Spatial Ecology of Bobcats *(Lynx rufus)* in the Appalachian Mountains of Western Virginia

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ABSTRACT

Despite the prevalent distribution of bobcats in western Virginia and the broader region of Appalachia, there is a paucity of information on their spatial ecology in this region. Due to the unique ecological conditions of Appalachia, and increasing public interest surrounding the role of bobcats as predators in the region, there is a need for local information on bobcat ecology. I utilized data from 20 GPS collared bobcats (14M, 6F) to investigate bobcat spatial ecology in the mountains of Western Virginia. Average resident male home range size was 33.9 ± 2.6 km^2, nearly 3 times larger than average resident female home range size (12.1 ± 2.4 km^2). Seasonal areas of use did not differ in size among seasons, but exhibited minor shifts in location and shape. Average male movement rates (232.3 ± 12.0 meters/hour) were 1.5 times greater than average female movement rates (154.4 ± 8.9 meters/hour). Male movement rates increased during the dispersal season and female movement rates increased during the denning/kitten-rearing season. Second order resource selection analysis indicates that bobcats of both sexes select home ranges at higher elevations than expected at random, and that selection varies between sexes and among seasons. Third order resource selection analysis indicates that bobcats select for locations near open canopy structure, and avoid forest interior. These findings build upon previous findings regarding bobcat diet and population dynamics to provide a comprehensive understanding of basic bobcat ecology in western Virginia, and will inform further research investigating predator/prey interactions.

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GENERAL AUDIENCE ABSTRACT

Despite the prevalent distribution of bobcats in western Virginia and the broader region of Appalachia, there is a paucity of information on their spatial ecology in this region. Due to the unique ecological conditions of Appalachia, and increasing public interest surrounding the role of bobcats as predators in the region, there is a need for local information on bobcat ecology. I utilized data from 20 GPS collared bobcats (14M, 6F) to investigate bobcat spatial ecology in the mountains of Western Virginia. I found that male bobcats use more space than females, with home ranges nearly 3 times larger and movement rates 1.5 times higher. I found that home ranges do not expand or contract throughout the year, but do shift in shape slightly. I found that bobcats select home ranges at higher elevations, indicating that home ranges are predominately located on ridges. I found that selection of home ranges differed between sexes and seasons, indicating that shifts in home range shape throughout the year reflect varying habitat selection. Within their home ranges, I found that bobcats select for areas of open canopy resulting from fields, fire, and timber harvest; and avoid areas of forest interior. These findings build upon previous findings regarding bobcat diet and population dynamics to provide a comprehensive understanding of basic bobcat ecology in western Virginia, and will inform further research investigating predator/prey interactions.

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I. Introduction

Bobcats (*Lynx rufus*) are a mid-sized felid endemic to North America. The species' distribution ranges from central Mexico to southern Canada, and throughout the contiguous United States, with the exception of the state of Delaware (Kelly et al. 2016). Despite the lack of current broad-scale barriers to gene flow, two distinct subspecies are recognized, genetically divided by a longitudinal cline in the central United States potentially caused by aridification of the Great Plains during the Pleistocene epoch (Croteau et al. 2012, Kitchener et al. 2017, Reding et al. 2012). The subspecies distributed west of the Great Plains is *Lynx rufus fasciatus* and the subspecies distributed east of the Great Plains is *Lynx rufus rufus.* Similar to many predators in North America, bobcat populations historically suffered from wide-scale persecution, overharvest, and habitat degradation that led to extirpation and population declines in many areas during the early 21st century (Woolf and Hubert 1998). Following the creation of the conservation and management infrastructure broadly termed the North American Model of Wildlife Management, bobcats have exhibited distribution-wide population increases and recolonized most areas from which they were extirpated (Roberts and Crimmins 2010). Bobcats are currently listed as a species of Least Concern by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Kelly et al. 2016). Bobcat populations in Virginia mirror these distribution-wide trends, with harvest metrics suggesting increases in abundance over recent decades (Figure 1). Other states in the region encompassing the central Appalachian Mountains (hereafter Appalachia), including West Virginia, Tennessee, Kentucky, and North Carolina, likewise report stable or increasing bobcat populations (Roberts and Crimmins 2010).

Despite the apparent increases in abundance of bobcats in Virginia, information on their local ecology is scarce. The recent Virginia Appalachian Coyote Study (VACS) conducted in western Virginia provided insight into bobcat population dynamics and diet through the use of genetic and morphological scat analysis. Spatially-explicit population analysis, conducted using fecal DNA collected during VACS, estimated bobcat population densities ranging from 5.93/100 to 20.27/100 km^2, twice that of coyote population densities in the area (Morin et al. 2018). Diet analysis from VACS found white-tailed deer (*Odocoileus virgiananus*) was a relatively common diet item of bobcats (Morin et al. 2016). This finding added to concerns of local sportsmen surrounding declines in white-tailed deer harvest in western counties that coincided with apparent increases in bobcat, coyote, and black bear populations; thereby prompting increased interest in the predation behavior of these carnivore species. While recent studies have examined the ecology of coyotes and black bears in Virginia, a comprehensive study of bobcat ecology has not been previously conducted in Virginia, with local information on bobcat spatial ecology nonexistent. Information on bobcat home ranges, movement characteristics, and habitat selection is highly relevant when drawing inference regarding predator/prey interactions, and when considering future wildlife management decisions more broadly.

While bobcat spatial ecology has been studied intensely in some areas, information from Appalachia is lacking. The vast majority of bobcat studies in eastern North America have taken place in low-relief areas of the Southeast or far Northeast (Figure 2). Some aspects of bobcat ecology vary widely between these regions. For example, home range sizes in southwestern Georgia have been estimated at 8.2 km^2 for males and 5.2 km^2 for females (Cochrane et al. 2006), while in the northeast they were dramatically larger at 143.9 km^2 for males and 32.5 km^2 for females in northern New York (Fox 1990). This positive latitudinal trend in bobcat home range sizes is common across their distribution, and is commonly attributed to varying prey availability (Ferguson et al. 2009, Litvaitis et al. 1986, Knick 1990). Existing information on bobcat spatial ecology in Appalachia comes from 2 studies conducted during the 1980's, in eastern Tennessee (Kitchings and Story 1984) and eastern Kentucky (Whitaker et al. 1987). Bobcat home range estimates in eastern Kentucky were 59.4 km^2 for males and 4.7 km^2 for females (Whitaker et al. 1987), and in eastern Tennessee were 76.77 km^2 and 25.90 km^2 for females (Kitchings and Story 1984).

In general, many previous bobcat studies that have been conducted were initiated during the 1980s, following sharp increases in fur prices during the mid-1970s that led to a nationwide upsurge in bobcat harvest (Woolf and Hubert 1998). Current information is important, due to both technological and ecological changes. Telemetry is essential to monitor movements of highly-mobile and elusive bobcats, and until the mid-2000s, all bobcat telemetry was conducted using VHF tracking collars. VHF telemetry is logistically difficult, particularly in the rugged topography of Appalachia, where acquiring a VHF signal can be challenging and locational error can be large. The previous bobcat space use studies in Appalachia suffered from small sample sizes of relocations with a temporal bias, with Whitaker et al. (1987) averaging 20-30 relocations per season for each bobcat and 80% of relocations triangulated during the day. These constraints resulted in a very coarse examination of space use and neither study examined resource selection at any scale.

More important than technological changes, Appalachian ecosystems have changed considerably since the 1980s. Appalachia was almost entirely deforested by the early 20th century, and forests regenerated in an altered disturbance regime (Nowacki and Abrams 2008). Additionally, timber harvest on National Forest lands, which compose much of Appalachian forests, declined sharply in the 1990s (Oswalt et al. 2009). Thus, forests in Appalachia are largely 30-40 years more mature at the present than they were in the 1980s. Further, the suppression of forest fire, invasive pests and diseases, and shifts in native wildlife communities, among other factors, have altered plant communities within Appalachian forests (Lafon et al. 2017, Lovett et al. 2006, Nowacki and Abrams 2008). Due to these factors, forests in Appalachia have an increasingly bare understory and fewer mast producing overstory species. This is important to bobcat ecology because, as ambush predators, bobcats have been found to select for dense understory in forested ecosystems (Godbois et al. 2004, Kolowski and Woolf 2002, Litvaitis et al. 1986, Tucker et al. 2008).

Prey availability also appears to have changed since the 1980s, which is likely tied to the aforementioned shifts in forested plant communities. In the Appalachian Mountains of western Virginia, white-tailed deer harvest has declined drastically, as much as 73% on public lands in some counties (VDGIF 2015). A bobcat diet study in western Virginia conducted during the 1950s by Progulske (1955) found cottontail rabbits (*Sylvilagus* spp.*)* were the most common diet item, however results from the recent VACS found squirrels (*Scurius* spp.) to be the most common diet item (Morin et al. 2016). This apparent diet shift may reflect reduced availability of rabbits associated with the loss of early successional habitat as forests mature. Another relevant ecological change that has occurred since the 1980s is the colonization of the region by coyotes (*Canis latrans*). Coyote-bobcat diet niche overlap was found to be 73% in Bath County in western Virginia (Morin et al. 2016). Beyond competing for resources, coyotes have potential to kill bobcats, particularly juveniles or smaller females (Anderson 1990, Gibson and Kamler 2002), although the frequency with which this occurs is unknown.

Due to the lack of information on bobcat spatial ecology in western Virginia, and the limitations of previous research in the broader region of Appalachia, I have conducted a thorough examination of bobcat space use in the Appalachian Mountains of western Virginia. Findings from this research will provide local information to managers of both wildlife and habitat, and can be used to inform future management decisions. A primary focus of this research is to inform further research into potential impacts of bobcats on white-tailed deer populations in western Virginia. If bobcat populations continue to increase, their interactions with other wildlife species will be an increasingly important consideration for managers. Of equal importance is the addition of this region-specific information to the broader body of knowledge surrounding space use of solitary carnivores and bobcats specifically. By capturing detailed information on regional variation in bobcat space use, we can better understand the factors driving their spatial ecology.

Literature Cited:

Anderson, E. M. 1990. Bobcat diurnal loafing sites in southeastern Colorado. Journal of Wildlife Management 54(4):600.

Cochrane, J. C., J. D. Kirby, I. G. Jones, L. M. Conner, and R. J. Warren. 2006. Spatial organization of adult bobcats in a longleaf pine-wiregrass ecosystem in southwestern Georgia. Southeastern Naturalist 5(4):711–724.

Croteau, E. K., E. J. Heist, C. K. Nielsen, J. R. Hutchinson, and E. C. Hellgren. 2012. Microsatellites and mitochondrial DNA reveal regional population structure in bobcats (Lynx rufus) of North America. Conservation Genetics 13:1637–1651.

Ferguson, A. W., N. A. Currit, and F. W. Weckerly. 2009. Isometric scaling in home-range size of male and female bobcats (Lynx rufus). Canadian Journal of Zoology 87:1052–1060.

Fox, L. B. 1990. Ecology and population biology of the bobcat (*Felis rufus*) in New York. PhD Dissertation, State University of New York College of Environmental Science and Forestry, Syracuse, New York.

Gipson, P. S., and J. F. Kamler. 2002. Bobcat killed by a coyote. Southwestern Naturalist 47(3):511.

Godbois, I. A., L. M. Conner, and R. J. Warren. 2004. Space-use patterns of bobcats relative to supplemental feeding of northern bobwhites. Journal of Wildlife Management 68:514–518.

Kelly, M., Morin, D. and C.A. Lopez-Gonzalez. 2016. Lynx rufus. The IUCN Red List of Threatened Species.

Kitchener A. C., Breitenmoser-Würsten Ch., Eizirik E., Gentry A., Werdelin L., Wilting A., Yamaguchi N., Abramov A. V., Christiansen P., Driscoll C., Duckworth J. W., Johnson W., Luo S.-J., Meijaard E., O'Donoghue P., Sanderson J., Seymour K., Bruford M., Groves C., Hoffmann M., Nowell K., Timmons Z. and S. Tobe. 2017. A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN/SSC Cat Specialist Group. Cat News Special Issue (11): 38-40.

Kitchings, J. T., and J. D. Story. 1984. Movements and dispersal of bobcats in east Tennessee. Journal of Wildlife Management 48(3):957.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 3–42.

Kolowski, J. M., and A. Woolf. 2002. Microhabitat use by bobcats in southern Illinois. Journal of Wildlife Management 66(3):822.

Lafon, C. W., A. T. Naito, H. D. Grissino-Mayer, S. P. Horn, and T. A. Waldrop. 2017. Fire history of the Appalachian region: gen. tech. rep. SRS-219. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 97 p.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50(1):110-117.

Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56:395.

Morin, D. J., S. D. Higdon, J. L. Holub, D. M. Montague, M. L. Fies, L. P. Waits, and M. J. Kelly. 2016. Bias in carnivore diet analysis resulting from misclassification of predator scats based on field identification: Bias and Uncertainty in Carnivore Scat Identification. Wildlife Society Bulletin 40(4):669–677.

Nielsen, C. K., and A. Woolf. 2003. Dispersal of juvenile male bobcats (Lynx rufus) in Southern Illinois. Trans. Ill. Stat Acad. Sci. 96: 313-318.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58:123–138.

Oswalt, Sonja N., T. G. Johnson, M. Howell, and J. W. Bentley. 2009. Fluctuations in National Forest timber harvest and removals: the southern regional perspective. Resource Bulletin, U.S. Department of Agriculture, Forest Service, Southern Research Station.

Progulske, D. R. 1955. Game animals utilized as food by the bobcat in the southern Appalachians. Journal of Wildlife Management 19(2):249.

Reding, D. M., A. M. Bronikowski, W. E. Johnson, and W. R. Clark. 2012. Pleistocene and ecological effects on continental-scale genetic differentiation in the bobcat (*Lynx rufus*): Continental Genetic Structure of Bobcats. Molecular Ecology 21:3078–3093.

Roberts, N. M., and S. M. Crimmins. 2010. Bobcat population status and management in North America: evidence of large-scale population increase. Journal of Fish and Wildlife Management 1(2):169–174.

Tucker, S. A., W. R. Clark, and T. E. Gosselink. 2008. Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. Journal of Wildlife Management 72(5):1114–1124.

Whitaker, J., Fredrick, R. B., and L.T. Edwards. 1987. Home-range size and overlap of eastern Kentucky bobcats. In Proceedings of the Southeastern Association of Fish and Wildlife Agencies 41: 417-423.

Woolf, A., and G.F. Hubert. 1998. Status and management of bobcats in the United States over three decades: 1970s-1990s. Wildlife Society Bulletin 26(2): 287-293.

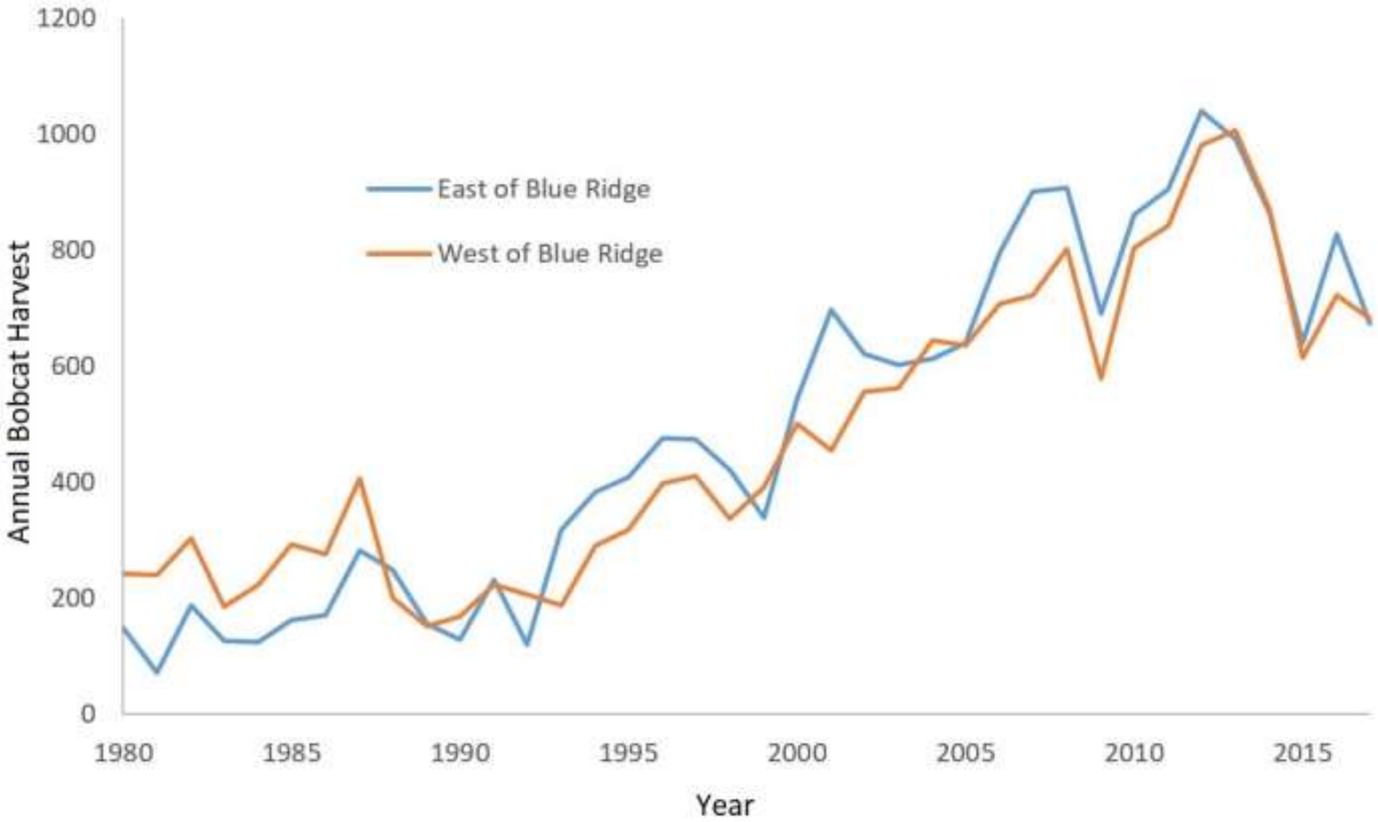

Figure 1. Annual number of bobcats harvested in Virginia from 1980 to 2017. Harvest numbers are separated into western and eastern Virginia by the Blue Ridge Mountains (VDGIF).

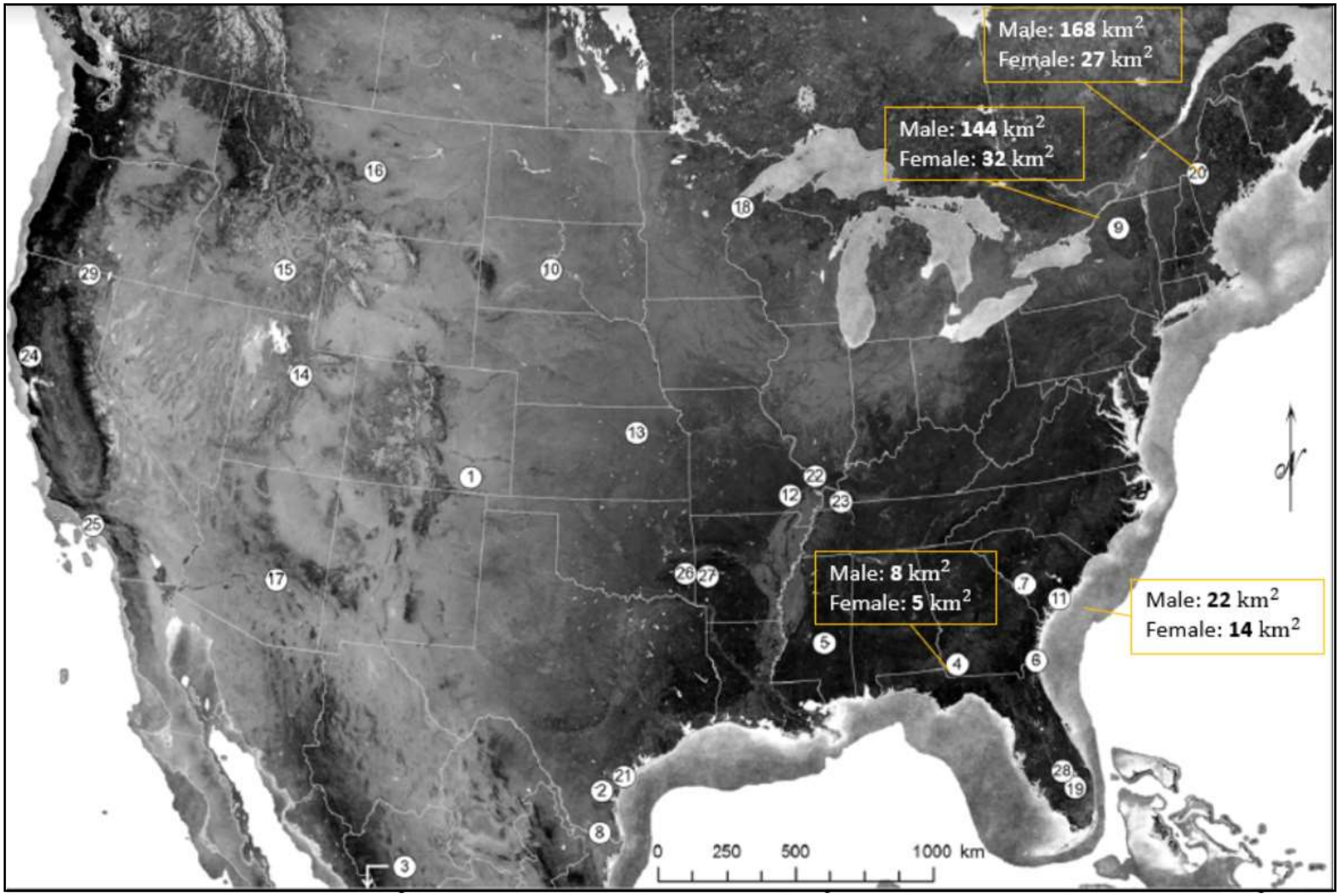

Figure 2. Figure from Ferguson et al. (2009) showing locations of bobcat home range estimates across the species distribution. Estimates of home range size from 4 sites in the eastern United States overlayed.

II. Bobcat space use dynamics in the Appalachian Mountains of western Virginia: the influence of sex and seasonality

Abstract:

Bobcats exhibit wide variability in space use throughout their broad distribution in North America. Region-specific knowledge on bobcat ecology is important because it provides insight into factors driving this variation and provides information useful to wildlife managers. Knowledge of bobcat spatial ecology in the central Appalachian Mountains is sparse, and nonexistent in the mountains of Virginia. In this study, I examined home ranges and seasonal areas of use (SAU), movements, and resource selection of bobcats in the mountains of western Virginia during 3 biological seasons: breeding (January-March), denning/kitten-rearing (April-September), and dispersal/pre-breeding (October-December). I observed sexual dimorphism for all space use metrics, with male SAUs approximately 3 times larger than female SAUs and male movement rates 1.5 times higher than females during all seasons, and resource selection differed between sexes. There was no seasonal effect on SAU size for either sex. Female movement rates were significantly higher during the denning season, and male movement rates were significantly higher during the dispersal season. There was a seasonal effect on 2nd order resource selection for both sexes, with seasonal changes in all covariates observed; and elevation, distance to field, and distance to deciduous forest having the strongest effect. There was also a seasonal effect on 3rd order resource selection for males, with selection for slope, elevation, and distance to deciduous forest differing among seasons. Seasonal variation in space use patterns is likely influenced by changes in reproductive behavior through time, and spatiotemporal variation in prey availability is likely another important driver of seasonal shifts in resource selection. The sexual dimorphism

and seasonal dynamics in bobcat space use have management and research implications; mortality risk and detection probability may change across sexes and seasons. Due to the prevalence of forest in the region, future research should investigate the influence of finer-scale forest structure on bobcat space use.

Introduction:

An understanding of animal spatial ecology is critical for managing and conserving wildlife populations (Manly 2002, Millspaugh and Marzluf 2001). Knowledge regarding space use and habitat requirements of wildlife provides insight into fundamental ecological processes such as population dynamics, behavioral interactions, and foraging behavior (Borger et al. 2008, Boyce et al. 2002, Johnson 1980). This information can be vital for informing population and land management decisions.

Bobcats are distributed throughout much of North America, and thus inhabit a wide variety of ecosystems, ranging from deserts to boreal forests (Kelly et al. 2016). Due to the wide variety of ecosystems in which bobcats occur, there is considerable variability in many facets of their spatial ecology. Despite this variability, there are patterns in bobcat spatial ecology that are evident across their distribution, largely driven by their foraging and reproductive strategies. Bobcats are solitary, territorial, and have a polygynous breeding strategy (McCord and Cordoza 1982). Thus, males should seek to maintain home ranges that overlap the home ranges of multiple females, and defend against other males competing for mates (Sandell 1989). Females raise young alone, and therefore must maintain home ranges that allow access to sufficient resources to support cost of reproduction, but also minimize energy expenditure to ensure reproductive success (Sandell 1989). These selective pressures are evident in the sexually dimorphic space use patterns of bobcats.

Male bobcat home ranges are on average 1.7 times larger than those of females, and scale isometrically with female home ranges (Ferguson et al. 2009). The body morphology of bobcats is also sexually dimorphic, with males being larger in size, and this difference is more pronounced in mountainous areas (Sikes and Kennedy 1993). Sikes and Kennedy (1993) suggest this dimorphism may be an expression of competing selective pressures for small body size to minimize energy expenditure and large body size to maximize breeding success. The sexual dimorphism in body size observed in bobcats may act synergistically with differing reproductive strategies to further differences in space use between sexes. Since males have larger bodies, and therefore increased metabolic requirements, they may require a larger home range, or they may need to use a home range more intensively to acquire resources (i.e. prey). Bobcats are obligate carnivores, as are all felids, and thus rely on the acquisition of sufficient prey to meet energetic requirements. Regional variation in bobcat home range size is likely driven primarily by prey availability; specifically, as prey availability increases, individuals are able to acquire necessary resources in a smaller area (Ferguson et al. 2009, Litvaitis et al. 1986, Knick 1990). This is evidenced by distinct latitudinal trends in bobcat home range size, with home range estimates being larger in northern latitudes, and smaller in the generally more productive southern latitudes (Elizalde-Arellano et al. 2012). Further, Ferguson et al. (2009) found a negative correlation between bobcat home range size and normalized difference vegetation index values.

Although bobcats are solitary and territorial, their degree of territoriality is poorly understood and varies widely. Home ranges often overlap, the extent of which can depend on relatedness, prey abundance, and population density, among other factors (Cochrane et al. 2006, Diefenbach et al. 2006, Kapfer 2014). Typically, intersexual home range overlap is more common and extensive than intrasexual overlap (Cochrane et al. 2006, Diefenbach et al. 2006, Nielsen and Woolf 2001). Negative relationships between female-female home range overlap and reproductive success have been found, indicating that females require exclusive areas to bear kittens (Diefenbach et al. 2006, Knick 1990, Lembeck and Gould 1979). Females in close proximity can trigger physiological responses that reduce fecundity (Diefenbach et al. 2006, Stys and Leopold 1993). Physical territorial conflicts are thought to be largely avoided by communicating through urine spraying, feces deposition, physical scrapes, olfactory investigation, and vocalizations, with urine spraying and olfactory investigation being the most commonly used communication behaviors (Allen et al. 2015).

Mirroring the sexually dimorphic pattern in home range size, many studies have found male movement rates to be higher than female movement rates (Bailey 1974, Chamberlain et al. 2003, Kitchings and Story 1979, Knowles 1985, Lariviere and Walton 1997). However, not all studies have found higher movement rates in males, and many bobcat space use publications do not report movement rates and even fewer compare rates between sexes. This lack of published movement data may largely be due to the use of VHF telemetry prior to the mid-2000s and the associated difficulties in acquiring short time interval locations. Further, many early bobcat studies used daily relocations to assess movement rates, which have been found to inaccurately portray real movement rates of bobcats (Laundre et al. 1987). The use of GPS telemetry in more recent bobcat studies has allowed for much higher sample sizes of sequential points and decreased locational error, resulting in more reliable movement analysis. Abouelezz et al. (2018) found males to move at nearly twice the rate of females in the mountains of Vermont, using 20-25 minute GPS intervals. Rockhill et al. (2013) did not find a sex effect on movement rates in eastern North Carolina, using GPS collars on 1 and 2 hour fix intervals. Elizalde-Arellano et al. (2012) also did not find a significant sex effect on movement rates in a low-relief area of the Chihuahuan desert, using 30 minute to 1 hour GPS fix intervals.

Bobcats exhibit male-biased dispersal, evidenced by more long-distance dispersal events observed in males and genetic relatedness being higher amongst females living in close proximity (Croteau et al. 2010, Janecka et al. 2007). Past studies examining bobcat dispersal have found that bobcats exhibit 2 types of dispersal: erratic and prolonged dispersal or straight-line and rapid dispersal (Johnson et al. 2010, Kamler et al. 2000, Nielsen and Woolf 2003). Despite the male bias, females can exhibit dispersal movements, but a smaller proportion disperse and generally at shorter distances (Janecka et al. 2007, Johnson et al. 2010, Kamler et al. 2000, Nielsen and Woolf 2003). A notable exception is a female bobcat that was tagged in New Jersey and recaptured in Pennsylvania 175 km from the initial capture site (Lovallo and Fowles 2018)

Bobcats have been found to select for areas of dense understory vegetation and young forest (Conner and Leopold 1996, Kolowski and Woolf 2002, Litvaitis et al. 1986, Mosby et al. 2012, Tucker et al. 2008). Bobcats are ambush predators, adapted to hunting in dense cover (Jaques and Jenks 2008, Labisky and Boulay 1998, McCord and Cordoza 1982). Further, bobcat resource selection is heavily influenced by varying prey availability, which is often higher in the same type of dense cover (Chamberlain et al. 2003, Fuller et al. 1985, Litvaitis et al. 1986, Knick 1990, Knowles 1985, McCord 1974). In addition to foraging, there is evidence that the same cover types are used for loafing areas and den sites (Anderson 1990, Kirby et al. 2010, Kitchings and Story 1984, Svoboda et al. 2013). Female bobcats have also been found to select for steep, rocky areas, presumably for use as denning cover (Anderson 1990, Mosby et al. 2012). Predation on female and juvenile bobcats by coyotes has been observed, as has bobcat kittens escaping coyote predation (Anderson 1990, Gibson and Kamler 2002). Thus, steep, rocky areas may serve as escape cover for comparatively small females and their vulnerable young, which they must leave alone frequently to forage since they raise kittens without assistance.

Home range characteristics, movement rates, and resource selection have all been found to vary seasonally, however many bobcat space use studies have not observed seasonal variability in home range size. Seasonal variability in bobcat space use is largely attributed to reproductive behavior and varying prey abundance in regions with pronounced seasonality, thus seasonal changes are generally more common in northern latitudes (Anderson 1987, Chamberlain et al. 2003, Cochrane et al. 2006, Conner et al. 1992, Knick 1990, Koehler and Hornocker 1989, Litvaitis et al. 1987, Lovallo and Anderson 1996, Tucker et al. 2008). Bobcats are spontaneous ovulators, with the peak of estrous occurring in February and March (Stys and Leopold 1993). The gestation period is 60-70 days, thus parturition usually occurs in April and May (Stys and Leopold 1993, Winegarner and Winegarner 1982). Bobcats generally produce only one litter per year, but are capable of having a second litter, usually in October following the loss of a first litter during pregnancy or shortly after parturition (Stys and Leopold 1993, Winegarner and Winegarner 1982). Kittens will feed exclusively on mother's milk for approximately their first 2 months, then they will nurse daily and consume small prey delivered by the mother for an additional 2 months, presumably learning to hunt in the later phases of this period and onward (Winegarner and Winegarner 1982). It is evident that kittens rely heavily on their mother during this approximately 4-month period, and that kitten-bearing females are under significant pressure to acquire abundant prey, both to produce milk and solid food. Yearling bobcats will stop traveling with their mothers prior to the breeding season, but remain in the area until the following summer or autumn, when they will initiate dispersal and make transient movements during the pre-breeding months (Kamler et al. 2000, Nielsen and Woolf 2003).

When home range sizes varies seasonally, they are typically smaller during summer months when prey is more available and females restrict movements closer to den sites, and larger during winter months when prey may be less available and males are breeding multiple females (Chamberlain et al. 2003, Cochrane et al. 2006, Lovallo and Anderson 1996, Rucker et al. 1989, Tucker et al. 2008). Although females may have smaller home ranges during the kitten-rearing season, their activity and movement rates have been found to increase during this time, indicating more intensive use of home ranges, most likely associated with providing food for their young (Chamberlain et al. 1999, Elizalde-Arellano et al. 2012, Lancia 1986). Both sexes have been found to increase movement rates during winter months, which has been attributed to breeding behavior, decreases in prey, and hunting pressure (Chamberlain et al. 2003, Rucker et al. 1989). It is important to note that dispersal also coincides with the autumn and winter months.

Seasonal variation in bobcat resource selection has been attributed to seasonally varying prey availability, interspecific and intraspecific competition, reproductive behavior, and thermoregulation (Chamberlain et al. 2003, Godbois et al. 2003, Koehler and Hornocker 1991, Lovallo and Anderson 1996, Mautz and Pekins 1989, Rucker et al. 1989). In northern latitudes, where winters are more severe, bobcats may shift to larger prey items during winter as small mammal availability decreases, and resource selection patterns shift accordingly (Lovallo and Anderson 1996). Chamberlain et al. (2003) found that the relatively stable availability of prey in southern latitudes allows bobcats to exploit the same prey items throughout the year instead of seasonally shifting prey selection, but they may still shift resource selection patterns seasonally to best exploit those prey items. Kolowski and Woolf (2002) attributed increased winter selection of log-wood ground cover and woody understory stem density to the absence of green herbaceous vegetation, supporting the suggestion by Chamberlain et al. (2003) that seasonal shifts in resource selection may be necessary to best exploit prey resources, even if diet composition remains static. These shifts could reflect seasonal shifts in resource selection of prey, or seasonal changes in concealment cover to facilitate foraging. However, bobcat prey availability can shift seasonally even in southern latitudes, as bobcats were found to prey on the temporally-pulsed resource of white-tailed deer fawns in both Georgia and Louisiana (Nelson et al. 2015, Shuman et al. 2017). Thermoregulation is also an important driver of bobcat resource selection. Bobcats have relatively poor cold thermoregulatory abilities compared to some other sympatric homeotherms (i.e. red fox (*Vulpes vulpes)*), and likely rely on thermal refugia and behaviors (i.e. sunning) to mitigate extreme cold (Mautz and Pekins 1989). There is also evidence that bobcats are poorly adapted physically to deep snow and may reduce their movements during the winter months (Bailey 1974, Koehler and Hornocker 1989). Bobcats have been found to increase use of rock outcrops, thick vegetation, and lowland conifers for winter refugia (Bailey 1974, Fuller et al. 1985, Lovallo and Anderson 1996). Godbois et al. (2003) suggested that bobcat resource selection in southwestern Georgia was partially driven by bobcats seeking refuge from summer heat.

Region-specific information on bobcat ecology is important due to the wide variety of ecosystems they inhabit, as it affords insight into distribution-wide patterns, drivers of regional variation, and provides local knowledge to managers. In many states, bobcats are managed as a furbearer or game species that is also known to consume other game species as prey. A local understanding of bobcat spatial ecology, especially as it relates to population dynamics and predator-prey interactions, will result in more effective strategies to manage bobcats as a furbearer/game species, while also considering possible predation impacts on other species. Information on bobcat spatial ecology is currently nonexistent in the state of Virginia, and sparse in the broader Central Appalachian region that contains western Virginia, western Maryland, West Virginia, eastern Kentucky, eastern Tennessee, and western North Carolina (hereafter referred to as Appalachia). Existing bobcat space use information for the region comes from 2 studies conducted during the 1980s in eastern Tennessee and eastern Kentucky, both of which had small sample sizes and used VHF telemetry in rugged topography (Kitchings and Story 1984, Whitaker et al. 1987). Extensive bobcat space use research has been conducted in the lowland Southeast, Northeast, and Midwest regions, yet these areas represent considerably different ecosystems than Appalachia. For example, Appalachia contains the highest elevations in the eastern United States, and a diversity of other factors that separate the region ecologically from adjacent regions. Within recent decades, bobcat populations in Appalachia have recovered from reductions in abundance and distribution observed in the early 20th century, yet larger carnivores, namely wolves (*Canis lupus*) and mountain lions (*Puma concolor*) remain extirpated, with the exception of black bears (*Ursus americanus*). Thus, bobcats occupy a niche as one of the dominant carnivore species in the region, with potential to influence the distribution and abundance of herbivores such as white-tailed deer (*Odocoileus virginianus*). Due to these considerations, there is a need to fill the gap in bobcat spatial ecology knowledge in Appalachia.

I examined home ranges, movements, and resource selection of bobcats in the Appalachian Mountains of western Virginia. I investigated the effects of sex and season on these facets of bobcat space use, and interpreted findings in the context of reproductive and foraging strategies. I predicted that home range estimates would be more similar to estimates from northern latitudes due to the high elevation of mountains in the study area, that male home ranges would be larger than those of females, and that male home ranges would be larger during breeding season and female home ranges smaller during denning season. I predicted that male movement rates would be higher than female movement rates, and that male movement rates would be largest during dispersal and breeding season and female movement rates highest during denning season. Lastly, I predicted that bobcats of both sexes would select for areas of dense cover and potentially abundant prey.

Methods:

Study site

Our study area encompasses the western half of Bath County, Virginia, adjacent to the border with West Virginia (Figure 1). Bath County is located in the Ridge and Valley physiographic province of the Appalachian Mountain range, characterized by parallel, northeast-southwest oriented ridges with narrow valleys interspersed. Elevation ranges from 343 meters to 1363 meters. Average monthly temperature can range from 0.8 C to 25.2 C, with a mean minimum temperature of 4.7 C in January and a mean maximum temperature of 31.7 C in July (National Oceanic and Atmospheric Administration, public data 2012). Average annual precipitation was 97.8 cm (National Oceanic and Atmospheric Administration, public data 2012). The forest structure primarily consists of mature deciduous forest, with common overstory species including oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and tulip poplar (*Liriodendron tulipifera*). Evergreen conifers are present in some forest stands, with common species including pine (*Pinus* spp.), hemlock (*Tsuga* spp.), and red cedar (*Juniperus virginiana).* Common midstory and understory species include rhododendron (*Rhododendron* spp.), flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum*), witch hazel

(*Hamamelis virginiana*), eastern redbud (*Cercis canadensis),* striped maple (*Acer pensylvanicum*), witch hobble (*Viburnum lantanoides),* mountain laurel (*Kalmia latifolia)*, blueberry (*Vaccinium* spp.), multiflora rose *(Rosa multiflora)*, raspberry and wineberry *(Rubus* spp.), common greenbrier (*Smilax rotundifolia),* and a wide diversity of herbaceous groundcover including ferns. Other than bobcats, the guild of white-tailed deer predators includes coyotes (*Canis latrans*), black bears (*Ursus americanus*). Common bobcat prey species, based on relative frequency of occurrence, are squirrels (*Sciurus* spp.), voles *(Microtus spp., Myodes gapperi)*, mice (*Peromyscus* spp.), and eastern cottontail rabbits *(Sylvilagus floridanus*, Morin et al. 2016). White-tailed deer (*Odocoileus virginianus*) also appear as a common diet item, although the contributions of predation versus scavenging are poorly understood. Bath County exemplifies the forest-dominated landscape of Appalachia, with public, forested land on the steep ridges and slopes, and narrow strips of private, low intensity development and agriculture in the flatter valley bottoms. Bath County is 89.4% forested land cover, most of which consists of contiguous swaths of forest managed by government agencies.

Bobcat Capture and Telemetry

I captured bobcats using cage traps (Camtrip Cages, Bartsow, California, USA and Briarpatch Cages, Rigby, Idaho, USA) in accordance with Virginia Tech IACUC protocol #16-071. I checked traps twice daily (morning and afternoon). Once captured, I immobilized bobcats with a mixture of 10 mg/kg ketamine hydrochloride and 1mg/kg xylazine using hand injection with syringe. I monitored and recorded respiratory rates, heart rates, and temperatures every 5-10 minutes. I used tooth growth and condition, body morphology, and teat/scrotum characteristics to determine whether bobcats were juvenile or adult (Jackson et al. 1988). I fitted adult bobcats with Iridium GPS collars (Telonics, Mesa, Arizona, USA and Advanced Telemetry Systems, Isanti, Minnesota, USA). All bobcats captured were marked with color-coded, numbered ear tags. Following handling, I reversed the xylazine with 0.125 mg/kg Yohimbine, administered either rectally or intravenously, and allowed bobcats to recover in the cage trap for 30 minutes to 1 hour before release.

GPS collars were cycled between 1, 2, and 4-hour GPS fix intervals. However, since I compared across seasons for these analyses, any locations more frequent than 4 hours were removed to maintain a constant sampling schedule across seasons. Iridium communication was scheduled for every 2 to 4 days. Overall, fix success was low for the Telonics sensors and high for the ATS sensors (Table 1). Poor Iridium fix success was a large contributing factor to the Telonics collar performance. The collars used Telonics' proprietary Quick Fix Pseudoranging (QFP) technology, which rapidly acquires GPS information necessary to acquire a fix, to be post-processed later, in order to reduce the battery power necessary to search for satellites and acquire a fix. QFP locations have a larger storage size than traditional GPS locations (~5 times larger), thus fewer locations can fit in each Iridium message. Due to the large storage size of QFP, Iridium messages became backlogged quickly when Iridium uplinks were missed. At a certain threshold, the Telonics collars store the oldest backlogged Iridium locations on-board the collar, only to be recovered by direct download with a cable. As a result, telemetry data for the bobcats wearing Telonics collars have some large gaps, sometimes several days long, randomly spread throughout their collar deployment. Additionally, the ATS collars had a software bug that caused them to randomly switch to a 12 -our fix interval, which happened rarely over the deployment life of each collar. It would typically take at least a week to recognize the interval change, remotely send a command to change back to the 4 hour interval, and have that command reach the collar. Thus, the ATS collar data has randomly interspersed periods of 12 hour fix rates.

Season Classification

I classified 3 seasons of interest based on the reproductive timeline and life history of bobcats. I classified seasons as breeding, denning/kitten-rearing, and dispersal/pre-breeding. I classified January 1 through March 31 as the breeding season, to overlap with the estrus cycle of females. I classified denning/kitten rearing season as April 1 through September 30, since parturition typically peaks in April or May and kittens nurse for up to 4 months (Stys and Leopold 1993, Winegarner and Winegarner 1982). I classified the dispersal/pre-breeding season as October 1 through December 31. Some previous bobcat space use studies examining seasonal effects have divided the year into only 2 seasons, essentially consisting of breeding (October through April) and denning (May through September) periods (Bailey 1974, Lovallo and Anderson 1996, Tucker et al. 2008). I argue the approach of Chamberlain et al. (2003) to divide the year into 3 seasons, breeding, kitten-rearing, and what they termed "winter", is more accurate. Bobcats are not breeding during autumn and early winter, evidenced by the lack of parturition during winter months; instead, entirely different ecological pressures are occurring during that time. Presumably, resident females will seek to restore body mass depleted during the kitten-rearing period, and resident males will aim to maximize body mass in preparation for the breeding season. Yearling bobcats will likely initiate dispersal immediately prior to, or during, this time period. Thus, the months of October through December represent a distinct period of bobcat behavior.

Home Range Analysis

I estimated bobcat home ranges using the autocorrelated kernel density estimator (AKDE; Fleming et al. 2015) in the continuous-time movement modeling package (ctmm, Fleming and Calabrese 2018) in R version 3.5.3 (R Core Team 2019). Traditional home range estimators were developed for VHF telemetry data or adapted from statistical techniques not developed for animal tracking data (i.e. conventional kernel density estimation), and assume independent and identically distributed data, an assumption violated by animal tracking data, which is autocorrelated and nonstationary (Fleming et al. 2015). Walter et al. (2015) termed these traditional estimators as first and second-generation estimators, while they termed recently developed estimators that account for autocorrelation by incorporating a temporal component as third-generation estimators, and they concluded that third-generation estimators are the most reliable. Examples of other third generation estimators are dynamic Brownian bridge movement models (DBBMM, Kraunstauber et al. 2012) and movement-based kernel density estimation (MKDE, Benhamou 2011). The AKDE is a third-generation estimator that assumes the data represent a sample from a nonstationary, autocorrelated continuous movement process, by incorporating the movement of animals through an autocorrelation function derived from movement models fitted to the data (Fleming et al. 2015). Furthermore, AKDE reduces to conventional KDE when locations are distant enough to be truly independent, and can correct for missing locations and irregular sampling schedules through an optimal weighting method (Fleming et al. 2018). Due to missing data in the Telonics collars, and irregular sampling schedule of the ATS collars, the AKDE home range estimator is the best fit for this relocation data.

I estimated 95% annual home ranges and 50% core areas for bobcats with at least 4 months of relocation data, during at least 2 seasons. I estimated 95% seasonal areas of use (hereafter SAU) and 50% seasonal core areas for bobcats with locations collected for at least 1 month in a given season. Bobcats are territorial and highly mobile, and regularly mark home ranges (Allen et al. 2015). Variograms for the resident bobcats reach an asymptote around 24-48 hours, indicating near-daily home range crossing, thus a month of relocations is likely sufficient to accurately portray SAUs. As with all analyses, the seasons of interest were based on reproductive processes and classified as breeding, denning, and dispersal. I fit linear mixed effects models using restricted maximum likelihood, with area of either 50% seasonal core area or 95% SAU as the response variables. I used a natural logarithm transformation for home range and core area sizes to meet assumptions of normality. Both the interaction and main effects of sex and season were included as predictors, and animal-specific intercepts were treated as random effects. I performed mixed modeling in the package lme4 (Bates et al. 2015) and the significance of factors and degrees of freedom were assessed using Satterthwaite's method for approximating degrees of freedom in the lmerTest R package (Kuznetsova et al. 2017).

I also estimated annual home ranges by creating 95% minimum convex polygons (MCP) for resident bobcats with sufficient monitoring based on the aforementioned criteria. I estimated MCPs for use in regional comparisons. Since previous studies on bobcat space use most often estimated home range size using MCPs, I opted to use the same estimator as these studies to minimize differences in home range size resulting from variation in analytical techniques.

Movement Analysis

I estimated each bobcat’s movement rates in meters moved per hour, calculated as the straight-line step length between successive locations divided by the time lag. I only used steps with a 4 hour time lag in calculation of movement rates. As described previously, steps with shorter time lags were removed to allow comparison across seasons. Steps with time lags longer than 4 hours were not examined either to maintain consistent representation of the distances moved. Seasonal movement rates were only examined for bobcats that were monitored for at least a month in a given season. I assigned each step to the appropriate season. I used a generalized linear mixed effects model (GLMM) with a gamma distribution and log link to model movement rates as a function of sex and season. Both the main effects and interaction of sex and season were included as predictors. Animal-specific intercepts were again treated as random effects. Significance of covariates was determined using Walds Z-test.

Resource Selection Analysis

I examined seasonal bobcat resource selection at 2 hierarchical scales (Johnson 1980), selection of home ranges within the landscape (2^{nd} order) and selection of locations with home ranges (3^{rd} order), by creating resource selection functions (RSF) in a use-availability framework (Manly 2002). I examined 2^{nd} order selection for both sexes, but was only able to examine 3^{rd} order resource selection for males due to the small sample size of females with suitable fix success. Due to poor fix success of the Telonics collars, and the potential bias of topography and elevation on GPS fix success, only bobcats wearing ATS collars were included in 3^{rd} order resource selection analysis. This reduced the sample size to 3 female bobcats, 1 of which was only monitored for ~2.5 months during the breeding season due to an April mortality.

Resource Selection Data

For resource selection analysis, I included land cover and topographical based covariates. The land cover covariates I included are distance to deciduous forest, distance to mixed forest, and distance to fields, which I derived from the 30m resolution 2011 National Land Cover Database (NLCD). The deciduous forest covariate simply consists of the Deciduous Forest class in the NLCD. To create the mixed forest covariate, I combined the Evergreen Forest and Mixed Forest NLCD classes. I named this covariate “mixed forest” because NLCD classifies forest as evergreen when more than 75% of the tree species maintain their leaves all year, and forest stands that are exclusively evergreen are exceedingly rare in the study area, thus even the cells classified as evergreen likely contain a mixture of deciduous trees. To create the field covariate, I combined the Pasture/Hay and Cultivated Crops NLCD classes. The majority of unforested area in the study area consists of fields, which are primarily used for cattle and hay production; and other fields (e.g. large fields surrounding residences) are generally classified as Pasture/Hay since they are often indiscernible from pasture.

Lastly, I created distance raster layers by calculating Euclidian distance to each of these land cover variables using the Euclidean Distance tool in ArcGis 10.6 (ESRI, Redlands, CA, USA). We used distance-based land cover covariates because they remove the need to base inference on reference categories, reduces the influence of telemetry error, and the effects of these land cover types can extend beyond their boundaries (e.g. edge effects surrounding fields).

I did not include development due to the unique variability in development types in the study area. For example, within the study area lies the largest pumped-storage hydroelectric power station in the world (Bath County Pumped Storage Station), an embankment dam (Gathright Dam), a luxury resort with a golf course and ski slope (The Homestead Resort), a municipal airport (Ingalls Field), and small towns. All of these are classified as Developed, High Intensity or Developed, Medium Intensity by the NLCD, despite the vast differences in human presence and activity, among other factors. Regardless of the variability in development types, impervious surfaces compose <1% of Bath County (VGIN 2016), and many bobcats were not near developed areas.

Topographical covariates included elevation and slope. Elevation values were extracted directly from a digital elevation model (DEM, United States Geological Survey 2013). Slope was calculated using the DEM with the Slope tool in ArcGIS 10.6 (ESRI, Redlands, CA, USA). Both topographical layers have a 30m resolution.

2nd order resource selection

I examined 2nd order resource selection across seasons for all bobcats, with the exception of 2 males that exhibited transient movements and were presumably dispersing. These 2 males had home ranges approximately twice the average male home range area. I characterized 2nd order availability by simulating random circular polygons, following Katnik and Wielgus (2005) finding that randomly located, simulated home ranges are superior to landscape proportions for estimating availability. I examined resource selection of SAUs on the landscape using an approach similar to that used by Pollentier et al. (2017). Instead of simulating polygons throughout the study area for each individual, simulated polygon centers were constrained within a 5.3km buffer surrounding the centroid of each bobcat's seasonal locations. I defined the constraining buffer radius of 5.3km based on the largest annual home range area of the 2 dispersing bobcats (88.5km^2), as 5.3km would be the radius of said home range if it was circular. This area should reflect available habitat more accurately than the entire study area, since it is based on approximate area traversed by dispersing bobcats prior to establishing a home range, and habitat on distant portions of the study area may not realistically be available. I simulated 10 polygons equivalent in size to each respective bobcat SAU. I then systematically extracted covariate values from every 10th raster cell within all polygons, both simulated and real SAUs. I sampled every 10th raster cell instead of all raster cells to increase computational speed. Using a portion of the bobcats (n=6), I compared models using values extracted from every 10th raster cell and from all raster cells, and results were highly similar, with significance and direction of all coefficient estimates identical.

3rd order resource selection

I examined 3rd order resource selection for male bobcats affixed with ATS collars (n=7). To characterize seasonal 3rd order availability, I randomly simulated 10 points within each bobcat's SAU for every real location. This resulted in ~200 random points per square kilometer. I clipped each bobcat's real seasonal locations within SAU borders to remove extraterritorial forays from analysis. I then extracted the mean covariate values of all raster cells within a 100m buffer surrounding real locations and simulated points, to account for GPS collar error and implicit uncertainty in animal movement.

Resource selection model development

To model 2nd and 3rd order bobcat resource selection, I developed RSFs using binomial generalized linear mixed models (GLMM) in the Program R package lme4 (Bates et al. 2015). The binary response variable for 2nd order resource selection was whether a raster cell was extracted from a real seasonal home range (used = 1) or a simulated polygon (available = 0). The binary response variable for 3rd order resource selection was whether a point was a real location (used = 1) or a random point (available = 0). Predictor variables for both scales were distance to deciduous forest, distance to mixed forest, distance to fields, elevation, and slope. No covariates were highly correlated (all $r < 0.5$). I included season as an interaction term with all main effects. For 2nd order selection, I created 2 separate models for male and female bobcats respectively, each consisting of the 5 main effects with a season interaction. For 3rd order selection, I created one model for male bobcats consisting of the 5 main effects with a season interaction. I rescaled all covariates by mean-centering at zero then dividing them by their standard deviation to reduce model convergence issues. I included animal-specific random intercepts to account for variation in sampling duration among individuals (Gillies et al. 2006). I evaluated selection or avoidance based on whether or not a coefficient significantly differs from zero ($\alpha = 0.05$). Significance of covariates was determined using Walds Z-test. I inferred selection if used points were closer to habitat variables than random locations, and avoidance if used points were further from habitat variables than random locations.

Results:

I attached GPS collars to 20 bobcats (14 male, 6 female) from January 2017 through April 2018. Number of locations per bobcat ranged from 259 to 1979, with a mean of 933 (Table 1). Length of collar deployments ranged from 55 days to 393 days, with a mean deployment length of 259 days (Table 1). The mean GPS collar fix success was 85% for ATS and 54% for Telonics. The mean ATS fix rate was lowered slightly by the fix success of 2 females that experienced a drastic decrease in fix success during the period encompassing parturition and denning. Weekly fix success for these females was approximately 90% prior to the denning period, then decreased in April and May, when bobcats typically give birth. The average fix success for the 7 males included in 3rd order resource selection analysis was 89%, and did not vary widely across seasons.

I estimated home ranges and core areas for 16 resident bobcats (11 males, 5 females) and 2 dispersing males, excluding 2 bobcats (1 male, 1 female) that were monitored for less than 4 months and only during 1 season. I estimated 41 SAUs and seasonal core areas using relocation data from bobcats that met the 1 month minimum criteria, resulting in 410 simulated polygons. This included 13 bobcats in the breeding season (8 males, 5 females), 15 bobcats in the denning season (11 males, 4 females), and 13 bobcats in the dispersal season (9 males, 4 females). On average, resident male home ranges were 33.9 ± 2.6 km^2 and were approximately 3 times larger than resident female home ranges (12.1 ± 2.4 km^2, Figure 2), and resident male core areas were 8.6 ± 0.8 km^2 and were also approximately 3 times larger than resident female core areas (3.2 ± 0.7 km^2, Figure 3). The annual home ranges of the 2 dispersing males were 84.8 km^2 and 88.5 km^2 respectively. When using a 95% MCP, for the purpose of comparison, I estimated annual home ranges of resident bobcats in this study area to be 53.7 ± 6.0 km^2 for males and 15.7 ± 3.2 km^2 for females. There was a significant sex effect on SAU and seasonal core area size (Table 2). On average, males SAUs and seasonal core areas were larger than female SAUs during all seasons (Figure 2, Figure 3). There was no effect of season on SAU or seasonal core area size (Table 2, Figure 2, Figure 3). Average SAU size of females (11.8 ± 1.2 km^2) and average SAU size of males (32.8 ± 2.0 km^2) were similar to average annual home range size of each sex respectively, indicating that SAUs do not shift location extensively throughout the year.

I estimated annual movement rates for all bobcats (n=20), and seasonal movement rates for bobcats with at least 1 month of relocations within a given season. Average male movement rates (232.3 ± 12.0 meters/hour) were approximately 1.5 times higher than average female movement rates (154.4 ± 8.9 meters/hour). There was a significant effect of sex and season on seasonal movement rates (Table 3). Male movement rates were higher than female movement rates during all seasons (Figure 4). Female movement rates were significantly higher during the denning season (Table 3, Figure 4). Male movement rates were significantly higher during the dispersal season (Table 3, Figure 4).

I conducted 2nd order resource selection for all bobcats with the exception of the 2 dispersers (12 males, 6 females). For females, elevation, distance to deciduous forest, and distance to fields were the strongest predictors of 2nd order resource selection (Table 4, Figure 5). During all seasons, females selected SAUs that were at higher elevations, further from fields, and closer to deciduous forest than expected (Table 4, Figure 5). Females exhibited strongest 2nd order selection for higher elevations during the breeding season, less strong selection for high elevations during the dispersal season, and weakest selection for high elevations during the denning season (Table 4, Figure 5). Females exhibited strongest 2nd order avoidance of fields during the denning season, weaker avoidance of fields during the dispersal season, and weakest avoidance of fields during the breeding season (Table 4, Figure 5). Females exhibited strongest 2nd order selection for deciduous forest during the denning season (Table 4, Figure 5). Females exhibited strongest 2nd order selection for mixed forest during the dispersal and breeding seasons, but did not select or avoid mixed forest during the denning season (Table 4, Figure 5). Females exhibited 2nd order selection for steep slopes during the dispersal season, but exhibited 2nd order selection for gentle slopes during the breeding and denning seasons (Table 4, Figure 5).

For males, distance to fields and elevation were the strongest predictors of 2nd order resource selection (Table 4, Figure 6). During all seasons, males selected SAUs that were closer to fields and at higher elevations than expected (Table 4, Figure 6). Males exhibited strongest 2nd order selection for fields during the denning season and weakest selection for fields during the breeding season (Table 4, Figure 6). Males exhibited weakest 2nd order selection for high elevations during the breeding season compared to dispersal and denning seasons (Table 4, Figure 6). Males exhibited 2nd order selection for mixed forest during all seasons, but this selection was weakest during the denning season, following a similar pattern to females (Table 4, Figure 6). Males exhibited 2nd order selection for deciduous forest during the dispersal season, but avoided deciduous forest during breeding and denning seasons (Table 4, Figure 6). Slope was not a significant predictor of male 2nd order resource selection (Table 4, Figure 6).

I examined 3rd order resource selection across seasons only for male bobcats with fix success of 85% or higher (n=7), due to the small sample size of females with adequate fix success. Distance to deciduous forest, distance to fields, elevation, and slope were all significant predictors of male 3rd order resource selection (Table 5, Figure 7). Distance to mixed forest was the only covariate that was not a significant predictor of male 3rd order resource selection during any season (Table 5, Figure 7). Male bobcats exhibited 3rd order selection for deciduous forest during all seasons (Table 5, Figure 7). Male bobcats exhibited 3rd order selection for fields during all seasons, but this selection was stronger during the denning season (Table 5, Figure 7). Male bobcats exhibited 3rd order selection for high elevations during all seasons, with the strongest selection for high elevations during the dispersal season and weakest selection during the breeding season (Table 5, Figure 7). Lastly, male bobcats exhibited 3rd order selection for gentle slopes during the denning and dispersal seasons, but selected for steeper slopes during the breeding season (Table 5, Figure 7).

Discussion:

Bobcat space use is primarily driven by the need to reproduce and acquire prey, among other proximal factors. Differences in reproductive strategies between sexes likely explains most of the sexual dimorphism observed in bobcat space use patterns. Marked reproductive seasons and seasonal fluctuations in prey availability likely explains most of the seasonal variation in space use patterns that I observed.

Despite the fact that Appalachia contains conditions more similar to northern climates, these bobcat home range estimates fit closely with latitudinal trends, possibly because temperatures are not consistently as low and there is not a sustained, deep snowpack as found further north. Bobcats are poorly adapted to deep snow and snow depth is widely considered to limit the northern edge of the species distribution (Gooliaff and Hodges 2018). Northeastern home range estimates for bobcats were 143.9 km^2 for males and 32.5 km^2 for females in northern New York (Fox 1990), and were 95.7 km^2 for males and 31.2 km^2 for females in Maine (Litvaitis et al. 1986). Bobcat home range estimates in eastern Kentucky were 59.4 km^2 for males and 4.7 km^2 for females (Whitaker et al. 1987). Southeastern bobcat home range estimates were 8.2 km^2 for males and 5.2 km^2 for females in southwestern Georgia (Cochrane et al. 2006), and were 20.2 km^2 for males and 12.3 km^2 for females in Mississippi (Conner et al. 2001). Regional variation in bobcat home range size is often attributed to varying prey availability. For example, the relatively small home ranges that Cochrane et al. (2006) observed in southwestern Georgia occurred in a site that conducts supplemental feeding of bobwhite quail (*Colinus virginianus*), thereby boosting the population density of rodents, which compose the vast majority of bobcat diet in that site (Godbois et al. 2004). While this latitudinal gradient is probably largely driven by prey availability as many have suggested, I suggest that the importance of habitat quality in mediating prey availability is an important consideration. An example lies in the seasonally-flooded landscape of south Florida, where relatively large bobcat home ranges were reported despite far-southern latitudes, with female home ranges larger than my estimates for this study area (Maehr 1996, Wassmer et al. 1988). In those flooded sites, bobcats were likely avoiding areas of deep water with scarce prey availability, which has been found in Florida panthers (Frakes et al. 2015). McCord (1974) examined winter habitat selection in Massachusetts and found that trails, logs, plowed roads, and other areas of shallow snow were used “at every opportunity” when snow was deep. This heterogeneity of use within home ranges may explain why bobcat home ranges are so much larger in northern latitudes than observed in this site, and provide an explanation for when they are atypically large in cases such as south Florida.

Bobcats of both sexes exhibited selection for SAUs at higher elevations than random polygons during all seasons, indicating that bobcat home ranges mostly encompass ridges in the systematic topography of the Ridge and Valley province. Despite their use of the mountains, bobcats avoid steep slopes, with the exception of males during the breeding season. There were no significant shifts in SAU size, and average SAU size for both sexes did not differ widely from average annual home range size. Since annual home ranges are composed of space use across seasons, and I only calculated annual home ranges for bobcats with at least 2 seasons of relocations, the discrepancy in size between annual home range and SAUs for an animal serves as an index of the degree of seasonal shifts in SAU location and/or shape. For example, if the 3 SAUs for a bobcat did not overlap at all, then the annual home range would be larger than the individual SAUs; but if the SAUs overlap extensively, then the annual home range will be similar in size to the SAUs. A visual inspection of SAUs for individual bobcats illustrates their extensive overlap, and that some individuals exhibit more seasonal shifts in SAU location/shape than others (Figure 8). Bobcats have been found to exhibit a land tenure system, in which previously occupied home ranges are filled by other bobcats of the same sex (Anderson 1988, Benson et al. 2004, Litvaitis et al. 1987). Thus, the territorial spatial organization of bobcats may prohibit large seasonal range contractions or expansions or wide shifts in location, unless seasonal shifts in prey availability are so drastic to necessitate use of a larger area in winter months to acquire sufficient prey. I observed that the rare cases when resident bobcats did drastically shift SAUs often corresponded to the mortality of a neighboring resident, such as when M21 shifted its breeding SAU into the vacant home range resulting from the mortality of neighboring M22. Thus, it appears that seasonal shifts in SAU location are not drastic, but are more shifts in shape that reflect seasonal adjustments in resource selection, likely constrained by the territorially of neighbors.

My findings that male home ranges were larger than female home ranges were probably driven by males seeking to maximize breeding opportunities with multiple females, and females seeking to minimize energy expenditure, a space use pattern typical of solitary, polygynous carnivores (Sandell 1989). My findings of movement rates mirror the sexually dimorphic patterns that I observed in home range size. With larger home ranges, males must move greater distances to patrol and mark territories, and move between multiple female home ranges. In contrast, it benefits females to restrict space use to an area just large enough to acquire sufficient prey to maximize reproductive success, both to conserve energy and remain near young. Traveling uphill is energetically costly, particularly for larger mammals (Taylor et al. 1978). Perhaps sexual dimorphism in movement rates is more pronounced in mountainous topography, as females further seek to reduce energetic costs associated with locomotion, whereas males still seek the increased fitness associated with moving between multiple females and maintaining a large territory. This aligns with Sikes and Kennedy (1993) findings that eastern bobcats tend to be more sexually dimorphic in size in mountainous areas, and their suggestion that this is caused by selective pressure for smaller female body size to minimize energetic cost of locomotion. Additional evidence of topographically-driven sexual dimorphism in bobcat movement rates exists in the lack of sex effects on movement rates in low-relief areas of Mexico and North Carolina (Elizalde-Arellano et al. 2012, Rockhill et al. 2013), with only slightly higher (13%) male movement rates in an area of moderately rolling topography in Mississippi (Chamberlain et al. 2003), and findings of male movement rates approximately 50-100% higher in the mountains of Vermont (Abouelezz et al. 2018) and in my rugged study area.

Increased food intake, and resulting increases in body mass and nutritional reserves, may increase reproductive success through outcompeting conspecifics of the same sex, increased litter size, and increased body mass of neonates (Schoener 1971). To sustain the larger body mass and greater space use necessary to maximize breeding opportunities, males are under selective pressure to acquire more prey, or perhaps larger prey, throughout the year. Females have increased metabolic demands when rearing kittens, but must balance foraging time with lactation and protection of kittens. I suggest that the increase in female movement rates observed during the denning/kitten-rearing season is due to the need to increase food intake but also attend to and feed young, resulting in frequent movements between den sites and foraging sites. Chamberlain et al. (2003) remarked on previous findings that female cheetahs spend more time hunting during lactation when they require nearly double their normal food intake (Caro 1994), and that female bobcat activity rates have been found to increase during kitten rearing (Chamberlain 1999). Further, female 2nd order selection for more gentle slopes during the denning/kitten rearing season may reflect an effort to reduce metabolic costs of locomotion during pregnancy and lactation, or reflect selection of gentle slopes by prey. Conversely, females may exhibit 2nd order selection for steep slopes only during the dispersal season because this is the only season they do not have the increased metabolic demands of pregnancy and kitten rearing, although the driving factor behind selection for steep slopes is unclear. I hypothesize that although females exhibited 2nd order selection for more gentle slopes during the denning season, 3rd order resource selection analysis would show selection for steeper slopes within home ranges during this time as females spend stationary time in especially rugged den sites. In the Appalachian Mountains of Tennessee, Kitchings and Story (1984) found female bobcats using dens in rocky terrain within "heavily wooded" areas. Female selection of SAUs closest to deciduous forest, and furthest from fields, during the denning season supports use of predominantly forested areas during this time. Selection of denning SAUs in heavily forested areas may be partially attributed to protection of young. Male bobcats are selecting SAUs closer to fields than any other season at this time, and selecting locations near fields within those SAUs. While yet unobserved in bobcats, infanticide by males is common in many felid species (Logan and Sweanor 2001; Balme and Hunter 2013). Coyotes and black bears are also potentially selecting for areas near fields during this time to exploit resources such as soft mast and increased prey, such as rabbits, rodents, and white-tailed deer neonates; as both species are well-documented fawn predators (Carstensen et al. 2009, Kilgo et al. 2012, Kunkel and Mech 1994, Mathews and Porter 1988, Nelson et al. 2015, Shuman et al. 2017, Vreeland et al. 2004). Thus, females may be selecting den sites far from these potential kitten predators. Also, female selection of denning SAUs far from fields may be due to niche partitioning, as they avoid larger competitors during the period when those competitors converge on areas with more abundant food resources and females have highest metabolic demands. These factors of kitten protection and niche partitioning may act synergistically.

Despite the reproductive benefits of increasing food intake, increased foraging time during the breeding season may lead to decreased time searching for mates, thereby decreasing reproductive success when animals are not spatially grouped (Mosimann 1958). Thus, there is significant pressure for bobcats to increase nutritional reserves prior to the breeding season, at which point they must spend time and energy searching for mates. This pressure likely increases in northern latitudes, where bobcats are more widely dispersed on the landscape, and breeding season coincides with the coldest months and greatest need for thermoregulation. There is an additional cost of searching for mates in Appalachia, bobcats must search throughout the rugged drainages and coves of the heavily-eroded mountain range, resulting in increased cost of locomotion and potentially search time. I suggest that my findings of 3rd order selection for steeper slopes during the breeding season by males, while they select for low-relief terrain during all other seasons, is driven by mate-searching behavior. Similarly, I suggest that the increased movement rates of males during the dispersal season is partially caused by increased foraging time to increase nutritional reserves leading up to the breeding season.

Male movement rates could also be higher during dispersal season due to transient bobcats seeking home ranges prior to the breeding season, and increased territorial marking and patrolling by resident males in response to transients in close proximity. The dispersal behavior I observed of 2 male bobcats fits more closely with erratic and prolonged dispersal patterns than straight-line and rapid dispersal patterns, suggesting that interactions between resident and transient bobcats may be common as transients occupy temporary home ranges. Further, Morin et al. (2018) estimated bobcat populations in this study area to be approximately twice as dense during winter months, which was attributed to an influx of dispersing bobcats. The season I have classified as dispersal also overlaps with most hunting seasons, when increased mortality can occur resulting in home range vacancies. Of the 2 dispersing males, 1 of them (M09) appeared to occupy the home range of another GPS collared male (M08) following his hunting-caused mortality. In general, the spatial organization of bobcats is in flux during this season, particularly for males. Many bobcat space use studies have not examined the dispersal season separately from kitten-rearing and breeding seasons. Chamberlain et al. (2003) did examine this season separately, and found higher movement rates of both sexes. I recommend that future bobcat space use studies delineate this season and examine the role of dispersal behavior on population-level space use patterns.

Seasonal changes in prey availability likely explain many of the seasonal fluctuations in resource selection that I observed. The availability of prey and cover can change drastically across seasons in the deciduous forests of Appalachia. In our study area, the season we have termed “denning/kitten-rearing” also overlaps with the growing season, and the seasons we have termed “dispersal” and “breeding” overlap with the dormant season. During the growing season, herbaceous plants and deciduous trees provide much of the cover across the landscape. White-tailed deer fawns, juvenile cottontail rabbits, and many other common bobcat prey species are abundant and relatively easily acquired during this time. In contrast, cover provided by herbaceous plants and deciduous foliage is lacking during the dormant season, and prey abundance is generally lower due to the lack of newborn prey on the landscape and usual population losses that occur during the growing season months. Both sexes exhibited 2nd order selection for mixed forest during the dispersal and breeding seasons, but either exhibited weaker selection for, or did not select for, mixed forest during the denning season. Perhaps this reflects increased use of areas surrounding evergreen vegetation during the dormant season, when deciduous cover is lacking, to exploit shifts of prey into these areas. Similarly, I found male bobcats selected SAUs closer to fields during the denning season, which overlaps with the growing season. Female white-tailed deer have been found to select parturition sites, and white-tailed deer fawns to select bed sites, in areas with high visual obscurity, which often is high along field edges in this study area (Shuman et al. 2018). Likewise, cottontail rabbits select for grassy areas and dense vegetation found in overgrown fields and along field edges (Althoff et al. 1997, Bond et al. 2002). Male bobcats also exhibited 2nd order selection for deciduous forest only during the dispersal season, which overlaps with the peak of hard mast production. Squirrels are the most common diet item of bobcats in this study area (Morin et al. 2016), and both gray squirrels (*Sciurus carilonensis)* and fox squirrels (*Sciurus niger)* exhibit peaks in foraging behavior during this time (Fox 1982, Short and Duke 1971, Spritzer 2002). As suggested by Chamberlain et al. (2003), it appears that bobcats in this study area may seasonally shift resource selection to better exploit prey.

This study provides initial insights into bobcat spatial ecology in the mountains of western Virginia and the broader region, specifically resource selection which has remained largely unstudied in Appalachia until this research. Further, this is the first study to utilize GPS collars on bobcats in the central Appalachian Mountains. This study has illuminated the difficulties in conducting GPS telemetry in the dense canopy and rugged landscape of Appalachia, particularly on bobcats due to their size and life history. Extended GPS satellite search times are required to maintain adequate fix success, at the cost of battery life, which is already limited for relatively small bobcat collars. Even collars that otherwise performed well exhibited a sharp decrease in fix success in the time surrounding the denning season for females, as they frequented presumably rocky, steep, and/or densely vegetated den sites. The main limitation of this study was the poor fix success of some GPS collars, and the compounding effects with the already small sample size that prohibited 3rd order resource selection analysis for females. Despite this fact, GPS relocations certainly exceeded previous VHF-telemetry samples from the 1980’s in sample size, frequency, and locational accuracy; allowing more robust examination of home ranges and movement rates. While a 4 hour fix interval does not capture the finer-scale variation in bobcat movements, it is an improvement over prior daily-distance-moved metrics of earlier studies. Another limitation of this study was the broad delineation of forest into 2 categories: mixed and deciduous. Forested land cover composes ~90% of the study area, and a finer-scale examination of forest structure would allow a better understanding of varying bobcat resource selection on the landscape and within home ranges. Since understory and midstory vegetation are likely the most relevant aspects of the forest to bobcats, Light Detection and Ranging (LiDAR) data or manually-collected microhabitat data would provide further insight.

Management and Research Implications:

Bobcat populations appear to be relatively stable in Appalachia, with states in the region reporting stable or increasing population metrics (Roberts and Crimmins 2010), and a recent population study estimating densities in this study area that fit with regional patterns (Morin et al. 2018). Managers should be armed with local information to conduct science-based management on bobcat populations in the region, whether that management dictates reducing, maintaining, or increasing populations. Findings from this study illustrate the importance of forested habitat to female bobcats in Appalachia. Likewise, both sexes selected home ranges at higher elevations, indicating use of predominately forested ridges, likely due to conversion of valley bottoms to agriculture and development, and a corresponding avoidance of humans. Based on the foraging ecology of bobcats, a dense understory within these forests would improve habitat quality for bobcats and most of their primary prey items. When planning future land use in the region, particularly regarding development of ridges, planners should consider the importance of these landscape features to bobcats.

This study shows that male bobcats in Appalachia exhibit higher movement rates and have larger home ranges than females, which has both management and research implications.

Male bobcats are also more likely to select home ranges, and locations within home ranges, near fields. From a management standpoint, these findings suggest that male bobcats may have increased risk of mortality due to increased probability of being shot, trapped, or hit by a vehicle. Mortality rates on this study support this, with 29% of males dying from harvest or vehicle collisions versus no human-caused mortalities for females (1 female 6+ years of age died of unknown causes), although it is important to consider the relatively small sample size of females. Harvest data indicates an almost even sex ratio for bobcat trapping mortality, or even female-skewed ratio for bobcat hunting mortality (Michael Fies personal communication). Considering the smaller space use requirements of females, perhaps the sex ratio of overall bobcat population is female-skewed. If this is true, and males are more vulnerable to harvest, the observed sex ratio of harvested bobcats may be 1:1 but not indicative of the overall population sex ratio. If mortality is male-skewed, long-term negative impacts on population dynamics are less likely than high rates of female mortality, especially considering the polygynous reproductive strategy and land tenure based spatial organization of bobcats. Efforts to reduce populations through increased trapping harvest may not be highly effective if mortality is male-skewed. Researchers should consider these vast differences in space use between sexes when considering detectability of bobcats. This has implications for any population-level sampling efforts such as diet analysis or population estimation, as it is likely that detection probabilities will be higher for male bobcats due to their greater space use.

Male bobcats exhibited 2nd and 3rd order selection for fields, and this selection was strongest during the denning season at both scales. The denning season overlaps with the time period in which white-tailed deer fawns are present on the landscape, and it is possible that female deer select areas of high visual obscurity near field edges as fawn rearing areas. Thus, selection of fields during summer months may indicate that males are actively searching for fawns along field edges at this time. Further research should investigate where bobcat predation on fawns is most likely to occur, and if field edges are areas of high risk for white-tailed deer fawns.

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Literature Cited:

Abouelezz, H. G., T. M. Donovan, R. M. Mickey, J. D. Murdoch, M. Freeman, and K. Royar. 2018. Landscape composition mediates movement and habitat selection in bobcats (Lynx rufus): implications for conservation planning. Landscape Ecology 33:1301–1318.

Anderson, E. M. 1988. Effects of male removal on spatial distribution of bobcats. Journal of Mammalogy 69:637–641.

Anderson, E. M. 1990. Bobcat diurnal loafing sites in southeastern Colorado. Journal of Wildlife Management 54(4):600.

Anderson, E. M., and Lovallo, M. J. 2003. Bobcat and lynx. Wild mammals of North America: biology, management, and economics. Johns Hopkins Press: Baltimore, Maryland, 758-786.

Bailey, T. N. 1974. Social organization in a bobcat population. Journal of Wildlife Management 38:435.

Balme, G. A., and L.T. Hunter. 2013. Why leopards commit infanticide. Animal Behaviour, 86(4): 791-799.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67.

Benson, J. F., M. J. Chamberlain, and B. D. Leopold. 2004. Land tenure and occupation of vacant home ranges by bobcats (*Lynx rufus*). Journal of Mammalogy 85:983–988.

Börger, L., B. D. Dalziel, and J. M. Fryxell. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research: Home range modelling. Ecology Letters 11:637–650.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Caro, T. M. 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. Univ. of Chicago Press, Chicago, Illinois.

Carstensen, M., G. D. DelGiudice, B. A. Sampson, and D. W. Kuehn. 2009. Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. Journal of Wildlife Management 73:175–18

Chamberlain, M. J. 1999. Dietary patterns of sympatric bobcats and coyotes in central Mississippi. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies, 53:204–219.

Chamberlain, M. J., B. D. Leopold, L. W. Burger, B. W. Plowman, and L. M. Conner. 1999. Survival and cause-specific mortality of adult bobcats in central Mississippi. Journal of Wildlife Management 63:613.

Conner, L. M., Chamberlain, M. J., and B.D. Leopold. 2001. Bobcat home range size relative to habitat quality. In Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 55: 418-426.

Croteau, E. K., E. J. Heist, and C. K. Nielsen. 2010. Fine-scale population structure and sex-biased dispersal in bobcats (Lynx rufus) from southern Illinois. Canadian Journal of Zoology 88:536–545.

Christen H. Fleming and Justin M. Calabrese (2018). ctmm: Continuous-Time Movement Modeling. R package version 0.5.2.

Cochrane, J. C., J. D. Kirby, I. G. Jones, L. M. Conner, and R. J. Warren. 2006. Spatial Organization of adult bobcats in a longleaf pine-wiregrass ecosystem in Southwestern Georgia. Southeastern Naturalist 5(4):711–724.

Elizalde-Arellano, C., J. C. López-Vidal, L. Hernández, J. W. Laundré, F. A. Cervantes, and M. Alonso-Spilsbury. 2012. Home range size and activity patterns of Bobcats (Lynx rufus) in the southern part of their range in the Chihuahuan Desert, Mexico. The American Midland Naturalist 168:247–264.

Ferguson, A. W., N. A. Currit, and F. W. Weckerly. 2009. Isometric scaling in home-range size of male and female bobcats (Lynx rufus). Canadian Journal of Zoology 87:1052–1060.

Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96:1182–1188.

Fleming, C. H., D. Sheldon, W. F. Fagan, P. Leimgruber, T. Mueller, D. Nandintsetseg, M. J. Noonan, K. A. Olson, E. Setyawan, A. Sianipar, and J. M. Calabrese. 2018. Correcting for missing and irregular data in home-range estimation. Ecological Applications 28:1003–1010.

Fox, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. Evolution, 36(4): 800-809.

Fox, L. B. 1990. Ecology and population biology of the bobcat (*Felis rufus*) in New York. PhD Dissertation, State University of New York College of Environmental Science and Forestry, Syracuse, New York.

Frakes, R. A., Belden, R. C., Wood, B. E., and F.E. James. 2015. Landscape analysis of adult Florida panther habitat. PloS one, 10(7): e0133044.

Fuller, T. K., W. E. Berg, and D. W. Kuehn. 1985. Bobcat home range size and daytime cover-type use in northcentral Minnesota. Journal of Mammalogy 66:568–571.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals: Random effects in resource selection. Journal of Animal Ecology 75:887–898.

Gipson, P. S., and J. F. Kamler. 2002. Bobcat killed by a coyote. Southwestern Naturalist 47:511.

Godbois, I. A., L. M. Conner, and R. J. Warren. 2004. Space-use patterns of bobcats relative to supplemental feeding of northern bobwhites. Journal of Wildlife Management 68:514–518.

Gooliaff, T., and K. E. Hodges. 2018. Historical distributions of bobcats (*Lynx rufus*) and Canada lynx (*Lynx canadensis*) suggest no range shifts in British Columbia, Canada. Canadian Journal of Zoology 96:1299–1308.

Jackson, D. L., Gluesing, E. A., and H.A. Jacobson. 1988. Dental eruption in bobcats. Journal of Wildlife Management. 52(3): 515-517.

Jacques, C. N., and J. A. Jenks. 2008. Visual observation of bobcat predation on an adult female pronghorn in northwestern South Dakota. American Midland Naturalist 160:259–261.

Janečka, J. E., T. L. Blankenship, D. H. Hirth, C. William Kilpatrick, M. E. Tewes, and L. I. Grassman. 2007. Evidence for male-biased dispersal in bobcats (*Lynx rufus*) using relatedness analysis. Wildlife Biology 13:38–47.

Janečka, J. E., T. L. Blankenship, D. H. Hirth, M. E. Tewes, C. W. Kilpatrick, and L. I. Grassman. 2006. Kinship and social structure of bobcats (Lynx rufus) inferred from microsatellite and radio-telemetry data. Journal of Zoology 269:494–501.

Johnson, D. H. 1980. The Comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, S. A., H. D. Walker, and C. M. Hudson. 2010. Dispersal characteristics of juvenile bobcats in south-central Indiana. Journal of Wildlife Management 74(3):379–385.

Kamler J.F, Gipson P.S., and T. R. Snyder. 2000. Dispersal characteristics of young bobcats from northeastern Kansas. Southwestern Naturalist 45:543–546.

Katnik, D. D. and R.B. Wielgus. 2005. Landscape proportions versus Monte Carlo simulated home ranges for estimating habitat availability. Journal of Wildlife Management 69(1):20-32.

Kelly, M., Morin, D. and C.A. Lopez-Gonzalez. 2016. Lynx rufus. The IUCN Red List of Threatened Species.

Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management 76:1420–1430

Kirby, J. D., J. C. Rutledge, I. G. Jones, L. M. Conner, and R. J. Warren. 2010. Effects of Time of Day and Activity Status on Bobcat (Lynx rufus) Cover-type selection in southwestern Georgia. Southeastern Naturalist 9:317–326.

Kitchings, J. T., and J. D. Story. 1984. Movements and dispersal of bobcats in east Tennessee. Journal of Wildlife Management 48:957.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 3–42.

Knowles, P. R. 1985. Home range size and habitat selection of bobcats, Lynx rufus, in north-central Montana. Canadian Field-Naturalist 99: 6-12.

Koehler, G.M. and M.G. Hornocker. 1989. Influences of seasons on bobcats in Idaho. Journal of Wildlife Management. 53(1):197-202.

Koehler, G.M. and M.G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mammalogy. 72(2): 391-396.

Kunkel, K. E., and L. D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology. 72:1557–1565

Kuznetsova A., Brockhoff P.B., R.H.B. Christensen. 2017. “lmerTest Package: Tests in Linear Mixed Effects Models.” Journal of Statistical Software. 82(13): 1-26. <i13 (URL: http://doi.org/10.18637/jss.v082.i13>

Labisky, R. F., and M. C. Boulay. 1998. Behaviors of bobcats preying on white-tailed deer in the Everglades. American Midland Naturalist 139:275–281.

Lancia, R. A. 1986. Summer movement patterns and habitat use by bobcats on Croatan National Forest, North Carolina. Cats of the World: Biology, Conservation, and Management 425-436.

Lariviere, S., and L. R.Walton. 1997. Lynx rufus. Mammalian Species 563:1–8.

Laundre, J. W., T. D. Reynolds, S. T. Knick, and I. J. Ball. 1987. Accuracy of daily point relocations in assessing real movement of radio-marked animals. Journal of Wildlife Management 51(4):937-940.

Lembeck M. and G. I. Gould. 1979. Dynamics of harvested and unharvested bobcat population in California. Bobcat Research Conference Proceedings, National Wildlife Federation Scientific Technical Series 6:53–54.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1986. Bobcat Habitat Use and Home Range Size in Relation to Prey Density. Journal of Wildlife Management 50(1):110-117.

Litvaitis, J. A., J. T. Major, and J. A. Sherburne. 1987. Influence of season and human-induced mortality on spatial organization of bobcats (*Felis rufus*) in Maine. Journal of Mammalogy 68:100–106.

Logan, K. A., and L.L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press.

Lorber, J., M. A. Thomas-Van Gundy, and S. Croy. 2018. Characterizing effects of prescribed fire on forest canopy cover in the George Washington and Jefferson National Forests.

U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Lovallo, M. J. and E. M. Anderson. 1996. Bobcat (*Lynx rufus*) home range size and habitat use in northwest Wisconsin. American Midland Naturalist. 135(2): 241-252.

Lovallo, M. J., and G. Fowles. 2018. Long distance dispersal by a female Lynx rufus (bobcat) in the Mid-Atlantic Region. Northeastern Naturalist 25:3.

Maehr, D. S. 1996. Comparative ecology of bobcat, black bear, and Florida panther in south Florida. PhD Dissertation, University of Florida, Gainesville.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L. and W. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers. Secaucus, New Jersey.

Mathews, N. E. and W. F. Porter. 1988. Black bear predation of white-tailed deer neonates in the central Adirondacks. Canadian Journal of Zoology 66:1241–124

Mautz, W.W., and P.J. Pekins. 1989. Metabolic rate of bobcats as influenced by seasonal temperatures. Journal of Wildlife Management. 53(1):202-205.

McLean, M. L., T. S. McCay, and M. J. Lovallo. 2005. Influence of age, sex and time of year on diet of the bobcat (Lynx rufus) in Pennsylvania. American Midland Naturalist 153:450–453.

McCord, C. M. 1974. Selection of winter habitat by bobcats (Lynx rufus) on the Quabbin Reservation, Massachusetts. Journal of Mammalogy 55:428–437.

McCord, C. M. and J. E. Cordoza. 1982. Bobcat and lynx, p. 728-766. In: J. A. Chapman and G. A. Feldhamer (eds.). Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, MD.

Millspaugh, J. J., and J. M. Marzluff, editors. 2001. Radio tracking and animal populations. Academic Press, San Diego, California, USA

Mosimann, J. E. 1958. The Evolutionary significance of rare matings in animal populations. Evolution 12:246–261.

Morin, D. J., S. D. Higdon, J. L. Holub, D. M. Montague, M. L. Fies, L. P. Waits, and M. J. Kelly. 2016. Bias in carnivore diet analysis resulting from misclassification of predator scats based on field identification: bias and uncertainty in carnivore scat identification. Wildlife Society Bulletin 40:669–677.

Morin, D. J., L. P. Waits, D. C. McNitt, and M. J. Kelly. 2018. Efficient single-survey estimation of carnivore density using fecal DNA and spatial capture-recapture: a bobcat case study. Population Ecology 60:197–209.

Nelson, M. A., M. J. Cherry, M. B. Howze, R. J. Warren, and L. M. Conner. 2015. Coyote and bobcat predation on white-tailed deer fawns in a longleaf pine ecosystem in southwestern Georgia. Journal of the Southeastern Association of Fish and Wildlife Agencies 2: 208-213.

Nielsen, C. K., and A. Woolf. 2003. Dispersal of juvenile male bobcats (Lynx rufus) in southern Illinois. Trans. Ill. Stat Acad. Sci. 96: 313-318.

Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. Ecology 94:1456–1463.

Roberts, N. M., and S. M. Crimmins. 2010. Bobcat population status and management in North America: evidence of large-scale population increase. Journal of Fish and Wildlife Management 1(2):169–174.

Rockhill, A. P., C. S. DePerno, and R. A. Powell. 2013. The effect of illumination and time of day on movements of bobcats (Lynx rufus). PLoS ONE 8:e69213.

Rucker, R. A., M. L. Kennedy, G. A. Heidt, and M. J. Harvey. 1989. Population density, movements, and habitat use of bobcats in Arkansas. Southwestern Naturalist 34:101.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. In: Carnivore Behavior, Ecology, and Evolution (Ed. by J. L. Gittleman). 164–182. Ithaca, New York: Cornell University Press.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Short, H. L., and W.B. Duke. 1971. Seasonal food consumption and body weights of captive tree squirrels. Journal of Wildlife Management. 35(3):435-439.

Shuman, R. M., M. J. Cherry, T. N. Simoneaux, E. A. Dutoit, J. C. Kilgo, M. J. Chamberlain, and K. V. Miller. 2017. Survival of white-tailed deer neonates in Louisiana. Journal of Wildlife Management 81:834–845.

Sikes, R. S., and M. L. Kennedy. 1993. Geographic Variation in Sexual Dimorphism of the Bobcat (Felis rufus) in the Eastern United States. Southwestern Naturalist 38:336.

Spritzer, M. D. 2002. Diet, microhabitat use and seasonal activity patterns of gray squirrels (*Sciurus carolinensis*) in hammock and upland pine forest. American Midland Naturalist. 148(2): 271-282.

Stys, E. D., and B. D. Leopold. 1993. Reproductive biology and kitten growth of captive bobcats in Mississippi. Proceedings of the annual conference Southeastern Association of Fish and Wildlife Agencies. 47:80-89.

Svoboda, N. J., J. L. Belant, D. E. Beyer, J. F. Duquette, and J. A. Martin. 2013. Identifying bobcat *Lynx rufus* kill sites using a global positioning system. Wildlife Biology 19:78–86.

Taylor, C. R., Caldwell, S. L., and V.J. Rowntree. 1972. Running up and down hills: some consequences of size. Science 178(4065): 1096-1097.

Virginia Geographic Information Network. 2016. Land Cover Report: Classification Summary by County. Virginia Information Technologies Agency.

Vreeland, J. K., D. R. Diefenbach, and B. D. Wallingford. 2004. Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns. Wildlife Society Bulletin 32:542–553.

Walter, W. D., D. P. Onorato, and J. W. Fischer. 2015. Is there a single best estimator? Selection of home range estimators using area-under-the-curve. Movement Ecology 3:10.

Wassmer, D. A., Guenther, D. D., and J.N. Layne. 1988. Ecology of the bobcat in south-central Florida. Bull. Fla. State Mus. Biol. Sci. 33: 159-228.

Whitaker, J., Fredrick, R. B., and L.T. Edwards. 1987. Home-range size and overlap of eastern Kentucky bobcats. In Proceedings of the Southeastern Association of Fish and Wildlife Agencies 41: 417-423.

Winegarner, C. E., and M. S. Winegarner. 1982. Reproductive history of a bobcat. Journal of Mammalogy 63:680–682.

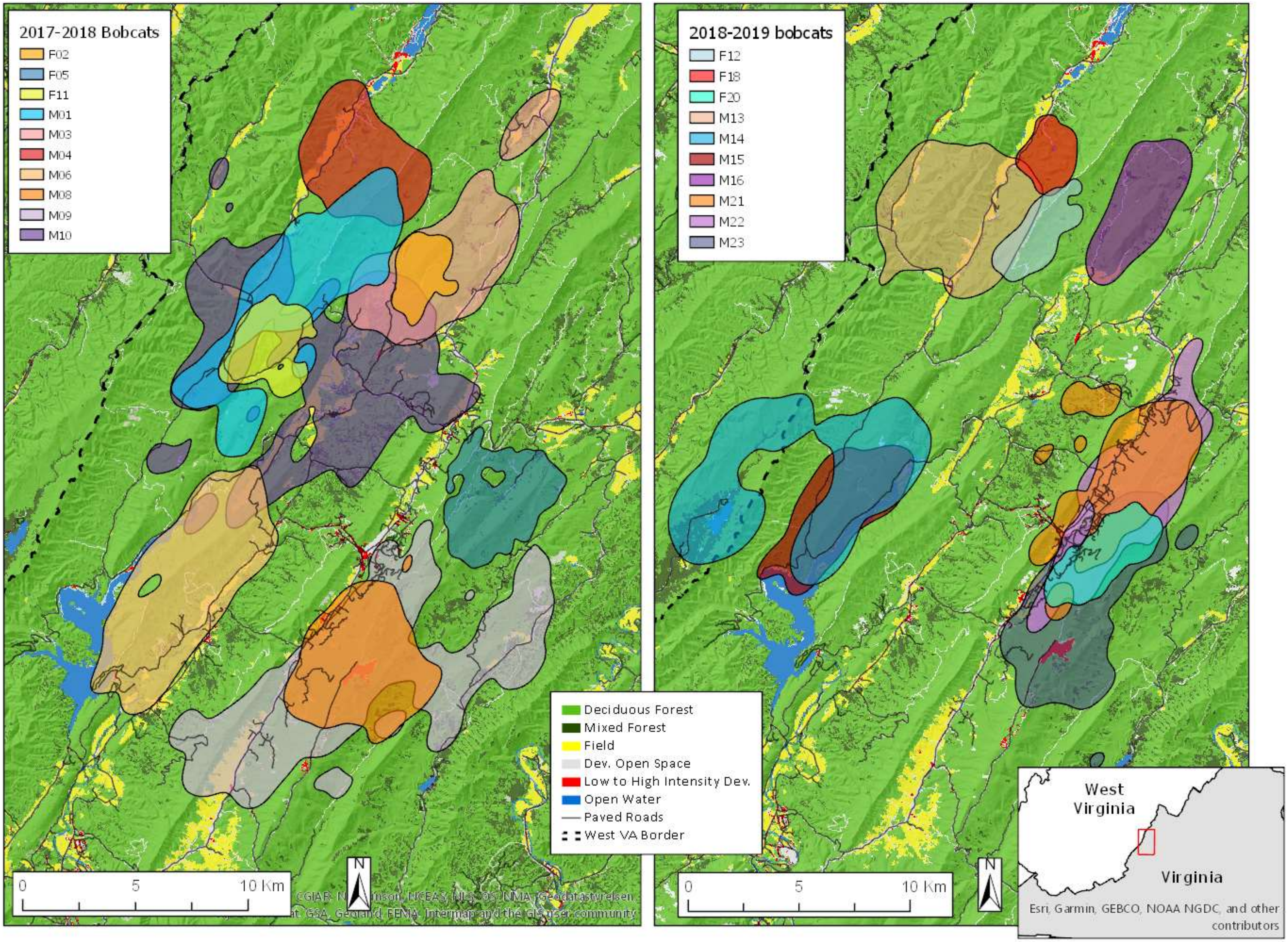

Figure 1. Map of study area with land cover and 95% home ranges of bobcats (n=20) monitored from 2017-2019 in Bath County, VA). Home ranges calculated using the autocorrelated kernel density estimator.

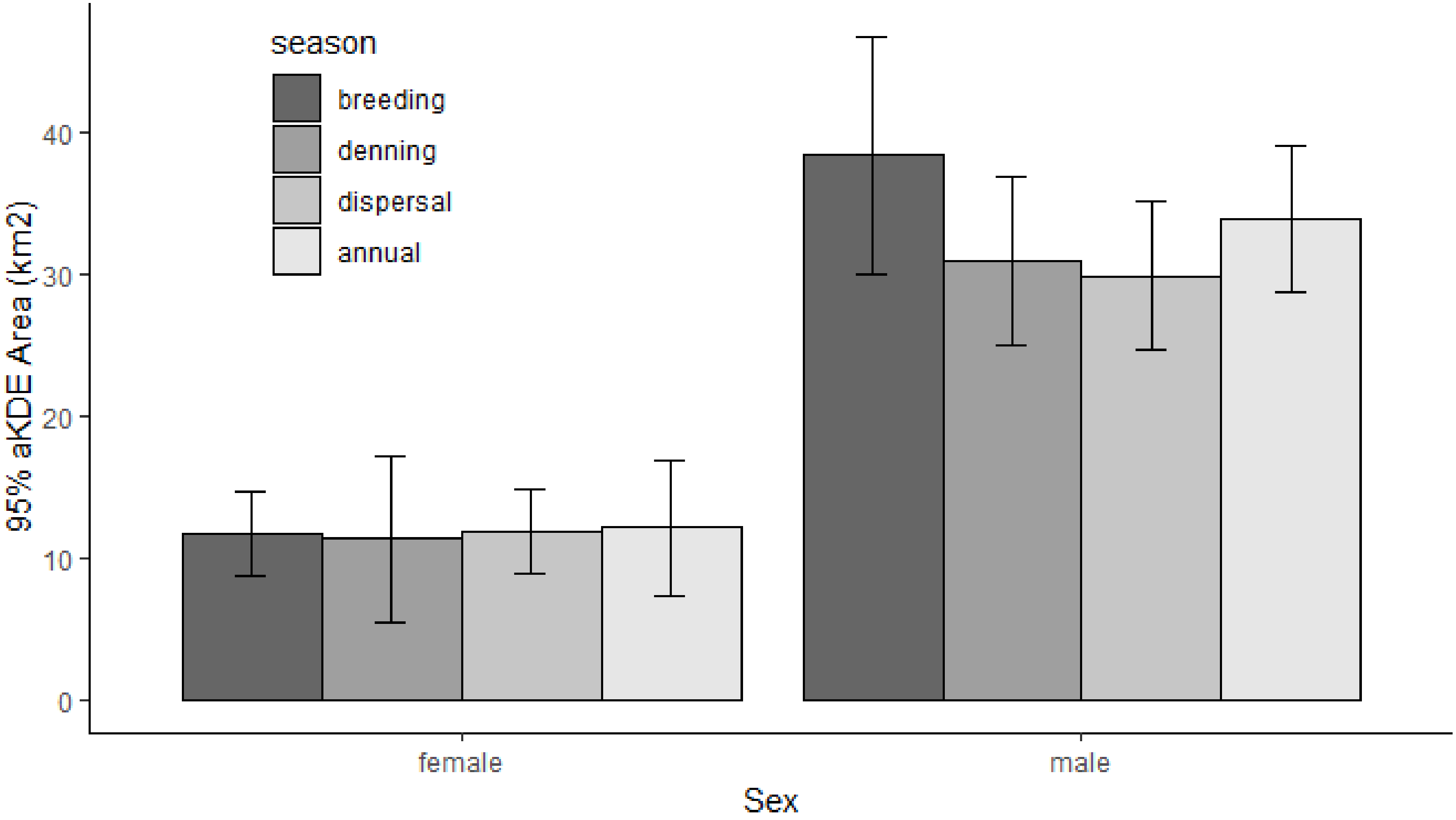

Figure 2. Means and 95% confidence intervals of 95% home ranges of female and male resident bobcats monitored during 2017-2019 in Bath County, VA, for breeding (n=12, 4 females, 8 males), denning/kitten-rearing (n=16, 5 females, 11 males), and dispersal/pre-breeding (n=15, 4 females, 11 males) seasons, and annual (n=16, 5 females, 11 males).. Home ranges calculated using the autocorrelated kernel density estimator.

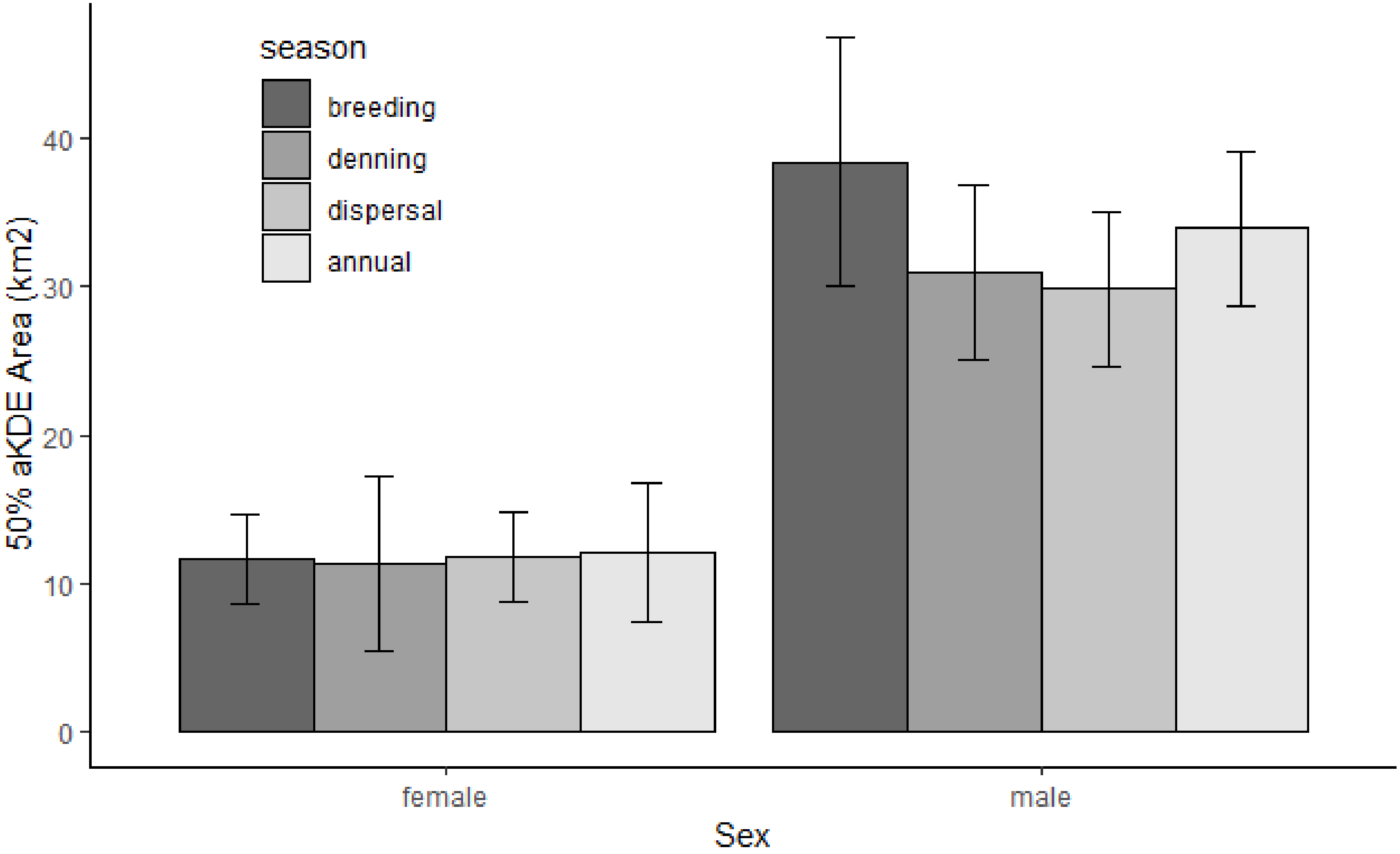

Figure 3. Means and 95% confidence intervals of 50% core use areas of female and male resident bobcats monitored during 2017-2019 in Bath County, VA, for breeding (n=12, 4 females, 8 males), denning/kitten-rearing (n=16, 5 females, 11 males), and dispersal/pre-breeding (n=15, 4 females, 11 males) seasons, and annually (n=16, 5 females, 11 males). Core use areas calculated using the autocorrelated kernel density estimator.

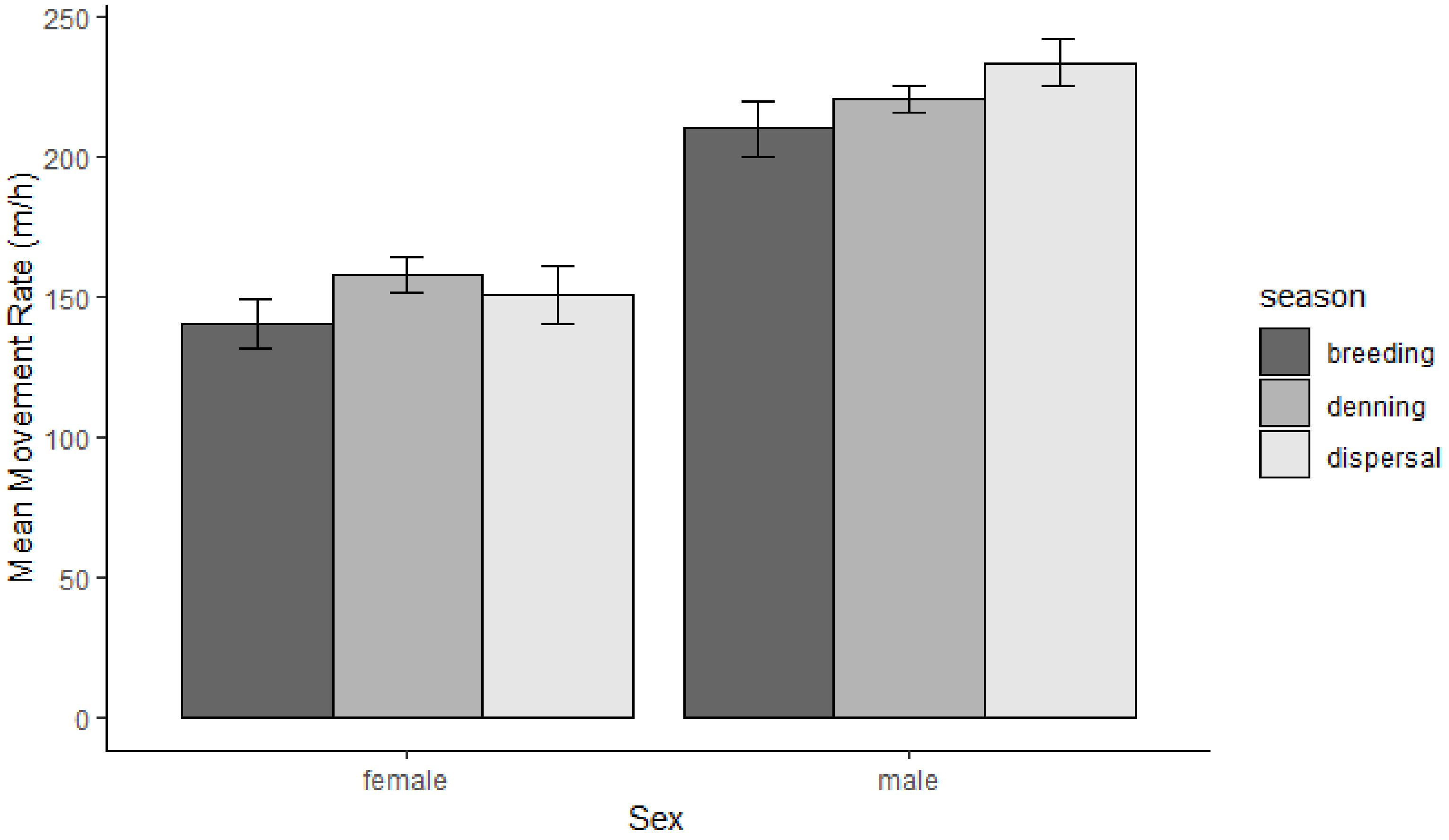

Figure 4. Means and 95% confidence intervals for movement rates of female and male bobcats monitored during 2017-2019 in Bath County, VA, for breeding (n=14, 5 females, 9 males), denning/kitten-rearing (n=17, 4 females, 13 males), and dispersal/pre-breeding (n=15, 4 females, 11 males) seasons. Movement rate is reported as meters moved per hour (m/h).

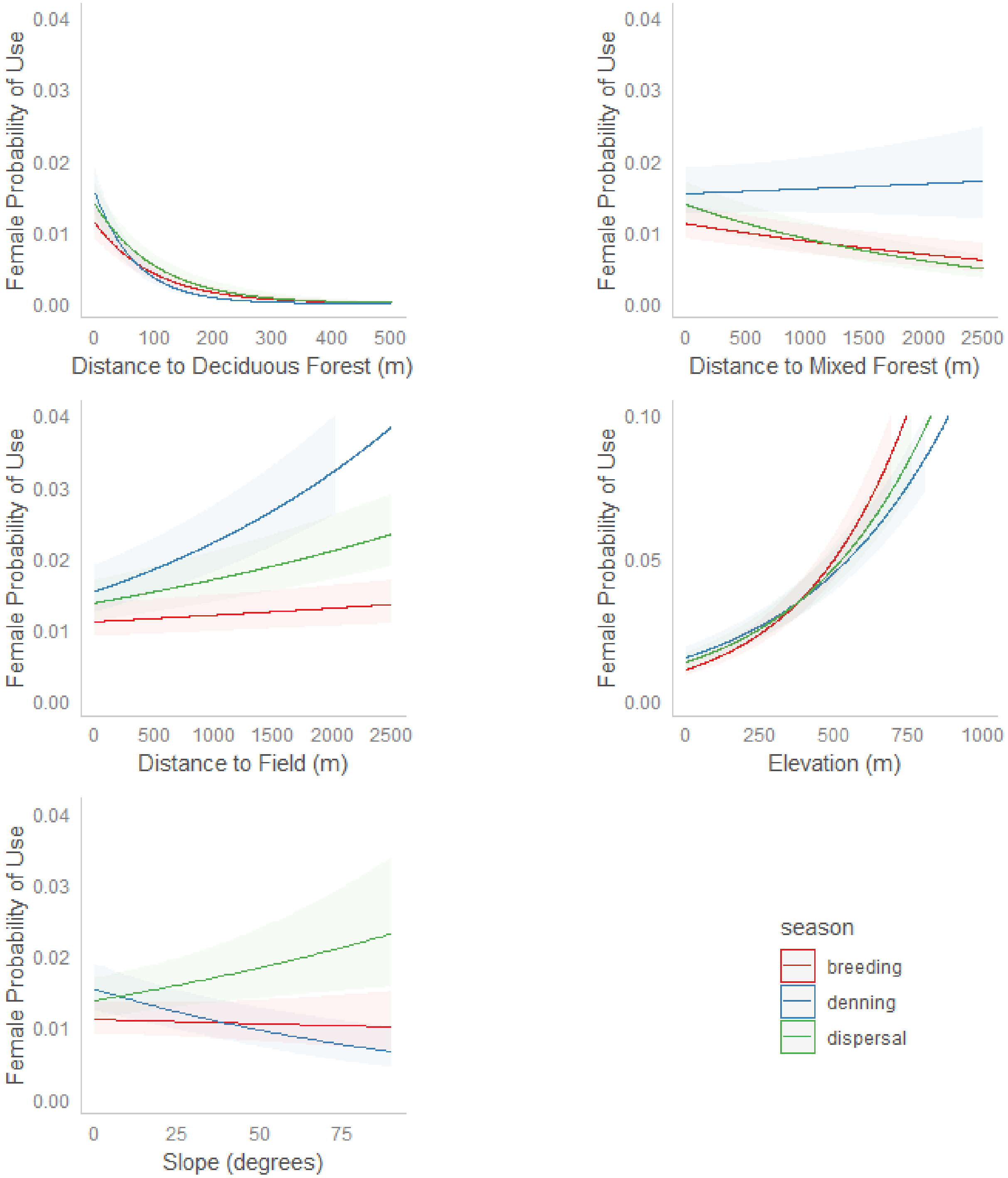

Figure 5. Relative probability of 2nd order selection with 95% confidence intervals for female bobcats monitored during 2017-2019 in Bath County, VA, for breeding (n=5), denning/kitten-rearing (n=4), and dispersal/pre-breeding (n=4) seasons.

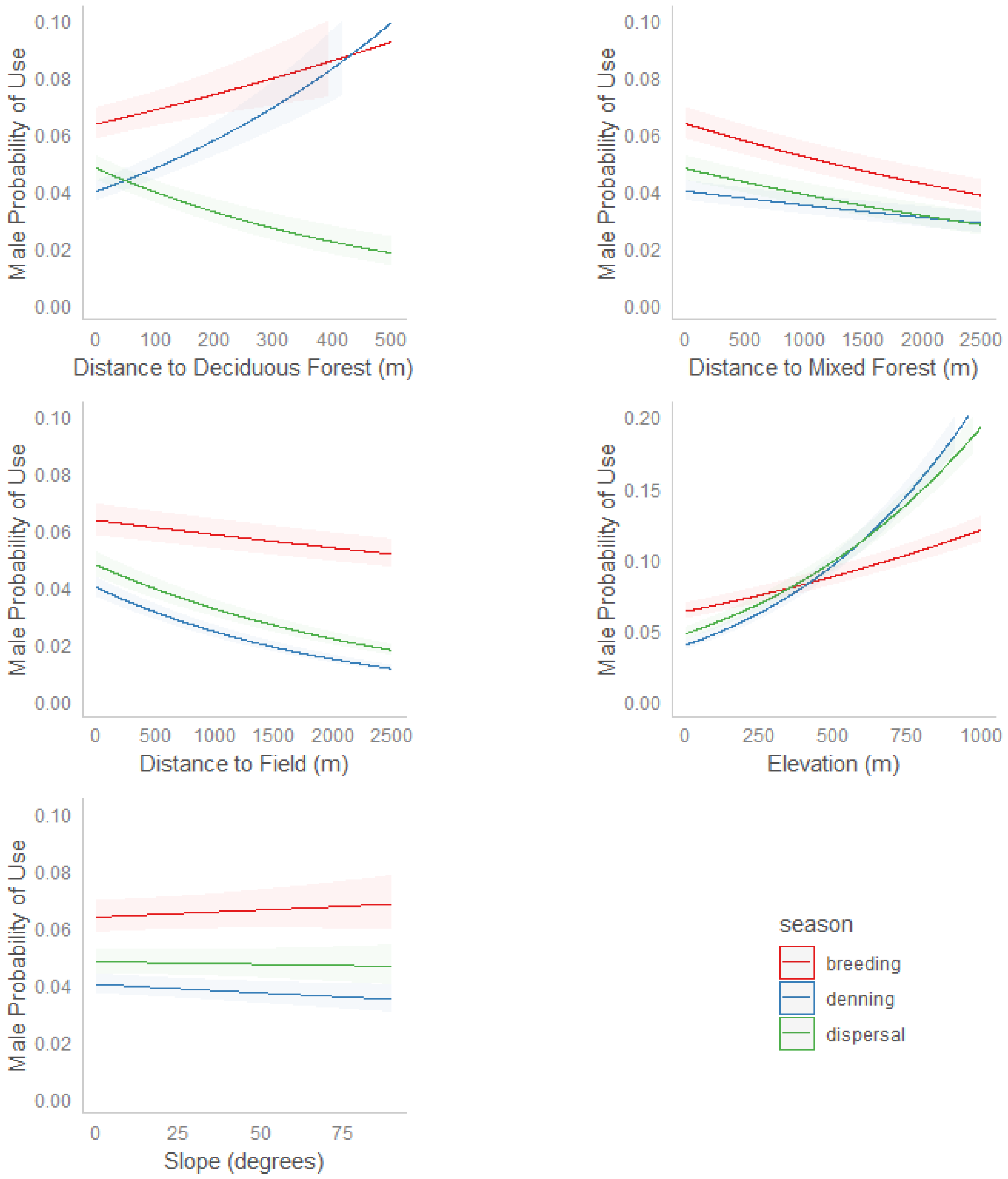

Figure 6. Relative probability of 2nd order selection with 95% confidence intervals for male bobcats monitored during 2017-2019 in Bath County, VA, for breeding (n=9), denning/kitten-rearing (n=13), and dispersal/pre-breeding (n=11) seasons.

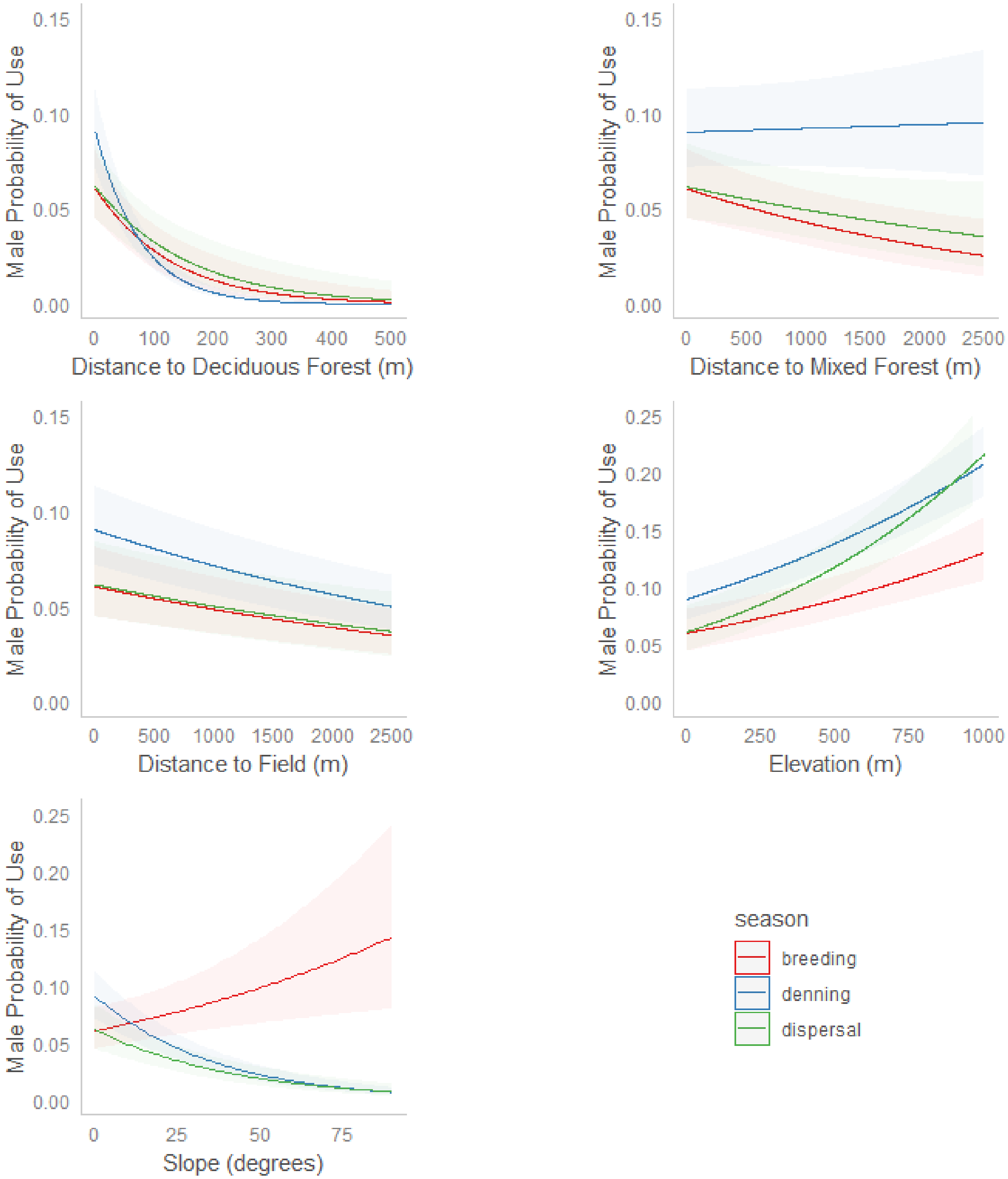

Figure 7. Relative probability of 3rd order selection with 95% confidence intervals for male bobcats monitored during 2017-2019 in Bath County, VA, for breeding (n=5), denning/kitten-rearing (n=7), and dispersal/pre-breeding (n=7) seasons.

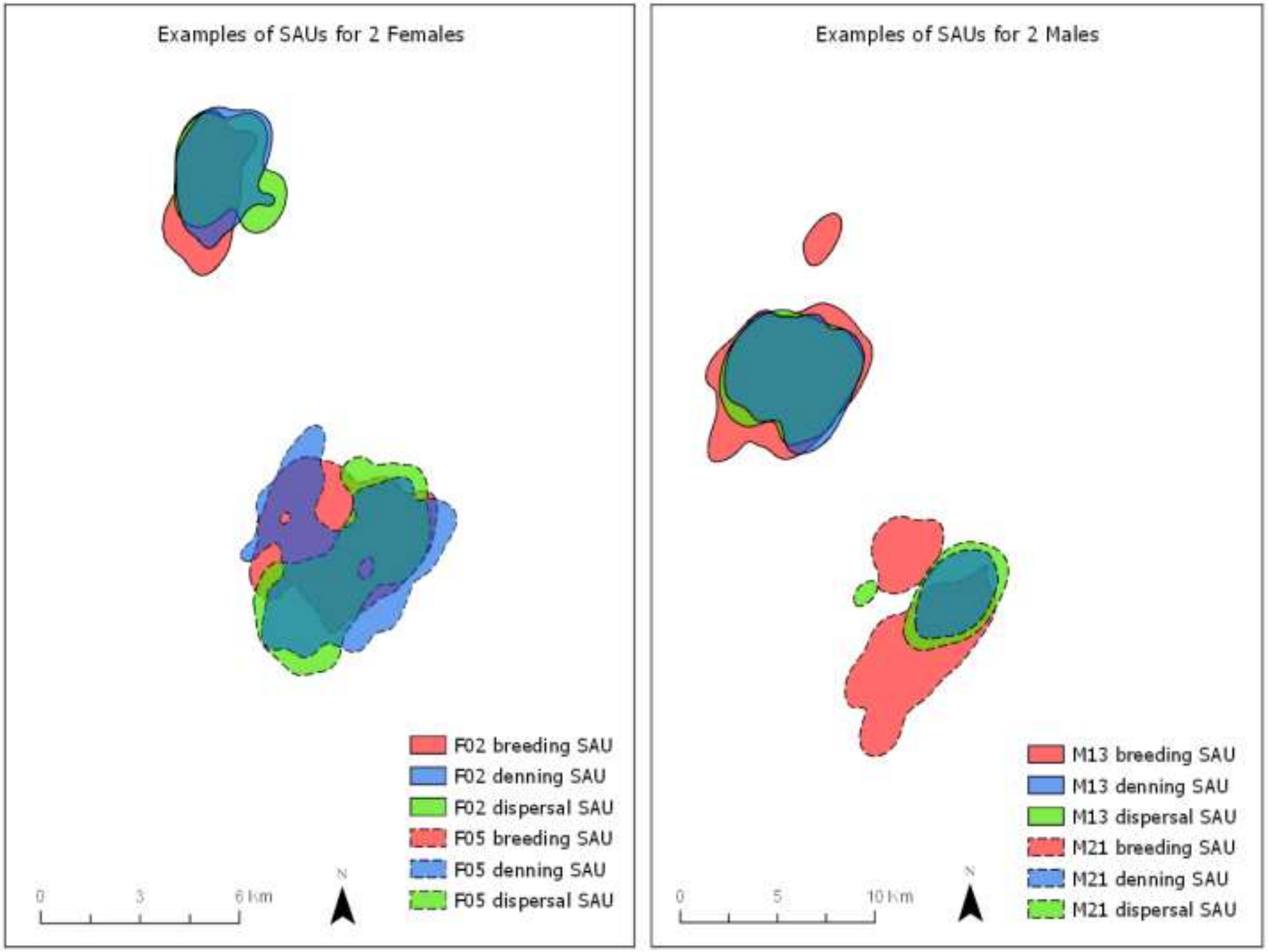

Figure 8. Breeding, denning, and dispersal seasonal areas of use (SAU) for 2 female and 2 male bobcats monitored during 2017-2019 in Bath County, Virginia. Note that SAUs overlap extensively, differing only slightly in location and shape. The wide shift in the breeding SAU for M21 followed the mortality of a neighboring male bobcat, potentially indicating a shift by M21 to fill the resulting home range vacancy.

Table 1. GPS collar fix success for bobcats (n=20, 6 female, 14 male) monitored during 2017-2019 in Bath County, VA. Telonics collars were deployed during 2017 and ATS collars were deployed during 2018. Weekly fix success of F18 and F20 sharply dropped during April and May, when those females were likely spending significant time lactating in den sites.

Bobcat ID	Collar Make	Number of locations	Days deployed	Fix success
F02	Telonics	907	282	68%
F05	Telonics	799	303	64%
F11	Telonics	454	239	41%
F12	ATS	351	85	94%
F18	ATS	552	151	51%
F20	ATS	1140	362	79%
M01	Telonics	789	268	71%
M03	Telonics	606	273	47%
M04	Telonics	599	242	45%
M06	Telonics	597	268	50%
M08	Telonics	990	233	60%
M09	Telonics	801	265	58%
M10	Telonics	490	236	36%
M13	ATS	1976	375	93%
M14	ATS	259	55	87%
M15	ATS	1123	249	85%
M16	ATS	1772	393	90%
M21	ATS	1762	363	87%
M22	ATS	873	178	91%
M23	ATS	1822	359	92%
Mean		933	259	69%
SE		116	20	4%
Male mean		1033	268	71%
Male SE		152	24	6%
Female mean		701	237	66%
Female SE		123	42	8%
Telonics mean		703	261	54%
Telonics SE		57	7	4%
ATS mean		1163	257	85%
ATS SE		204	41	4%

Table 2. Linear mixed model for bobcats monitored during 2017-2019 in Bath County, VA with log transformed home range area as response and reproductive season interacting with sex as predictor. Reference categories are sex=female and season=dispersal.

Model	Covariate	β	SE	df	t value	Pr(>|t|)
50% core	(Intercept)	0.979	0.213	24.48	4.598	< 0.001
	Breeding Season	0.022	0.170	21.11	0.132	0.896
	Denning season	0.042	0.184	23.55	0.230	0.820
	Male	1.086	0.249	24.20	4.360	< 0.001
	Breeding season: x male	0.164	0.207	21.44	0.793	0.437
	Denning season x male	0.025	0.210	23.11	0.121	0.905
95% home range	(Intercept)	2.370	0.202	26.95	11.755	< 0.001
	Breeding Season	0.020	0.177	21.62	0.111	0.913
	Denning season	-0.020	0.190	24.51	-0.103	0.918
	Male	1.098	0.236	26.69	4.658	< 0.001
	Breeding season x male	0.231	0.215	22.04	1.073	0.295
	Denning season x male	0.064	0.217	23.99	0.295	0.770

Table 3. Gamma generalized linear mixed-effects model for bobcats monitored during 2017-2019 in Bath County, VA, with movement rates as response and reproductive season interacting with sex as predictor. Reference categories are sex=female and season=den.

Covariate	β	SE	t value	Pr(>|z|)
(Intercept)	5.127	0.099	51.867	< 0.001
Breeding season	-0.150	0.072	-2.093	0.036
Dispersal season	-0.149	0.057	-2.605	0.009
Male	0.294	0.116	2.535	0.011
Breeding season x male	0.082	0.078	1.060	0.289
Dispersal season x male	0.189	0.064	2.968	0.003

Table 4. Model results for 2nd order resource selection functions (RSF) for 18 bobcats (12 male, 6 female) collared in Bath County, Virginia in years 2017-2019, including separate models for males and females. RSF models are binomial generalized linear mixed-effects models. Results include β coefficients (β), and standard errors (SE), z values, and p values from Wald tests. Reference category is season = dispersal.

Sex	Covariate	β	SE	Z value	P value
Female	deciduous	-0.244	0.027	-8.998	< 0.001
	mixed	-0.124	0.015	-8.553	< 0.001
	field	0.166	0.014	11.900	< 0.001
	elevation	0.381	0.016	24.386	< 0.001
	slope	0.044	0.016	2.796	0.005
	deciduous x breed	-0.006	0.037	-0.154	0.878
	deciduous x den	-0.126	0.043	-2.943	0.003
	mixed x breed	0.052	0.020	2.674	0.008
	mixed x den	0.137	0.024	5.679	< 0.001
	field x breed	-0.105	0.020	-5.162	< 0.001
	field x den	0.124	0.021	5.781	< 0.001
	elevation x breed	0.086	0.021	4.086	< 0.001
	elevation x den	-0.045	0.022	-2.064	0.039
	slope x breed	-0.053	0.023	-2.341	0.019
	slope x den	-0.116	0.023	-5.043	< 0.001
Male	deciduous	-0.054	0.008	-6.928	< 0.001
	mixed	-0.065	0.007	-9.933	< 0.001
	field	-0.293	0.008	-38.014	< 0.001
	elevation	0.234	0.006	36.515	< 0.001
	slope	-0.003	0.007	-0.490	0.624
	deciduous x breed	0.076	0.010	7.864	< 0.001
	deciduous x den	0.107	0.009	11.349	< 0.001
	mixed x breed	0.002	0.009	0.268	0.789
	mixed x den	0.025	0.009	2.878	0.004
	field x breed	0.229	0.010	23.579	< 0.001
	field x den	-0.075	0.010	-7.492	< 0.001
	elevation x breed	-0.128	0.009	-14.721	< 0.001
	elevation x den	0.048	0.008	5.767	< 0.001
	slope x breed	0.010	0.009	1.108	0.268
	slope x den	-0.011	0.009	-1.196	0.232

Table 5. Model results for 3rd order resource selection functions (RSF) for male bobcats (n=7) collared in Bath County, Virginia in 2018-2019. RSF model is a binomial generalized linear mixed-effects model. Results include β coefficients (β), and standard errors (SE), z values, and p values from Wald tests. Reference category is season = dispersal.

Covariate	β	SE	Z value	P value
deciduous	-0.179	0.046	-3.879	< 0.001
mixed	-0.054	0.029	-1.875	0.061
field	-0.133	0.036	-3.674	< 0.001
elevation	0.232	0.031	7.502	< 0.001
slope	-0.177	0.029	-6.152	< 0.001
deciduous x breed	-0.037	0.069	-0.541	0.588
deciduous x den	-0.195	0.053	-3.669	< 0.001
mixed x breed	-0.030	0.038	-0.792	0.428
mixed x den	0.059	0.032	1.840	0.066
field x breed	-0.010	0.044	-0.230	0.818
field x den	-0.025	0.040	-0.613	0.540
elevation x breed	-0.095	0.038	-2.522	0.012
elevation x den	-0.075	0.032	-2.338	0.019
slope x breed	0.253	0.039	6.499	< 0.001
slope x den	-0.036	0.033	-1.101	0.271

III. Influence of Prescribed Fire and Open Canopy Structure on Bobcat Space Use in Appalachian Forests

Abstract:

In the Appalachian Mountains, bobcat populations and the forest ecosystems they inhabit were greatly reduced by the early 20th century. As forest lands regenerated during the past century, bobcat populations increased and recolonized most of the species' former range. While forests have regenerated throughout the region, this regeneration has occurred with a drastically altered disturbance regime, resulting in a landscape increasingly dominated by contiguous swaths of mesic, closed-canopy forests. Due to their foraging strategies, bobcats are adapted to densely vegetated, productive understory in forested ecosystems. Considering these adaptations, the shifts in Appalachian forest structure likely have broad scale implications for bobcat habitat in the region. Despite the broad scale trends, land managers implement efforts to restore historic forest structure and increase productivity through the use of prescribed fire, timber harvest, and maintained wildlife clearings. I utilized GPS telemetry data from 10 GPS collared bobcats (7 male, 3 female) in 2018-2019 to examine resource selection in the heavily forested Appalachian Mountains of western Virginia. Specifically, I used resource selection analysis in a use-availability framework to examine how edge effects, prescribed fire, and timber harvest may influence how bobcats use space within their home ranges. I found that bobcats exhibited selection for forest-edge, open-canopy structure resulting from prescribed fire, and recently harvested forest stands. Bobcats exhibited avoidance of the forest interior. Selection was strongest for areas with open canopy structure resulting from prescribed fire and forest edge. Bobcats are likely selecting locations closer to these areas because of dense understory cover

where preferred prey species are more abundant. Land managers in Appalachia are steadily increasing the use of prescribed fire, however fire only occurs in a small portion of the Appalachian region and forest edges around open fields probably compose the majority of ideal bobcat habitat in most areas. The comparatively widespread use of fire in this study area has allowed novel insight into the effects of prescribed fire on bobcat space use and demonstrates the ecological importance of future efforts to restore historic fire cycles in Appalachia. As one of the largest carnivores in Appalachian ecosystems and the only wild felid remaining in the region, I suggest managers consider bobcat ecology when planning habitat management strategies and communicating those strategies to the public.

Introduction:

The ecosystems of the Appalachian Mountains have undergone dramatic shifts in recent centuries, primarily beginning with the arrival of European settlers and increasing over time. By the turn of the 20th century, the largest native grazers: elk (*Cervus canadensis*) and bison (*Bison bison*) were extirpated from the landscape, and widespread overharvest of timber followed by uncontrolled burning culminated in wide-scale deforestation throughout the region (Brooks 1965, Clarkson 1964, Davis 2003). Over the past century, forests have regenerated throughout much of Appalachia, yet largely in the absence of grazers or other broad-scale disturbance. Notably, these forests have regenerated during an era of fire suppression, despite the crucial role of frequent fire in shaping and maintaining Appalachian ecosystems (Lafon et al. 2017). The absence of fire appears to be spurring a broad shift from oak (*Quercus* spp.) and pine (*Pinus* spp.) dominated forests, to those dominated by maple (*Acer* spp.) and other mesophytic plant species (Lafon et al. 2017). More recently, changes in timber harvest strategies, agricultural practices, and the distribution of human populations have contributed to decreases in early successional forest throughout the eastern United States (Trani et al. 2001). Additionally, the concurrent introduction and proliferation of numerous exotic pests and pathogens, including the chestnut blight, Dutch elm disease, beech bark disease, gypsy moths, hemlock woolly adelgids, and emerald ash borers, among others, continues to drastically alter forest ecosystems in eastern North America (Lovett et al. 2006). These patterns of regeneration have led to the wide-scale maturation and "mesophication" of eastern forests, resulting in large unbroken swaths of mature, closed-canopy hardwood forest with relatively bare understory, and decreases in mast-producing, overstory species (Nowacki and Abrams 2008, Trani et al. 2001).

These landscape changes have considerable implications for wildlife (Litvaitis 2006), including bobcats (*Lynx rufus*), the only native felid species remaining in the Appalachian Mountains. Bobcats are ambush predators and obligate carnivores (Jaques and Jenks 2008, Labisky and Boulay 1998, McCord and Cordoza 1982). Thus, bobcats select for densely vegetated areas that provide concealment cover and abundant prey (Godbois et al. 2004, Kolowski and Woolf 2002, Litvaitis et al. 1986, Tucker et al. 2008). Bobcats have been found to select for areas with higher stem density and dense brush, and avoid sparse understories (Caine et al. 2003, Kolowski and Woolf 2002, Litvaitis et al. 1986, Tucker et al. 2008). Due to the aforementioned landscape patterns, the type of productive, densely-vegetated areas that bobcats select for are increasingly scarce in Appalachia. The low-relief valley bottoms generally consist of open fields used for cattle and hay production or development, and steeper, higher elevations generally consist of unproductive mesic forest, with little variation from this systematic pattern. These landscape patterns also have implications for bobcat prey. For example, suitable early successional habitat for common bobcat prey species like cottontail rabbits (*Sylvilagus floridanus*) and Appalachian cottontails (*S. obscurus*) is scarce throughout most of the forested areas of the Appalachian Mountain region. White-tailed deer (*Odocoileus virginianus*), a potentially important diet component for bobcats that is associated with younger forest conditions, have shown declines on public lands in western Virginia according to harvest metrics (VDGIF 2015). Within western Virginia, white-tailed deer densities were estimated to be lower in areas more predominately composed of National Forest lands (Montague et al. 2017). In the face of these broad scale patterns, land managers in the region have been implementing measures to restore historic forest structure and create productive areas of early successional forest, fields, and induced edge through timber harvest, mowing/disking, herbicidal treatments, and increasingly, through the use of prescribed fire.

On the George Washington and Jefferson National Forests (GWJNF) in western Virginia, the area treated with prescribed fire has increased steadily since 1998 (Lorber et al. 2018, Figure 1). The Heart of the Appalachians Fire Learning Network (FLN), one of four groups within the larger Central Appalachian FLN, is a driving force behind the increased utilization of prescribed fire in the region. The FLN engages federal, state, and private land managers in a collaborative effort to enhance their capacity to implement ecological fire management. In far western Virginia, almost all of the prescribed fire treatments are conducted on lands administered by the United States Forest Service (USFS) and properties owned by The Nature Conservancy (TNC). Burns are conducted during the spring, mostly in April and May, with smaller burns (less than 200 hectares) hand ignited and larger burns ignited with a combination of helicopter and hand ignition (Lorber et al. 2018). Currently, these fires cover a small spatial extent (generally 2-3% of the GWJNF), but they provide novel information on the response of local ecosystems to fire, which collaborators research and monitor to inform future management efforts.

Inverse to the increasing use of prescribed fire, the scale of timber harvest conducted by the USFS in western Virginia has declined in recent decades (Figure 2). This decline in timber harvest on National Forest in Virginia mirrors a nationwide trend, resulting from shifts in societal values and administrative policies within the USFS during the early 1990s (Oswalt et al. 2009). On National Forest within the Warm Springs Ranger District (~69,700 hectares), 1,556 hectares of forest was harvested from 1980 to 1989 by the USFS, 301 hectares harvested from 1990 to 1999, 66 hectares harvested from 2000 to 2009, and 397 hectares from 2010 to 2018 (Table 1). While quantity of timber harvest has decreased, the goal of timber harvest on National Forest has gone from being more strictly focused on timber production to an emphasis on the creation of wildlife habitat, among other ecologically focused goals. This emphasis has led to efforts such as The Lower Cowpasture Restoration and Management Project (LCRMP), which is a large landscape-scale effort currently underway in an 117,500 acre area across Bath, Allegheny, and Rockbridge counties in western Virginia. Upon completion, the LCRMP will include 3,422 acres of timber harvest, and prescribed fire treatments across an even larger area. This landscape scale effort differs from past timber harvest efforts that may have been more localized in their approach. The Virginia Department of Game and Inland Fisheries (VDGIF) has conducted timber operations more steadily on their lands in western Virginia. In recent years there has been a slight increase in timber harvest on Gathright Wildlife Management Area (Table 2), partially due to multi-agency initiatives such as Appalachian Mountains Joint Venture.

The USFS and VDGIF also maintain wildlife clearings on National Forest and Wildlife Management Areas (WMAs), which are created through timber harvest and land clearing, or management of previously occurring old fields. These clearings are typically planted with grasses or legumes, and maintained through subsequent mowing and/or burning. The clearings provide areas of increased herbaceous vegetation and insect abundance, which in turn provides forage for a suite of potential bobcat prey species, such as rodents, and wild turkey (*Meleagris gallopavo*),), and to a lesser extent, deer (Healy and Nenno 1983, Healy 1985, Stewart et al. 2000). Additionally, these openings create areas of forest edge where sunlight can penetrate into surrounding forest and create a dense vegetation structure ideal for ambush predators such as bobcats.

Human land use patterns on private land also act to mimic some historical landscape drivers, namely grazers, in the form of small-scale cattle and hay production. Historically, there were grasslands in Appalachia, and in western Virginia specifically, in which grazers shaped and maintained vegetative communities (Heus 2003, Mitchell 1972). Modern pastures do not reflect the historic flora and fauna of Appalachian grasslands because the grazers and the grasses consist of non-native taxa, however these areas do provide maintained openings that contain herbaceous forage for bobcat prey and allow sunlight to penetrate into the surrounding forest and create areas of induced edge. It is important to consider that in the predominately forested landscape of Appalachia, these private fields compose the vast majority of open habitat. Although land managers work to create areas of open canopy structure and wildlife clearings on public lands, logistical constraints and historic land use patterns cause these areas to be small in comparison to openings on private lands. While the forest edge surrounding fields may provide better bobcat habitat, the open areas within these fields is likely poor habitat due to the lack of cover, unless they are densely vegetated. In the Midwest, bobcats were found to avoid row crop agriculture and population abundance was negatively correlated with row crop agriculture (Nielson and Woolf 2002, Tucker et al. 2008), due to a lack of non-crop vegetative cover. The conversion of valley bottoms from rich riparian forests to agriculture and development has probably shifted bobcat space use from pre-settlement patterns, leading to increased use of the less productive ridges. A similar long-term space use trend has been suggested for the sympatric Allegheny woodrat (Mengak and Castelberry 2008), due to its dependence on acorn production in forested areas.

Proximal relationships between bobcat space use and timber harvest and prescribed fire have been discussed in previous research (i.e. implications of the habitat created by these practices). For example, Godbois et al. (2003) discussed the importance of prescribed fire in maintaining the type of upland pine stands that bobcats selected for in their study area. Likewise, Chamberlain et al. (2003) proposed that bobcat selection for mature pine stands in their area was due to thinning and burning that led to subsequent increases in herbaceous vegetation and prey resources, and found that early successional pine habitat also influenced resource selection. These discussions aside, research exploring the direct relationship between these habitat management practices and bobcat space use is scarce. Conner and Leopold (1996) found bobcats selected for young pine stands in central Mississippi, providing evidence for selection of recently harvested forest stands. Little et al. (2018) examined the effects of time since fire on bobcat space use in a longleaf pine (*Pinus palustris*) savanna, and found it did not influence space use in their system. However, almost the entirety of their study site was frequently burned (>3 year fire interval), preventing a comparison between infrequently/un-burned areas. The aforementioned analysis represents the only published research into the direct effects of fire on bobcat space use.

Scat analysis conducted by Morin et al. (2016) found common prey items for bobcats in western Virginia to consist of squirrels (*Sciurus* spp. and *Glaucomys* spp.), white-tailed deer, cottontail rabbits (*Sylvilagus floridanus*), voles (*Microtus* spp., *Myodes gapperi*) and mice (*Peromyscus* spp.). With the exception of squirrels, the taxa that comprise bobcat diet in western

Virginia are associated with early successional and edge habitats (Litvaitis 2001, Menzel et al. 1999). Additionally, direct relationships between fire and timber harvest and increases in abundance and/or activity of these species have been found (Cherry et al. 2018, Fisher and Wilkinson 2005, Harper et al. 2016, Hill 1981, Kaminski et al. 2007, Lochmiller et al. 1991, Vogl and Beck 1970). Oak mast is an important diet item for squirrels, and fire can be an important component in successful oak regeneration (Brose et al. 2013, Smith and Follmer 1972). It is noteworthy that voles occurred in bobcat scats more than twice as frequently as mice (*Peromyscous* spp.) in western Virginia (Morin et al. 2016). In a study examining small mammal communities across the gradient from forest opening to forest interior in the southern Appalachian Mountains, Menzel et al. (1999) caught over 3 times as many mice as voles, but found that voles were most abundant in forest edge, whereas mice were most abundant in forest interior. This higher occurrence of voles than mice in bobcat diet may reflect bobcat's use of forest edge over forest interior, resulting in increased availability of voles compared to mice. Previous findings regarding bobcat resource selection across the species distribution, combined with recent local findings of bobcat prey in western Virginia and the habitat associations of those prey, provide evidence that bobcats likely select for younger forest in the predominately mature expanses of forest in Appalachia.

As land managers plan management strategies, their actions should be informed by knowledge of local wildlife species and ecological processes, especially if the primary goal of those management strategies is to improve wildlife habitat and enhance ecosystem functionality. As one of the largest carnivores in Appalachian ecosystems, and the only remaining native felid species in the region, bobcats are a species deserving of relevance when planning habitat management actions. Currently, there is a paucity of information on the relationships between bobcat space use and the types of habitat management strategies most often utilized, and local information on these relationships is nonexistent in western Virginia and the broader Appalachian region. In this study, I utilized distance-based, resource selection analysis to investigate how bobcats use space on a landscape dominated by mature closed-canopy deciduous forest, particularly in the context of prescribed fire, timber harvest, and edge effects. I predicted that bobcats would select locations closer to forest edge, burned, and logged areas, than would be expected at random, thereby avoiding the forest interior.

Methods:

Study site

The study area encompasses the western half of Bath County, Virginia, adjacent to the border with West Virginia (Figure 3). Bath County is located in the Ridge and Valley physiographic province of the Appalachian Mountain range, characterized by parallel, north-south oriented ridges with narrow valleys. Elevation ranges from 343 meters to 1363 meters. Average monthly temperature can range from 0.8 C to 25.2 C, with a mean minimum temperature of 4.7 C in January and a mean maximum temperature of 31.7 C in July (National Oceanic and Atmospheric Administration, public data 2012). Average annual precipitation was 97.8 cm (National Oceanic and Atmospheric Administration, public data 2012). The forest structure primarily consists of mature deciduous forest, with common overstory species including oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and tulip poplar (*Liriodendron tulipifera*). Evergreen conifers are present in some forest stands, with common overstory species including pine (*Pinus* spp.), hemlock (*Tsuga* spp.), and red cedar (*Juniperus virginiana).* Common midstory and understory species include rhododendron (*Rhododendron* spp.), flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum*), eastern redbud (*Cercis canadensis),* striped maple (*Acer pensylvanicum*), witch hobble (*Viburnum lantanoides),* mountain laurel (*Kalmia latifolia),* blueberry (*Vaccinium* spp.), multiflora rose *(Rosa multiflora),* raspberry and wineberry *(Rubus* spp.), common greenbrier (*Smilax rotundifolia),* and a wide diversity of herbaceous groundcover including ferns. Other than bobcats, the carnivore guild includes coyotes (*Canis latrans*), black bears (*Ursus americanus*), and a diverse group of smaller carnivores. Bath County exemplifies the forest-dominated landscape of Appalachia, with public, forested land on the steep ridges, and narrow strips of private, low intensity development and agriculture in the flatter valley bottoms. Bath County is 89.4% forested land cover, most of which consists of contiguous swaths of forest managed by government agencies. Within Bath County, 50.7% of the land is federally managed National Forest, 5.1% is state managed Wildlife Management Area and State Park land, and 2.3% is land owned and managed by The Nature Conservancy. The use of prescribed fire is relatively widespread in the study area compared to surrounding areas, partially due to the LCRMP and the large proportion of USFS and TNC land.

Bobcat Capture and Monitoring

I captured bobcats using cage traps (Camtrip Cages, Bartsow, California, USA and Briarpatch Cages, Rigby, Idaho, USA) in accordance with Virginia Tech IACUC protocol #16-071. I checked traps twice daily (morning and afternoon). Once captured, I immobilized bobcats with a mixture of 10 mg/kg ketamine hydrochloride and 1mg/kg xylazine using hand injection with syringe. I monitored and recorded respiratory rates, heart rates, and temperatures every 5-10 minutes. I used tooth growth and condition, body morphology, and teat/scrotum characteristics to determine whether bobcats were juvenile or adult (Jackson et al. 1988). I fitted adult bobcats with Iridium GPS collars (Advanced Telemetry Systems, Isanti, Minnesota, USA). All bobcats captured were marked with color-coded numbered ear tags. Following handling, I reversed xylazine with 0.125 mg/kg yohimbine, administered either rectally or intravenously, and allowed bobcats to recover in the cage trap for 30 minutes to 1 hour before release. GPS collars were cycled between 2, 4, and 12 hour GPS fix intervals, with the more frequent fixes taken during early summer (May – July).

GIS data acquisition

I characterized relevant habitat variables using geographic information system (GIS) data from a variety of sources. Land cover data were acquired from the Virginia Geographic Information Network (VGIN), which produces 1m resolution land cover data via classification of aerial imagery. VGIN classifies land cover into 12 categories (Table 3), which I reclassified to characterize fields and early successional habitat (see below). I resampled the 1m resolution VGIN land cover raster to a 10m resolution to expedite computing speeds, using the “majority” resampling method.

GIS data on prescribed burn and wildfires were acquired from the United States Forest Service and The Nature Conservancy. Fire GIS data included results from an analysis on the effects of prescribed fire on forest canopy structure conducted by USFS and TNC, in which leaf-on, aerial imagery was used to digitize canopy openings created by prescribed fire treatments (Lorber et al. 2018).

Lastly, timber harvest and wildlife clearing data were collected from USFS and VDGIF. The USFS timber harvest dataset included polygons for all cuts, with associated stand/harvest information, dating back to 2003. A separate USFS dataset contained polygons for all wildlife clearings (i.e. clearings the USFS maintains through fire/mowing for the benefit of wildlife). The

VDGIF timber harvest and wildlife clearing data were extracted from a dataset created as a result of a forest inventory conducted for Gathright Wildlife Management Area in summer 2016. A small number of polygons denoting stands harvested post-2016 were acquired from the Virginia Department of Forestry and added to these data.

Data aggregation

To characterize edge effects around forest openings, I aggregated data from all sources into two types of openings, fields and early successional habitat. The "fields" class of opening consisted of combined Turf, Pasture, and Crops land cover classes, and all wildlife clearings. The "early" class of opening consisted of Shrub/Scrub and Harvested/Disturbed land cover classes, all timber harvest within 15 years, and canopy openings resulting from fire. I only included edges that interfaced with the Forest land cover class, to exclude field edges that may border other land cover types (e.g. development). I delineated between edge surrounding open fields and regenerating, early successional habitat due to structural differences. Forest edges surrounding open fields are a more permanent fixture on the landscape, present for decades or even centuries, providing opportunities for floristic succession within the edge. These edges around open fields are also typically more of a hard edge, exhibiting abrupt transitions in vegetative structure. Conversely, edges surrounding regenerating forest have a more dynamic and ephemeral nature. The edges surrounding regenerating forest will exhibit characteristics of a hard edge, but only briefly. As plant communities directly within the opening regenerate and succeed, they will create an increasingly soft edge, which will eventually merge with the surrounding forest. The "early" class of forest edge was not included as a covariate in models containing fire or timber harvest covariates, since a large portion of the "early" class is composed of those same burned and harvested forest stands.

I characterized forest interior as forest that is 300m or further from contrasting land cover types, following the delineation of forest core relevant to bobcats used by Abouelezz et al. (2018), since edge effects on primary forest processes can extend up to ~300m (Harper et al. 2005). I created the forest interior layer using the “forest” land cover category. I used the Erase tool in ArcGis 10.6 (ESRI, Redlands, CA, USA) to erase all harvested forest stands, fire-created canopy gaps, and wildlife clearings. I then created a 300m negative buffer in the remaining forest layer using the Buffer tool in ArcGis.

I characterized fire-created clearings using results from the analysis on effects of prescribed fire on forest canopy structure conducted by USFS and TNC (Lorber et al. 2018). The analysis delineated between 2 types of canopy openings created by prescribed fire: early and open. Early canopy openings were defined as those with less than 30% canopy cover. Open canopy openings were defined as those with between 30% and 50% canopy cover. For these analyses, open and early canopy openings were combined into one class with less than 50% canopy cover, because the two classes are largely interspersed and highly spatially correlated.

I characterized timber harvest by combining all cuts occurring after 2002 from VDGIF and USFS into one dataset. Initially, I hoped to delineate timber harvest by harvest prescription (i.e. shelterwood vs. clearcut) and time since harvest. However, due to the small sample size of bobcat home ranges that overlap differing prescriptions and/or ages of harvested stands, I had to combine all types and ages of cuts. Thus, all types of timber harvest within the past 15 years (since 2002) were combined into one timber harvest layer.

Lastly, I created distance raster layers by calculating Euclidian distance to each of these variables using the ‘Euclidean Distance’ tool in ArcGis 10.6 (ESRI, Redlands, CA, USA). The 5 resulting covariates are distance to forest edge surrounding fields, distance to forest edge surrounding early successional habitat, distance to forest interior, distance to fire-created canopy openings, and distance to timber harvest. Distance to forest interior was not strongly negatively correlated with any of the other covariates (r < 35%), since forest abuts land cover categories other than fields and early successional habitat (e.g. development, water, barren). We used distance-based covariates because they remove the need to arbitrarily select reference categories and the effects of the focal landscape processes can extend beyond their boundaries (see below).

Parsing of individuals

Due to the spatial organization of bobcat home ranges in relation to burned and harvested forest stands, certain individuals were removed from further analyses examining effects of fire and timber harvest. Since I used distance-based analysis, and not a categorical approach, I removed from analyses those that exceeded a maximum distance of 1 km from these areas, instead of simply removing individuals with home ranges that did not overlap areas of prescribed fire or timber harvest.

Even if a burned or harvested forest stand is not within an animal's home range, the effects of these disturbances could reach well beyond the stand's borders, and influence processes within nearby bobcat home ranges. Cherry et al. (2018) found that white-tailed deer are attracted to recently burned areas, but maintain unburned portions of their home ranges, increasing movement rates to access the burned areas. Similarly, female white-tailed deer were found to select fawn rearing areas near more productive agricultural areas, but avoid them within the actual fawn rearing area (Shuman et al. 2018). Therefore, prey species utilizing the openings may be more abundant or active throughout the broader area surrounding openings, not just within the opening's boundaries. For this reason, I based the maximum distance as a reasonable distance that a white-tailed deer, the most mobile of potentially important bobcat prey species in the study area, might move to access these areas.

The estimated home range size of white-tailed deer in a nearby and ecologically similar area in West Virginia, when averaged across sex and seasons, was approximately 1 square kilometer (Campbell et al. 2004). Based on these nearby estimates of white-tailed deer ranging behavior, I infer that bobcats could benefit from increased deer densities and abundance resulting from prescribed fire and timber harvest within an area as large as 1 square kilometer. Therefore, I chose 1 km as the maximum linear distance from burned or harvested forest stands that a bobcat could use and be included in analysis focusing on said variable.

Use and availability

To investigate bobcat resource selection in the context of canopy openings, I examined 3^{rd} order resource selection, or resource selection within the home range (Johnson 1980). I defined resource availability within a 95% minimum convex polygon (MCP) around each bobcat's locations. Within each individual's MCP, 10 simulated locations for each real location were randomly placed. For each covariate, I then calculated the mean value of raster cells within a 100m buffer surrounding each point, to account for GPS collar error and implicit uncertainty in animal movement. No covariates were highly correlated (all $r < 40\%$).

Resource selection model development

I developed resource selection functions (RSFs) to examine 3^{rd} order bobcat resource selection, with logistic regression using a generalized linear mixed model (GLMM) in the Program R package "lme4", in a use-availability framework (Bates et al. 2015, Manly et al. 2002). The binary response variable was whether a point was used or available (used = 1, available = 0). Predictor variables were the distances of each point to forest structure related habitat variables: forest edge surrounding fields, forest edge surrounding early successional habitat, fire-created canopy gaps, forest stands harvested within 15 years, and forest interior. I created 3 separate models that only included bobcats within 1km of covariates. A model including all covariates was not feasible since a very small portion of the bobcats were within 1km of both fire and timber harvest. A model with distance to forest edge surrounding fields, distance to forest edge surrounding all early successional habitat, and distance to forest interior as covariates included all individuals. Two separate models with distance to forest edge surrounding fields, and distance to fire-created canopy openings and distance to timber harvest respectively, as covariates included the individuals within 1km of those respective variables. I scaled all predictor values by mean-centering the distance values at 0, then dividing them by their standard deviation, to reduce model convergence issues. I included random intercepts for individual bobcats, to account for variation in sampling duration among individuals (Gillies et al. 2006). I evaluated selection or avoidance based on whether or not a coefficient significantly differs from zero ($\alpha = 0.05$). I inferred selection if used points were closer to habitat variables than random locations, and avoidance if used points were further from habitat variables than random locations. Each model contained 3 covariates, and I compared coefficient estimates from largest to smallest to evaluate relative importance of the various types of canopy openings.

Results:

I included 10 bobcats (7 male, 3 female) in these analysis, which were captured from January to April 2018. Other bobcats captured during 2017 and collared with Telonics GPS collars were not included in this analysis due to poor GPS fix success (<75%). Number of locations per bobcat ranged from 470 to 2371, with a mean of 1341 (Table 4). Length of collar deployments ranged from 8 weeks to 48 weeks, with a mean deployment length of 31 weeks (Table 4). The mean GPS collar fix success was 85%, however this mean is lowered by the fix success of 2 females that experienced a drastic decrease in fix success during the period surrounding parturition and denning. Weekly fix success for these females was approximately 90% prior to the denning period, then decreased in April and May, when bobcats typically birth young. Since missed fixes likely took place within the confines of a few localized den sites, instead of a canopy-driven fix bias across the landscape, I still included these 2 females in analysis. The mean fix success for the other 8 cats included in this analysis is 90%.

RSF model results provide evidence for selection of locations within home ranges that are closer to forest edge surrounding fields and early successional habitat, fire-created canopy openings, and harvested forest stands, than would be expected at random (Table 5). All model results provide evidence of bobcats avoiding forest interior, evidenced by selection of locations further from forest interior than expected at random (Table 5).

The model including all individuals (n=10), and only including distance to forest edge surrounding field and early successional edge and distance to forest interior as covariates, showed stronger selection for distance to forest edge surrounding early successional habitat (β = -0.276, SE = 0.013) than for distance to forest edge surrounding fields (β = -0.170, SE = 0.011). The model only including individuals within 1km of fire (n=8), which included distance to fire-created openings, distance to forest edge surrounding fields, and distance to forest interior as covariates, showed stronger selection for fire-created canopy openings (β = -0.309, SE = 0.015) than forest edge surrounding fields (β = -0.168, SE = 0.015). Lastly, the model only including individuals within 1km of timber harvest (n=8), which included distance to timber harvest, distance to forest edge surrounding fields, and distance to forest interior as covariates, showed stronger selection for forest edge surrounding fields (β = -0.243, SE = 0.013) than timber harvest (β = -0.045, SE = 0.013). All 3 of the models estimated a positive coefficient for distance to forest interior, indicating avoidance.

Discussion:

Variation in the availability of prey likely drives much of the resource selection patterns observed in bobcats (Conner and Leopold 1996, Godbois et al. 2004, Litvaitis et al. 1986, Kolowski and Wollf 2002). As obligate carnivores, bobcats must acquire sufficient prey to meet energetic requirements necessary to survive and reproduce, yet as ambush predators they also require sufficient concealment cover to utilize available prey, therefore these factors likely act synergistically. Prescribed fire, timber harvest, and edge effects are all mechanisms that can increase the availability of bobcat prey and cover on the landscape (Harper et. al. 2016, Litvaitis 2006, Masters et al. 1993, Williamson and Hirth 1985). The selection for locations closer to prescribed fire, timber harvest, and forest edge that I observed on this study most likely reflect utilization of prey and cover resulting from these habitat management practices.

The relative importance of prescribed fire as a factor influencing bobcat space use is apparent from the ranking of RSF covariates. Bobcats exhibited the strongest selection for locations near canopy openings resulting from prescribed fire, whereas the weakest selection was for timber harvest. While all canopy openings and forest edges allow increased sunlight to reach the forest floor and spur understory growth, whether created from fire, timber harvest, or permanent clearings, prescribed fire can influence the ecosystem in unique and complex ways. Years after a fire event, soil nutrients can continually increase due to the gradual sequestration of charcoal and growth of post-fire, nitrogen fixing vegetation (Certini 2005, Johnson and Curtis

2000). Fire can also benefit the growth of fire-adapted tree species, such as oaks which provide forage in the form of mast for common bobcat prey species like deer and squirrels, while inhibiting the success of mesophytic tree species such as maple (Brose et al. 2012, Nowacki and Abrams 2008).

The fact that selection for timber harvest was ranked lower than field edge, whereas canopy openings resulting from prescribed fire was ranked as stronger than field edge, may relate to the size, shape, and composition of the canopy openings resulting from these respective practices (Figure 3). Compared to the irregularly-shaped and clumped canopy openings created from prescribed fire, timber harvest operations in the study area typically have a more even-shaped edge and are more disjunct in space. This may be largely attributed to the logistical constraints of planning and executing timber harvests, such as the associated need to access and operate heavy equipment. Conversely, large fire treatments can be executed via helicopter ignition and spread more evenly across a topographical gradient. The resulting "patchy" distribution of canopy openings can then influence processes along an entire mountainside. Based on this, I would expect the burns to have more broad-scale impacts on landscape patterns, whereas the impacts of timber harvest may be more localized. This could explain the pronounced influence of prescribed fire on the space use of a wide-ranging species like bobcats, whereas the impacts of timber harvest, at least in the manner in which they have been executed within the mountainous study site, may be more relevant to less mobile species. It is important to note that bobcats are one of the most highly mobile terrestrial species within this ecosystem.

Projects like the LCRMP indicate an effort by the USFS to conduct timber harvest with landscape scale ecological processes in mind, which may allow logging-caused disturbance to play a more influential role on bobcat space use in the near future. As managers implement ecologically focused harvest prescriptions in combination with prescribed fire, it is likely these strategies will act synergistically to mimic historic patterns of forest disturbance. It is also possible that the lack of strong evidence regarding timber harvest is due to limitations of the data. A larger sample size of bobcats overlapping the diversity of harvest prescriptions would allow a finer scale examination of differences in harvest types and ages.

Although we found stronger selection for forest edge surrounding early successional habitat, bobcats are probably also selecting for locations within those openings once vegetation has regenerated enough to provide sufficient cover. This is less likely for openings consisting of fields, as bobcats are not well adapted to foraging in open areas. Furthermore the risk of traveling through open areas in the study area, particularly those on private land, can be high for bobcats. Attitudes towards predators appear generally negative in the study area due to perceived threats to game species and livestock, and 20% of the collared bobcats were shot or trapped. Despite these considerations, bobcats selected for locations near forest edge surrounding open fields, many of which are privately owned. This selection highlights the importance of edge habitat for bobcats in this system. Forest edge surrounding fields likely composes the majority of suitable bobcat habitat within the study area, which is an important consideration due to the fact that timber harvest and prescribed fire are utilized relatively frequently in the study area compared to the surrounding region. In many areas of rural Appalachia, forest edge surrounding open fields may compose the vast majority of suitable bobcat habitat, simultaneously providing increased prey and cover along with increased exposure to human conflict and risk.

Bobcat selection for locations further from forest interior than would be expected at random indicates avoidance of these areas. Based on the habitat associations of their prey, it is probable that prey densities are lower in the forest interior, as distance from cover and forage increases. Likewise, under the contiguous canopy of the forest interior, where the least sunlight can reach the forest floor, vegetative concealment cover is also at its lowest. This differs from the pre-European settlement forests in which bobcats evolved, where fires were frequent and wide-spread (Lafon 2017). Most pre-settlement fires consisted of low to mixed-severity burns that created open, “park-like” forests, with a lower density of trees on the landscape (Nowacki and Abrams 2008). Therefore, tree mortality, whether caused by fire, wind, or other factors, within the forest interior would open up much larger gaps in the canopy. Native grazers in the form of elk and bison may have acted to maintain many of these openings. Historically, the interior of forests in Appalachia were likely much better suited to the foraging ecology of bobcats. The even-aged regeneration of modern Appalachian forests, occurring with a lack of fire or grazers, has resulted in a densely-stocked and heavily-shaded forest interior that differs from the conditions in which bobcats evolved. The importance of forested habitat to bobcats in eastern North America has been shown repeatedly in past research (Abouelezz et al. 2018, Donovan et al. 2011, Lovallo and Anderson 1996, Tucker et al. 2008). These findings highlight that forest structure and composition should be considered as well.

Conducting this research in a study area with comparatively frequent and widespread use of prescribed fire has allowed novel insight into the effects of fire on bobcat space use, particularly in the forests of Appalachia. A limitation of this study was the relatively small sample size of bobcats, which was further decreased due to the removal of GPS collars with poor fix success. Reliable GPS relocation data were integral to this study due to the explicit consideration of canopy structure, and the potential for dense canopy to influence GPS fix success. A larger sample size of bobcats, covering a wide range of timber harvest prescriptions and stand ages, would allow a more in-depth analysis of the effects of timber harvest on bobcat space use. For example, very recently harvested stands that have not yet regenerated will be structurally different than 3 to 5 year old stands. Since I combined a range of harvest strategies and age, the findings regarding timber harvest are likely somewhat confounded by this variability. Thus, future studies investigating the effects of timber harvest on bobcat space use should specifically examine a range of harvest prescriptions and stand ages.

Management Implications:

Land managers in Appalachia primarily utilize timber harvest, and to a lesser extent prescribed fire, as the primary mechanisms to create productive, early successional forests to benefit wildlife species. As the use of prescribed fire increases, we recommend that managers consider these findings when planning future efforts and communicating them to the public. Creation of open canopy structure is one aspect of prescribed fire that is explicitly and quantitatively outlined in the GWJNF forest management plans, which state goal percentages of burn areas to convert to open canopy and early successional habitat. In these management plans, goals for creating open canopy structure suggest management for a particular suite of wildlife species (Lorber et al. 2018). Findings that bobcats select for areas closer to canopy openings resulting from prescribed fire could be used to inform future canopy structure goals when planning prescribed fire. If managers are interested in using fire specifically to the benefit of certain common bobcat prey species, they might aim for a higher percentage of canopy openings or wider distribution of canopy openings, to avoid attracting bobcats and their prey to the same localized areas. Due to the solitary and territorial behavior of bobcats, there is an upper limit on how many bobcats can realistically exhibit 3rd order selection for any particular area with open canopy, which may decrease risk for prey species via “predator-swamping”. Likewise, these considerations apply to the spatial organization of timber harvest and wildlife clearings.

Public perception of these habitat management strategies can sometimes be negative. It is likely that much of the general public does not understand the altered state of forest ecosystems in eastern North America. Much of the public communication regarding these management strategies is currently focused on certain migratory bird species (e.g. golden-winged warbler) or popular game species (e.g. white-tailed deer), which caters to the specific groups of birders and hunters. Bobcats are a charismatic species, generally appreciated by the general public, with the exception of some hunters concerned about the impacts of bobcats on commonly hunted game species (i.e. deer and turkey). I recommend that managers explicitly consider bobcat ecology, perhaps even using them as a flagship species, when communicating to the public regarding efforts to improve habitat through prescribed fire and timber harvest.

The scientific literature surrounding bobcats, although extensive in its examinations of space use, largely lacks research into relationships with specific habitat management strategies such as prescribed fire and timber harvest. Further research is needed to understand these relationships, their causal mechanisms, and how they might vary regionally across the vast distribution of bobcats. It is clear from long term trends of bobcat distribution and abundance that habitat is an essential consideration when managing and conserving populations. For example, the only areas where bobcats remain extirpated or scarce are in monoculture dominated agricultural landscapes such as the Midwest or Delmarva Peninsula (Roberts and Crimmins 2010). When considering issues regarding bobcat habitat, it is important for managers from state, federal, and nongovernmental land management organizations to communicate with each other, and convey information to private landowners and general public.

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Literature cited:

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67.

Benson, J. F., K. J. Mills, and B. R. Patterson. 2015. Resource selection by wolves at dens and rendezvous sites in Algonquin Park, Canada. Biological Conservation 182:223–232.

Brooks, M. 1965. The Appalachians. Houghton Mifflin Harcourt.

Brose, P. H., D. C. Dey, R. J. Phillips, and T. A. Waldrop. 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? Forest Science 59:322–334.

Cain, A., V., Tuovila, D., Hewitt, and M., Tewes. 2003. Effects of a highway and mitigation projects on bobcats in Southern Texas. Biological Conservation 114:189–197.

Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2004. Topographic home ranges of white-tailed deer in the Central Appalachians. Southeastern Naturalist 3:645–652.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143:1–10.

Chamberlain, M. J., B. D. Leopold, and L. M. Conner. 2003. Space use, movements and habitat selection of adult bobcats (Lynx rufus) in central Mississippi. American Midland Naturalist 149:395–405.

Cherry, M. J., R. B. Chandler, E. P. Garrison, D. A. Crawford, B. D. Kelly, D. B. Shindle, K. G. Godsea, K. V. Miller, and L. M. Conner. 2018. Wildfire affects space use and movement of white-tailed deer in a tropical pyric landscape. Forest Ecology and Management 409:161–169.

Clarkson, R.B. 1964. Tumult on the mountains: lumbering in West Virginia 1770-1920. Parsons, WV: McClain Printing Company. 400 p.

Conner, L. M., and B. D Leopold. 1996. Bobcat habitat use at multiple spatial scales. In Proc Annu Conf Southeast Assoc Fish Wildl Agencies. 50: 622-631.

Conner, L. M., and B. D. Leopold. 1998. A multivariate habitat model for female bobcats: a GIS approach. In Proceedings of the annual conference of the Southeastern Association of Fish and Wildlife Agencies. 52: 232-243.

Conner, L. M., and B. W. Plowman. 2001. Using Euclidean distances to assess nonrandom habitat use. Pages 275–290 *in*. Radio Tracking and Animal Populations. Elsevier.

Conner, L. M., M. D. Smith, and L. W. Burger. 2003. A comparison of distance-based and classification-based analyses of habitat use. Ecology 84:526–531.

Davis, D. E. 2003. Where there are mountains: an environmental history of the southern Appalachians. University of Georgia Press.

Eby, S. L., T. M. Anderson, E. P. Mayemba, and M. E. Ritchie. 2014. The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. J. Fryxell, editor. Journal of Animal Ecology 83:1196–1205.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35:51–81.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals: Random effects in resource selection. Journal of Animal Ecology 75:887–898.

Godbois, I. A., L. M. Conner, and R. J. Warren. 2003. Habitat use of bobcats at two spatial scales in southwestern Georgia. Proc. Southeast Assoc. Fish Wild Agencies. 57:228-234.

Godbois, I. A., L. M. Conner, and R. J. Warren. 2004. Space-use patterns of bobcats relative to supplemental feeding of northern Bobwhites. Journal of Wildlife Management 68:514–518.

Harper, C. A., W. M. Ford, M. A. Lashley, C. E. Moorman, and R. B. Standiford. 2016. Fire effects on wildlife in the central hardwoods and Appalachian Regions, USA. Fire Ecology 12:127–159.

Healy, W. M., and E. S. Nenno. 1983. Minimum maintenance versus intensive management of clearings for wild turkeys. Wildlife Society Bulletin 11:113-120.

Healy, W. M. 1985. Turkey poult feeding activity, invertebrate abundance, and vegetation structure. Journal of Wildlife Management 49:466.

Heus, P. 2003. An historical prairie remnant in Virginia. Native Plants Journal, *4*(2): 104-106.

Hill, E. P. 1981. Prescribed fire and rabbits in southern forests. Pages 103–108 Prescribed fire and wildfire in southern forests: Proc. Symp. Belle W. Baruch For. Sci.Inst., Clemson University, Clemson, S.C

Jackson, D. L., Gluesing, E. A., and H.A. Jacobson. 1988. Dental eruption in bobcats. Journal of Wildlife Management. 52(3): 515-517.

Jacques, C. N., and J. A. Jenks. 2008. Visual observation of bobcat predation on an adult female pronghorn in northwestern South Dakota. American Midland Naturalist 160:259–261.

Johnson, D. W., and P. S. Curtis. 2001. Effects of forest management on soil C and N storage: meta-analysis. Forest Ecology and Management 140:227–238.

Kaminski, J. A., M. L. Davis, M.J. Kelly, and P. D. Keyser. 2007. Disturbance effects on small mammal species in a managed Appalachian Forest. American Midland Naturalist 157:385–397

Kolowski, J. M., and A. Woolf. 2002. Microhabitat use by bobcats in southern Illinois. Journal of Wildlife Management 66(3):822.

Labisky, R. F., and M. C. Boulay. 1998. Behaviors of bobcats preying on white-tailed deer in the Everglades. American Midland Naturalist 139:275–281.

Lafon, C. W., A. T. Naito, H. D. Grissino-Mayer, S. P. Horn, and T. A. Waldrop. 2017. Fire history of the Appalachian Region: Gen. Tech. Rep. SRS-219. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 97 p.

Little, A. R., Conner, M.L., Chamberlain, M. J., Nibbelink, N. P. and R. J. Warren. 2018. Adult bobcat (Lynx rufus) habitat selection in a longleaf pine savanna. Ecological Processes 7:20.

Litvaitis, J. A. 2006. Importance of early successional habitats to mammals in eastern forests. Wildlife Society Bulletin (1973-2006) 29:466–473.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110.

Lochmiller, R. L., J. F. Boggs, S. T. McMurry, D. M. Leslie, and D. M. Engle. 1991. Response of cottontail rabbit populations to herbicide and fire applications on Cross Timbers Rangeland. Journal of Range Management 44:150.

Lorber, J., M. A. Thomas-Van Gundy, and S. Croy. 2018. Characterizing effects of prescribed fire on forest canopy cover in the George Washington and Jefferson National Forests. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in Eastern North America. BioScience 56:395.

Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., and W.P. Erickson. 2007. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media.

Masters, R. E., Lochmiller, R. L., and D.M. Engle. 1993. Effects of timber harvest and prescribed fire on white-tailed deer forage production. Wildlife Society Bulletin. 21(4): 401-411.

McCord, C. M. 1974. Selection of winter habitat by bobcats (Lynx rufus) on the Quabbin Reservation, Massachusetts. Journal of Mammalogy, *55*(2): 428-437.

McCord, C. M. and J. E. Cordoza. 1982. Bobcat and lynx, p. 728-766. In: J. A. Chapman and G. A. Feldhamer (eds.). Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore.

Mengak, M. T., and S. B. Castleberry. 2008. Influence of acorn mast on Allegheny woodrat population trends in Virginia. Northeastern Naturalist 15:475–484.

Menzel, M. A., W. M. Ford, J. Laerm, and D. Krishon. 1999. Forest to wildlife opening: habitat gradient analysis among small mammals in the southern Appalachians. Forest Ecology and Management 114:227–232.

Mitchell, R. D. 1972. The Shenandoah Valley Frontier. Annals of the Association of American Geographers 62:461–486.

Montague, D. M., R. D. Montague, M. L. Fies, and M. J. Kelly. 2017. Using distance-sampling to estimate density of white-tailed deer in forested, mountainous landscapes in Virginia. Northeastern Naturalist 24:505–519.

Morin, D. J., S. D. Higdon, J. L. Holub, D. M. Montague, M. L. Fies, L. P. Waits, and M. J. Kelly. 2016. Bias in carnivore diet analysis resulting from misclassification of predator scats based on field identification: Bias and Uncertainty in Carnivore Scat Identification. Wildlife Society Bulletin 40(4):669–677.

Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. Ecology 94:1456–1463.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and “mesophication” of forests in the eastern United States. BioScience 58:123–138.

Oswalt, Sonja N., T. G. Johnson, M. Howell, and J. W. Bentley. 2009. Fluctuations in National Forest timber harvest and removals: the southern regional perspective. Resource Bulletin, U.S. Department of Agriculture, Forest Service, Southern Research Station.

Roberts, N. M., and S. M. Crimmins. 2010. Bobcat population status and management in North America: evidence of large-scale population increase. Journal of Fish and Wildlife Management 1:169–174.

Shuman, R. M., Cherry, M. J., Dutoit, E. A., Simoneaux, T. N., Miller, K. V., and M. J. Chamberlain. 2018. Resource selection by parturient and post-parturient white-tailed deer and their fawns. Journal of the Southeastern Association of Fish and Wildlife Agencies 5:78–84.

Smith, C. C., and D. Follmer. 1972. Food preferences of squirrels. Ecology 53:82–91.

Stewart, K. M., T. E. Fulbright, and D. L. Drawe. 2000. White-tailed deer use of clearings relative to forage availability. Journal of Wildlife Management 64:733.

Trani, M. K., Brooks, R. T., Schmidt, T. L., Rudis, V. A., and C.M. Gabbard. 2001. Patterns and trends of early successional forests in the eastern United States. Wildlife Society Bulletin. 29 (2): 413-424

Tucker, S. A., W. R. Clark, and T. E. Gosselink. 2008. Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. Journal of Wildlife Management 72(5):1114–1124.

USDA Forest Service. 2004. Revised land and resource management plan Jefferson National Forest. Management Bull. R8-MB 115A. Roanoke, VA: U.S. Department of Agriculture, Forest Service, Southern Region, Jefferson National Forest. 396 p.

USDA Forest Service. 2014. Revised land and resource management plan George Washington National Forest. Management Bull. R8-MB 143A. Roanoke, VA: U.S. Department of Agriculture, Forest Service, Region 8, George Washington National Forest. 374 p.

VDGIF. 2015. Virginia deer management plan, 2015-2024. Virginia Department of Game and Inland Fisheries, Richmond, Virginia, USA.

Vogl, R. J., and A. M. Beck. 1970. Response of white-tailed deer to a Wisconsin wildfire. American Midland Naturalist 84:270.

Williamson, S. J., and D. H. Hirth. 1985. An evaluation of edge Use by White-Tailed Deer. Wildlife Society Bulletin. 1393: 252-257.

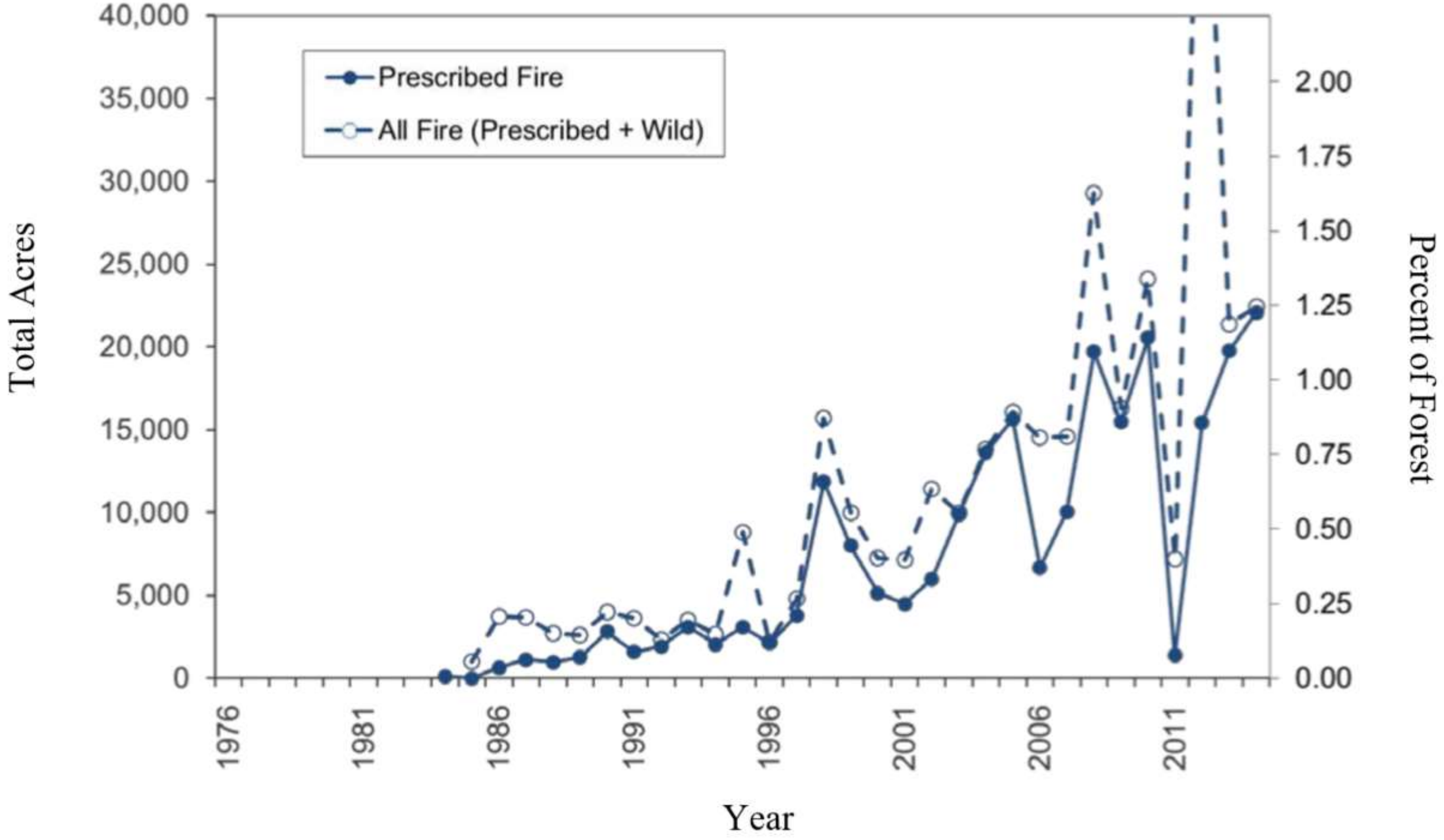

Figure 1. George Washington and Jefferson National Forests, Virginia, prescribed fire and wild fire management history, 1986-2014. During 2012, all fires burned 58,954 acres (3.28%). Data provided by USFS (VDGIF 2015).

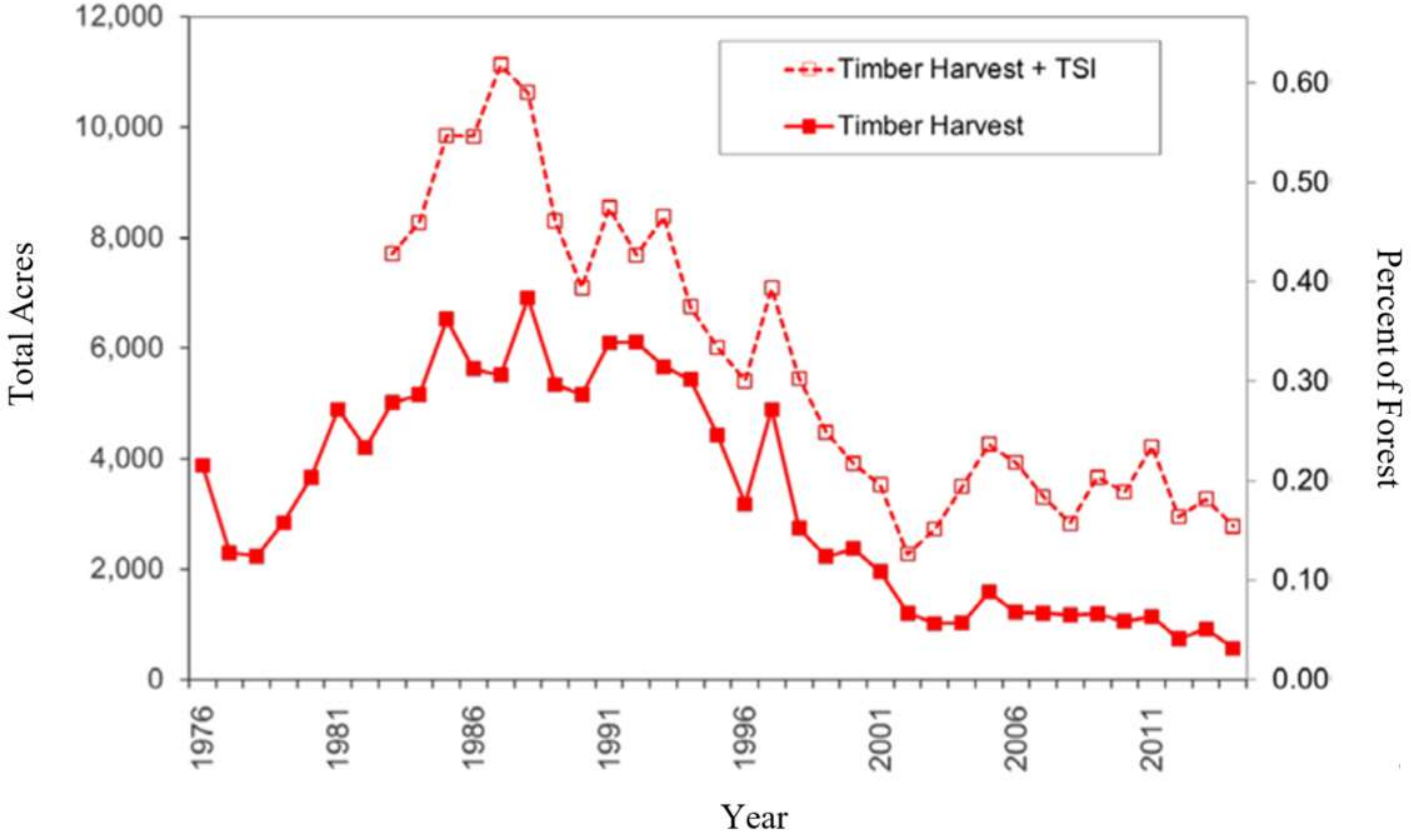

Figure 2. George Washington and Jefferson National Forests, Virginia, timber harvest and timber stand improvement (TSI) history, 1976-2014 (data provided by the USFS, VDGIF 2015).

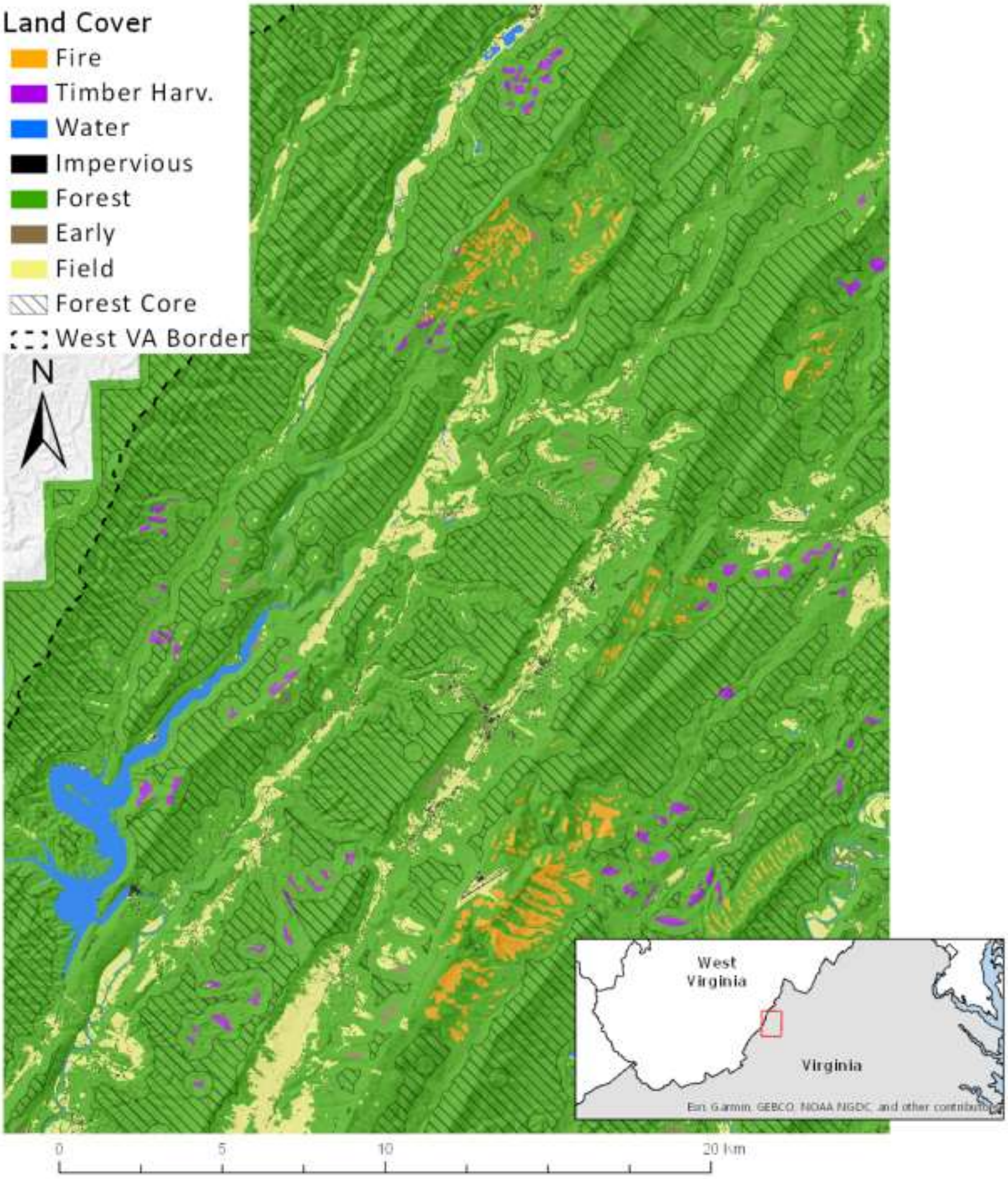

Figure 3. Map of study area in Bath County, Virginia showing areas of timber harvest, fire-created canopy openings, other early succesional areas, fields, and forest interior (>300m from edge).

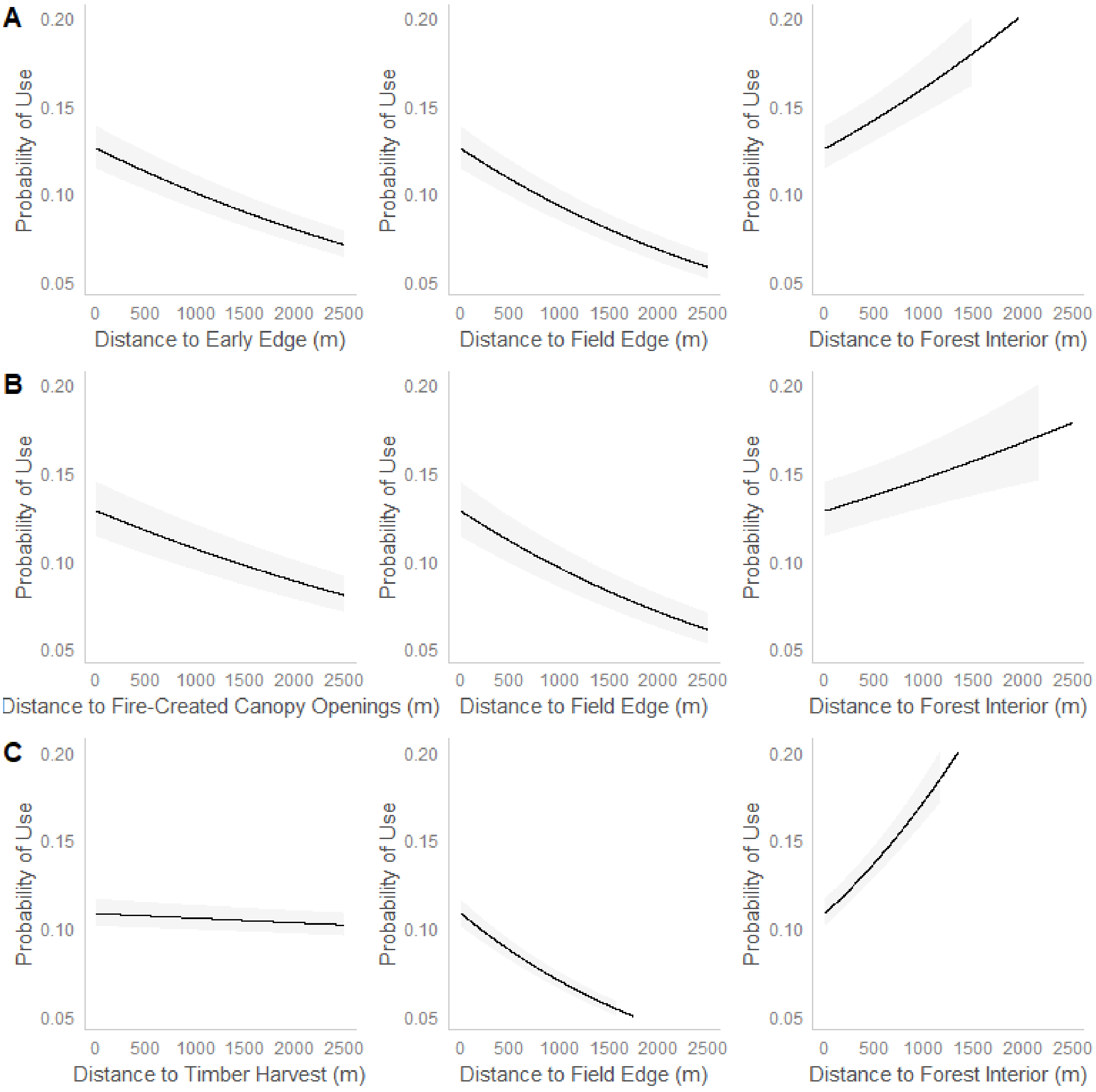

Figure 4. Effects of distance to forest edge surrounding fields, distance to forest edge surrounding early succesional habitat, distance to canopy openings resulting from fire, distance to timber harvest, and distance to forest interior on relative probability of bobcat use in Bath County, Virginia, with 95% confidence intervals. Results are from 3 separate 3rd order resource selection functions including all individuals (n=10, Model A), only individuals within 1km of fire-created canopy openings (n=8, Model B), and only individuals within 1km of timber harvest (n=8, Model C).

Table 1. Total hectares of timber harvested areas on National Forest lands in the Warm Springs Ranger District, Bath County, Virginia from 1980 to 2008 (unpublished data, 1978 – 2008 records acquired from USFS, subsequent years compiled using USFS timber harvest GIS data).

Year	Hectares	Total Hectares
1978	206	413
1979	207	
1980	13	1556
1981	94	
1982	35	
1983	176	
1984	302	
1985	56	
1986	176	
1987	363	
1988	218	
1989	124	
1990	60	745
1991	126	
1992	155	
1993	14	
1994	88	
1995	66	
1996	122	
1997	63	
1998	51	
1999	0	
2000	51	163
2001	22	
2002	0	
2003	0	
2004	17	
2005	0	
2006	0	
2007	0	
2008	74	
2009	0	
2010	0	397
2011	0	
2012	29	
2013	7	
2014	57	
2015	93	
2016	30	
2017	109	
2018	72	

Table 2. Total hectares of timber harvested areas on Gathright Wildlife Management Area in western Bath County, Virginia. Summary compiled from Timber Inventory of Gathright Wildlife Management Area conducted in March 2016, and data from subsequent years acquired from VDGIF).

Year	**Hectares**	**Total Hectares**
1985	2	11
1990	9	59
1994	5	
1995	29	
1997	10	
1998	6	
2003	17	29
2004	4	
2005	5	
2009	2	
2010	1	88
2011	27	
2016	36	
2018	24	

Table 3. All land cover categories composing the Virginia Geographic Information Network (VGIN) Virginia Land Cover Product

11 - Open Water	Drainage network and basins such as rivers, streams, lakes, canals, waterways, reservoirs, ponds, bays, estuaries, and ocean as defined by the NHD.
21 - Extracted Impervious	Areas characterized by a high percentage of constructed materials such as asphalt and concrete, buildings and parking lots, and infrastructure as defined by the EPA, that extends beyond local planimetric data provided.
22 - External Impervious	Locally maintained planimetric data such as buildings, parking lots, edge of pavement, roads, and any other paved surface data.
31 - Barren	Areas with little or no vegetation characterized by bedrock, desert pavement, beach and other sand/rock/clay accumulations, as well as areas of extractive mining activities with significant surface expression as defined by the EPA.
41 - Forest	Areas characterized by tree cover of natural or semi-natural woody vegetation as defined by the EPA, encompassing an acre in size; this class includes deciduous, evergreen, and mixed foliage types
42 - Tree	Characterized by tree cover of natural or semi-natural woody vegetation as defined by the EPA, that does not encompass at least an acre in size; this class includes deciduous, evergreen, and mixed foliage types.
51 - Scrub/Shrub	Areas characterized by natural or semi-natural woody vegetation with aerial stems generally less than 6 meters tall; features classified here will include those that would otherwise be determined Harvested/Disturbed but appear to show unmanaged stunted growth, or managed as easements.
61 - Harvested/Disturbed	Areas of forest clear-cut, temporary clearing of vegetation, and other dynamically changing land cover due to land use activities as defined by the EPA; these features should be categorized only where there is 30% canopy cover or less.
71 - TurfGrass	Primarily grasses; including vegetation planted in developed settings for erosion control or aesthetic purposes, as well as natural herbaceous vegetation and undeveloped land, including upland grasses and forbs, as defined by the EPA.
81 - Pasture	Areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops as defined by the EPA.
82 - Cropland	Characterized by herbaceous vegetation that has been planted or is intensively managed for the production of food, feed, or fiber, or is maintained in developed settings for specific purposes as defined by the EPA.
91 - NWI/Other	Areas where forest, shrubland vegetation, or perennial vegetation accounts for 25% to 100% of the cover and the soil or substrate is periodically saturated with or covered with water, as provided by the TMI & NWI; this class has an additional attributed subclass to correspond with the extracted software output had external wetland data not been incorporated.

Table 4. Number of GPS locations for each of 20 collared bobcats in Bath County, Virginia in years 2017-2019, and total, mean, and standard error (SE) number of locations for all bobcats, and for males and females.

Bobcat ID	**Number of Locations**	**Weeks Deployed**	**Fix Success**
F12	575	12	94%
M13	2371	48	93%
M14	470	8	87%
M15	1418	36	85%
M16	2077	44	90%
F18	758	39	51%
F20	1273	22	79%
M21	1634	38	87%
M22	1144	25	91%
M23	1685	38	92%
Total	13405	310	
Mean	1341	31	85%
SE	198	4	4%
Male Mean	1543	34	89%
Male SE	235	5	1%
Female Mean	869	24	75%
Female SE	209	8	12%

Table 5. Model results for resource selection functions for 10 bobcats collared in Bath County, Virginia in years 2017-2019, including separate models for various covariate combinations. Models are binomial generalized linear mixed-effects models. Results include β coefficients (β), and standard errors (SE), z values, and p values from Wald tests.

Model	**Covariate**	**β**	**SE**	**Z value**	**P value**
A.) All individuals n=10 (7 male, 3 female)	early edge^{a}	-0.276	0.013	-21.525	<0.001
	field edge^{b}	-0.170	0.011	-15.666	<0.001
	forest interior^{e}	0.074	0.010	7.690	<0.001
B.) Individuals within 1km of fire n=8 (5 male, 3 female)	fire^{c}	-0.309	0.015	-20.531	<0.001
	field edge^{b}	-0.168	0.011	-14.702	<0.001
	forest interior^{e}	0.041	0.011	3.919	<0.001
C.) Individuals within 1km of timber harvest n=8 (6 male, 2 female)	timber^{d}	-0.045	0.013	-3.573	<0.001
	field edge^{b}	-0.243	0.013	-19.137	<0.001
	forest interior^{e}	0.144	0.011	13.570	<0.001

a) The “early edge” covariate is the distance to edge surrounding combined shrub/scrub and harvested/disturbed land cover classes, all timber harvest within15 years, and canopy openings resulting from fire.
b) The “field edge” covariate is the distance to edge surrounding combined turf, pasture, and crops land cover classes, and all wildlife clearings.
c) The “fire” covariate is the distance to open canopy structure resluting from prescribed fire.
d) The “timber harvest” covariate is the distance to all timber harvest on public lands within 15 years.
e) The “forest interior” covariate is the distance to forest that is 300m or further from contrasting land cover types.

IV. Research Notes

A Note on Dispersal:

I observed movement patterns indicative of dispersal behavior in 2 male bobcats, M09 and M10. The bobcats were captured on the same day (April 9, 2017, Table 1). Tooth eruption indicated that both individuals were mature, but notable lack of wear or yellowing indicated they were young, perhaps 2 or 3 years of age. M09 was monitored for 265 days. M10 was monitored for 236 days. Unfortunately, M10 had the worst fix success of any bobcat (36%), yet this still provided 490 relocations throughout the deployment. M09 was known to survive at least until April 2019, when the bobcat was captured by a remote camera within the area it appeared to finally establish a home range. M10 was killed during April 2018 due to becoming ensnared in a neck snare placed for coyotes on private land. M10 was killed near the area it finally appeared to establish a home range prior to the battery exhausting in the GPS collar. GPS relocations, combined with the most recent observations of each individual, indicate that both bobcats established home ranges towards the end of 2017.

Previous studies examining bobcat dispersal have reported 2 types of dispersal movements: erratic and prolonged dispersal or straight-line and rapid dispersal (Johnson et al. 2010, Kamler et al. 2000, Nielsen and Woolf 2003). The dispersal movements of both M09 and M10 fit more closely with the erratic and prolonged type of dispersal movements, as opposed to straight-line. Straight-line movements are often dozens of kilometers, and sometimes exceed 100km (Johnson et al. 2010, Kamler et al. 2000, Nielsen and Woolf 2003). The longest distance between areas each bobcat used was less than 20km, and the movements between those areas were not in a straight-line. Both bobcats spent several weeks in an area before transitioning to another nearby area, repeating this pattern. Both bobcats would periodically return to areas they previously used, particularly M09. Following the mortality of M08, a resident male bobcat that overlapped an area previously used by M09, M09 returned to that area and filled the vacant home range of M08.

A Note on Mortality:

I observed an overall mortality rate of 35% within the GPS-collared sample of bobcats (n=20, 14 male, 6 female, Table 1). The overall mortality rate for males was 43% and the overall mortality rate for females was 17%. The approximate annual mortality rates, since the battery life of all collars did not reach 1 year, was 29% for males in 2017 and 57% for males in 2018, and 0% for females in 2017 and 33% for females in 2018. The average monitoring duration for males was 268 ± 24 days and for females was 237 ± 42 days, although this includes monitoring that ended prematurely due to mortalities. The most common cause of mortality for males was trapping by landowners and fur trappers, with 2 males unintentionally trapped in coyote neck snares on private lands and 1 intentionally trapped in a foot hold trap by a fur trapper on Gathright WMA. Other mortality causes for males include 1 opportunistically harvested by a deer hunter, 1 hit by a vehicle on state route 220, and 1 dead from pneumonia. The cause of death for the 1 female that died is uncertain, but the age of that female was estimated to be over 6 years of age.

Space Use Surrounding White-tailed Deer Fawning:

Due to the interest in the potential impacts of bobcat predation on white-tailed deer, I examined bobcat movements and resource selection during the neonatal life stage, when deer are most susceptible to mortality. Specifically, I examined bobcat space use during the time period that coincides with the earliest stage of a fawn's life and the highest probability of mortality (Cook et al. 1971, Kilgo et al. 2012). This time of peak mortality generally occurs during the first weeks of life when deer fawns are least mobile and cannot evade predators as easily (Shuman et al, 2017), which I will hereafter refer to as the limited mobility period (LMP). Bobcats are known fawn predators, with nearly all fawn mortality studies conducted in sites where bobcats occur observing some level of bobcat predation on fawns (Ballard et al. 1999, Boulay 1992, Cook et al. 1971, Epstein et al. 1983, Kilgo et al. 2012, Nelson et al. 2015, Roberts 2007, Shuman et al. 2017, Vreeland et al. 2004). Fawn predation rates by bobcats vary widely and appear to be lower in areas of low deer density (Chitwood et al. 2015, Kilgo et al. 2012, Nelson et al. 2015), perhaps reflecting an opportunistic foraging strategy in which fawns are preyed upon when encountered versus intensive fawn-searching behavior.

If bobcats are intensively searching for fawns during the limited mobility period, this change in foraging behavior should be detectable in bobcat space use metrics. I examined bobcat resource selection during the LMP, and compared bobcat movement rates during the LMP to the time periods immediately before and after the LMP. For movement analysis, I used the local LMP proposed by VDGIF biologists of 21 May – 30 June, resulting from fawn datasets on several Virginia Military Installations and interviews with deer biologists in the region (Michael Fies personal communication). I calculated movement rates, and modeled the effect of sex and time period, using the methods outlined in Chapter 1 (page 43). The time periods I compared were the previously defined LMP, a 41-day period before the LMP, and a 41-day period following the LMP. I only examined movement rates for individuals that were monitored during all time periods. I examined 3rd order (within home range) resource selection, using the methods outlined in Chapter 2 (pages 99-104). The covariates I included were distance to early successional forest edge, distance to field edge, distance to forest interior, elevation, and slope. Instead of examining resource selection with the 41-day defined LMP, I examined all of June and July due to model convergence issues with the shorter 41-day time period. I only included individuals with greater than 85% GPS fix success and relocation data across the entire time period.

I examined movement rates for 17 bobcats (13 males, 4 females). I did not find any significant effects of time period on movement rates (Table 2). Although not significant ($p > 0.05$) for either sex, the mean movement rate was slightly lower during the post LMP period for both sexes (Figure 1). I examined resource selection for 6 males. The resource selection results were similar to findings in my other resource selection analysis examining annual or seasonal resource selection. During June and July, male bobcats exhibited 3rd order selection for forest edge surrounding early successional forest and fields, high elevations, and gentle slopes (Table 3, Figure 2). The strongest predictors were distance to forest edge along fields and elevation (Table 3). Distance to forest interior was not a significant predictor of male 3rd order resource selection during June and July (Table 3). This contrasts my annual resource selection findings in Chapter 2, in which distance to forest edge surrounding early successional forest was a stronger predictor than distance to forest edge surrounding fields, and bobcats exhibited avoidance of forest interior.

In summary, I did not find evidence that bobcats shift movement rates during the white-tailed deer LMP, but I did find evidence that male bobcat resource selection patterns differ slightly around that time period compared to annual patterns. Selection for field edges appears to be stronger compared to early successional forest during these months, and there is no avoidance of forest interior, as seen on an annual time scale. I believe that these resource selection patterns are largely due to the emergence of herbaceous understory vegetation during the growing season. Fields and their edges are more densely vegetated during the growing season, and by June and July herbaceous vegetative cover will be relatively dense. The understory of the forest interior, mostly bare during the dormant season, may have extensive growth of ferns and other shade-tolerant herbaceous plant species. This emergence of herbaceous vegetation results in concealment cover in areas that may not have sufficient cover during dormant months. During the dormant season, the dense woody vegetation in early successional forest may compose a higher proportion of the dense cover on the landscape. It is possible that deer are selecting fawn-rearing areas near fields, and bobcats are selecting for similar areas to pursue fawns. Shuman et al. (2018) found female white-tailed deer were found to select fawn rearing areas near more productive agricultural areas. Future research in Bath County should investigate fawn-rearing site selection by female deer, and determine if these areas are more likely to be near fields than early successional forest. If so, this may provide evidence that relatively strong selection for field edges by bobcats during June and July corresponds to the distribution of fawns. However, it is important to note that abundance of some other prey species (i.e. cottontail rabbits) is also expected to be higher near fields during the same time period

Literature Cited:

Anderson, E. M. 1990. Bobcat diurnal loafing sites in southeastern Colorado. Journal of Wildlife Management 54(4):600.

Ballard, W. B., H. A. Whitlaw, S. J. Young, R. A. Jenkins, and G. J. Forbes. 1999. Predation and survival of white-tailed deer fawns in northcentral New Brunswick. Journal of Wildlife Management 63:574–579.

Boulay, M. C. 1992. Mortality and recruitment of white-tailed deer fawns in the wet prairie/tree island habitat of the Everglades. M.S. thesis. University of Florida, Gainesville.

Chitwood, M. C., Lashley, M. A., Kilgo, J. C., Moorman, C. E., and C.S. Deperno. 2015. White-tailed deer population dynamics and adult female survival in the presence of a novel predator. The Journal of Wildlife Management *79*(2): 211-219.

Cook, R. S., M. White, D. O. Trainer, and W. C. Glazener. 1971. Mortality of young white-tailed deer fawns in south Texas. Journal of Wildlife Management 35:47–56.

Epstein, M. B., G. A. Feldhamer, and R. L. Joyner. 1983. Predation on white-tailed deer fawns by bobcat, foxes, and alligators: predator assessment. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 37:161–172.

Johnson, S. A., H. D. Walker, and C. M. Hudson. 2010. Dispersal characteristics of juvenile bobcats in south-central Indiana. Journal of Wildlife Management 74(3):379–385.

Kelly, M., Morin, D. and C.A. Lopez-Gonzalez. 2016. Lynx rufus. The IUCN Red List of Threatened Species.

Kilgo, J. C., Ray, H. S., Vukovich, M., Goode, M. J., and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management *76*(7), 1420-1430

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 3–42.

Kolowski, J. M., and A. Woolf. 2002. Microhabitat use by bobcats in southern Illinois. Journal of Wildlife Management 66(3):822.

Nelson, M. A., M. J. Cherry, M. B. Howze, R. J. Warren, and L. M. Conner. 2015. Coyote and Bobcat Predation on White-tailed Deer Fawns in a Longleaf Pine Ecosystem in Southwestern Georgia. Journal of the Southeastern Association of Fish and Wildlife Agencies 2: 208-213.

Nielsen, C. K., and A. Woolf. 2003. Dispersal of juvenile male bobcats (Lynx rufus) in southern Illinois. Trans. Ill. Stat Acad. Sci. 96: 313-318.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and “mesophication” of forests in the eastern United States. BioScience 58:123–138.

Roberts, S. B. 2007. Ecology of white-tailed deer and bobcats on Kiawah Island, South Carolina: Implications for suburban habitat preservation. Doctoral dissertation. University of Georgia, Athens.

Shuman, R. M., M. J. Cherry, T. N. Simoneaux, E. A. Dutoit, J. C. Kilgo, M. J. Chamberlain, and K. V. Miller. 2017. Survival of white-tailed deer neonates in Louisiana: Neonate Survival in Louisiana. Journal of Wildlife Management 81:834–845.

Shuman, R. M., Cherry, M. J., Dutoit, E. A., Simoneaux, T. N., Miller, K. V., and M. J. Chamberlain. 2018. Resource selection by parturient and post-parturient white-tailed deer and their fawns. Journal of the Southeastern Association of Fish and Wildlife Agencies 5:78–84.

Vreeland, J. K., D. R. Diefenbach, and B. D. Wallingford. 2004. Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns. Wildlife Society Bulletin 32:542–553.

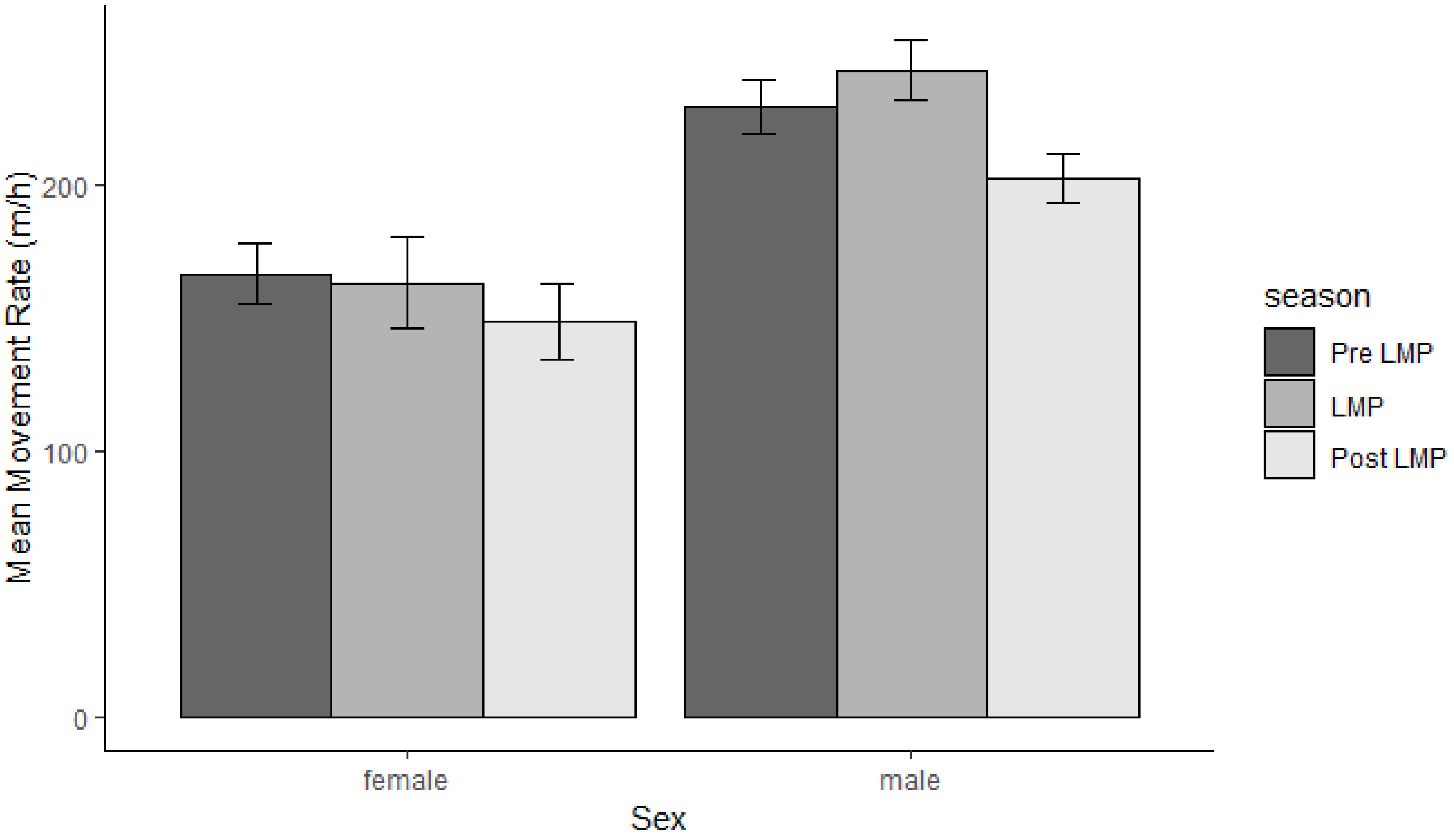

Figure 1. Means and 95% confidence intervals for movement rates of female (n=4) and male (n=13) bobcats monitored during 2017-2019. Time periods examined are surrounding the white-tailed deer limited mobility period (LMP) from May 21 through June 30, the 41 day preceding the LMP, and the 41 day period following the LMP. Movement rate is reported as meters moved per hour (m/h)

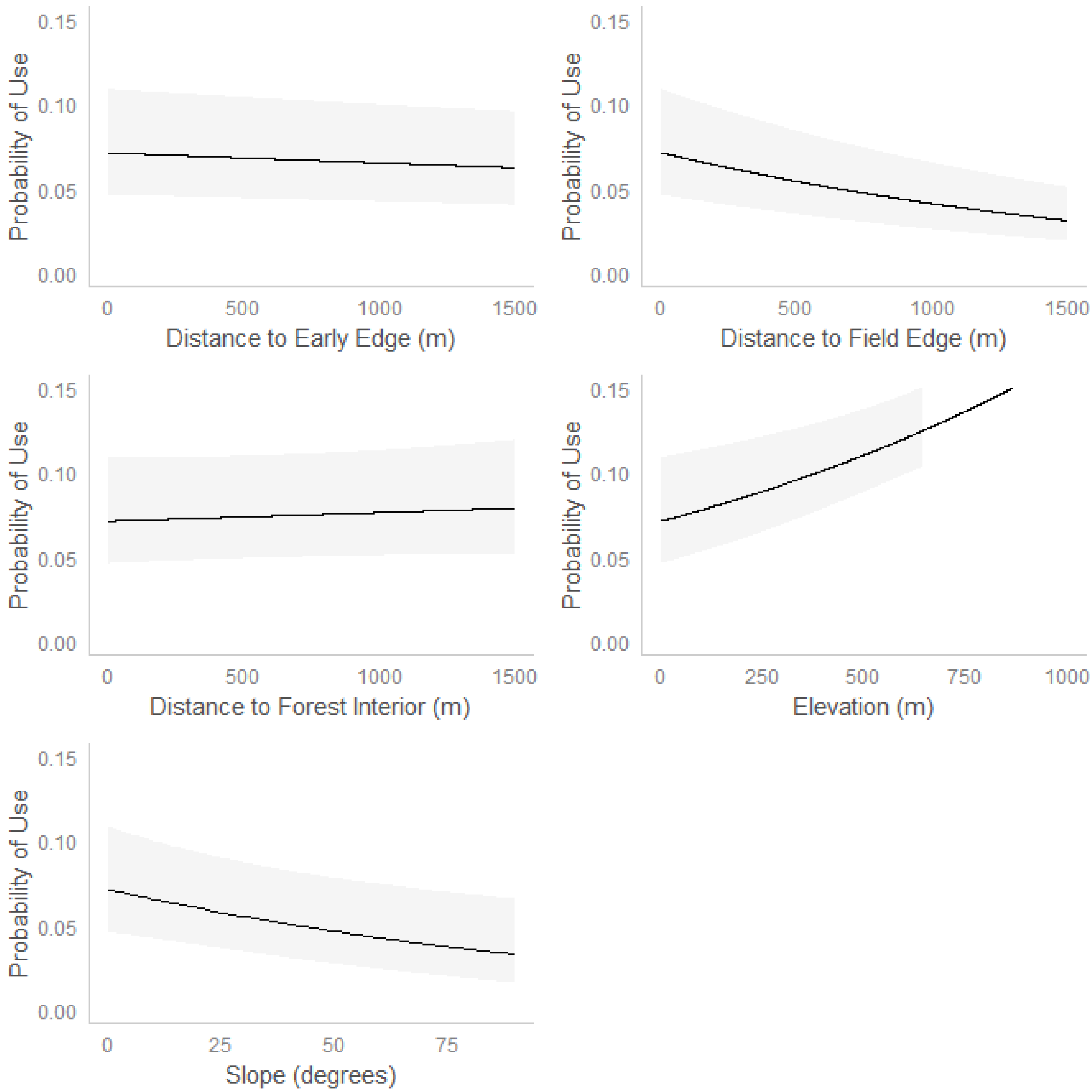

Figure 3. Relative probability of 3rd order resource selection with 95% confidence intervals for male bobcats (n=6) from June 1 – July 31, 2018 in Bath County, VA.

Table 1. Capture-related information for bobcats captured and monitored from 2017-2019 in Bath County, Virginia.

ID	Sex	Capture Date	Capture Area	Collar Type	Ear Tag	Weight (kg)	Age Class	Neck Circ. (cm)	Head Circ. (cm)	Girth (cm)	Shoulder Height (cm)	Body Length (cm)	Zygomatic Breadth (cm)	Head Length (cm)	Mortality
1	M	1/26/2017	Back Creek Mt.	Telonics	R. white	9.0	A	25.5	35	NA	NA	NA	NA	NA	NA
2	F	2/2/2017	Hidden Valley	Telonics	L. green	7.2	A(>5)	23	29	36.5	34	74	NA	16	NA
3	M	2/3/2017	Hidden Valley	Telonics	R. black	11.4	A	27	33.5	50.5	44.5	68	9.3	17.5	NA
4	M	2/7/2017	Back Creek Mt.	Telonics	R. blue	11.2	A	29.5	32.5	61.5	37	76	NA	18	NA
5	F	2/17/2017	Warm Springs Mt.	Telonics	L. white	6.9	A	23	28	38	35	72	NA	15	NA
6	M	2/18/2017	Coles Mt.	Telonics	R. yellow	11.2	A	28.5	34.5	43	33	72	NA	17	NA
7	F	3/25/2017	Back Creek Mt.	None	L. red	4.7	A	19.5	24.5	33	28.5	61	6.4	13.5	NA
8	M	4/4/2017	Warm Springs Mt.	Telonics	R. red	7.8	A	24.5	30.5	39	38	62	7.8	15.5	Shot by deer hunter
9	M	4/9/2017	Warm Springs Mt.	Telonics	R. green	8.2	A	24.5	29	39.1	35.5	64.5	8.3	16	NA
10	M	4/9/2017	Gathright	Telonics	R. green	10.5	A	26	31.5	43.5	42	68	7.8	16.5	Trapped in coyote snare
11	F	10/11/2017	Back Creek Valley	Telonics	L. purple	NA	A	22.5	25	NA	NA	68	NA	15	NA
12	F	1/20/2018	Back Creek Mt.	ATS	L. orange	8.5	A(>5)	23	27.5	36	36	72	NA	16	Emaciated/potential pnuemonia
13	M	2/1/2018	Back Creek Mt.	ATS	R. yellow	11.6	A	27	33	43	39	74	8.8	15	Trapped in coyote snare
14	M	2/14/2018	Gathright	ATS	R. red	NA	A	24	29	40	35	76	NA	17	Pneumonia
15	M	2/22/2018	Gathright	ATS	R. purple	11.9	A	27	32	42	38	78	NA	16.5	Trapped on Gathright (foothold)
16	M	3/3/2018	Hidden Valley	ATS	R. yellow	10	A	27	32	43.5	37	70	NA	17	NA
17	F	3/6/2018	Back Creek Mt.	None	None	6.5	A	19	24	NA	NA	NA	NA	NA	NA
18	F	3/15/2018	Back Creek Valley	ATS	L. yellow	6.0	A	19	24.5	36	NA	71	8.9	15	NA
19	M	3/16/2018	Hidden Valley	Lotek	R. green	7.0	A	22.5	28.5	34	38	73	8.2	15	NA
20	F	4/2/2018	Warm Springs Mt.	ATS	L. orange	6.0	A	21	26	33.5	31	71	7.4	14.5	NA
21	M	4/2/2018	Warm Springs Mt.	ATS	R. white	NA	A	23	31	36	36	80	9.1	16	NA
22	M	4/12/2018	Warm Springs Mt.	ATS	R. red	8.5	A	22	28.5	35	34	79	NA	16	Vehicle collision (rt. 220)
23	M	4/12/2018	Warm Springs Mt.	ATS	R. purple	10.5	A	26	32	41	39	34	8.6	17	NA
Male mean						9.9	-	25.6	31.5	42.2	37.6	69.6	8.5	16.4	-
Male SE						0.4	-	0.6	0.6	1.9	0.8	3.1	0.1	0.2	-
Female mean						6.5	-	21.3	26.1	35.5	32.9	69.9	7.6	15	-
Female SE						0.5	-	0.8	0.8	0.8	1.3	1.8	0.5	0.4	-

Table 2. Gamma generalized linear mixed-effects model for bobcats monitored during the time periods surrounding the white-tailed deer limited mobility period (LMP) in 2017-2019 in Bath County, VA, with movement rates as response and time period interacting with sex as predictor. Reference categories are sex=female and time period= pre LMP.

Covariate	β	SE	t value	Pr(>|z|)
(Intercept)	5.111	0.125	40.918	<0.001
LMP	-0.015	0.080	-0.187	0.852
Post LMP	-0.128	0.077	-1.675	0.094
Male	0.308	0.143	2.146	0.032
LMP x male	0.051	0.090	0.566	0.572
Post LMP x male	-0.031	0.086	-0.360	0.719

Table 3. Model results for a 3rd order resource selection functions for 6 male bobcats in Bath County, Virginia in during June and July of 2018. Model is a generalized linear mixed-effects model with a binomial distribution. Results include β coefficients (β), and standard errors (SE), z values, and p values from Wald tests.

Covariate	β	SE	Z value	P value
Early edge[a]	-0.089	0.034	-2.607	0.009
Field edge[b]	-0.262	0.032	-8.149	<0.001
Forest interior[c]	0.020	0.029	0.686	0.493
Elevation	0.154	0.045	3.389	0.001
Slope	-0.074	0.027	-2.719	0.007

[a] The “early edge” covariate is the distance to forest edge surrounding combined shrub/scrub and harvested/disturbed land cover classes, all timber harvest within15 years, and canopy openings resulting from fire.

[b] The “field edge” covariate is the distance to forest edge surrounding combined turf, pasture, and crops land cover classes, and all wildlife clearings.

[c] The “forest interior” covariate is the distance to forest that is 300m or further from contrasting land cover types.