Survival and Habitat Use of Non-breeding Northern Bobwhites on Private Lands in Ohio

THESIS

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By

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ABSTRACT

Despite a long history of research and accumulated knowledge of factors affecting population growth rates, conservation efforts aimed at reversing population declines of northern bobwhites (*Colinus virginianus*) have been largely ineffective. Bobwhite population decline and range contraction across the Midwest was driven primarily by changes in land-use practices related to large-scale intensive agriculture, urbanization, and forest succession. Although changes in agricultural landscapes have contributed substantially to the decline, such landscapes remain the only area where active management may improve population growth rates. To understand the ecology of bobwhites in agricultural landscapes in Ohio, I used radio-telemetry to investigate survival and habitat use during the non-breeding season (October- March) on 4 private land study sites in southwestern Ohio during 2009-2011. Known-fates survival estimates were low in both years ($\hat{S}_{2009\text{-}2010}$=0.05, 95% CI=0.03, 0.11, $\hat{S}_{2010\text{-}2011}$=0.12, 95% CI=0.07, 0.20) and lowest weekly survival coincided with periods of prolonged snow cover. Compositional analysis revealed that coveys used habitat non-randomly at 3 scales; positioning of home ranges within study areas ($\Lambda = 0.320$, $P < 0.001$), positioning of core areas within home range ($\Lambda = 0.599$, $P = 0.002$), and point locations within home ranges ($\Lambda = 0.058$, $P = 0.002$). Early successional woody vegetation (e.g. fencerows and ditches) was the most preferred habitat type at all scales. Differences in selection among study sites revealed that home ranges were preferentially established in areas with grassland cover on 2 agricultural study sites, but not at the site with the greatest amount of grassland cover. Bobwhites mostly used habitat edges such that interior portions of grass and crop fields were used less as they increased in area. Thus small fields with high edge to interior ratios are most advantageous.

I tested the influence of habitat use on individual survival by comparing models representing habitat use at 4 spatial scales; site, landscape (78.5 ha buffer), home range, and microhabitat use. Support for different models at 2 scales showed scale-dependent effects of habitat on survival. Higher woody edge density within home ranges was associated with higher survival whereas increasing perennial cover within a 78.5 ha buffer around individuals was related to diminished survival. This relationship suggested that survival was influenced by habitat availability at smaller scales and by factors that affect predator distribution at larger scales. Given the important influence of low non-breeding season survival on population growth rates, management strategies should focus on improving non-breeding season survival in this population by providing woody cover near food sources (e.g. grasslands and row crop fields). Intermediate amounts of grassland and row crop habitat are important in agricultural landscapes, but overrepresentation of any 1 cover type will diminish the suitability of the site for bobwhites during the non-breeding season. Practices focused on improving woody edge habitat along forests are likely to only marginally affect crop production but could significantly improve the amount of usable habitat for bobwhites in agricultural landscapes.

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On a personal level, I would like to thank my friends and family for their support through the last 2 years. My parents have been exceedingly supportive and helpful throughout my education. In my youth, my father and grandfather instilled a passion in me for wildlife conservation from the view of an Indiana duck blind, and without this passion I'm unsure where I would be today.

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Major Field: Environment and Natural Resources

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CHAPTER 1: INTRODUCTION

Northern bobwhites (*Colinus virginianus*; hereafter bobwhite) have declined across most of their range since the industrial revolution in the late 1800's (Leopold 1931, Stoddard 1931, Brennan 1991). During that time, agricultural practices characterized by small and diverse crop fields were replaced by more mechanized and clean farming techniques (Leopold 1931). The trend of agricultural intensification continued throughout the 20th century and well into the 21st century, leading to increasingly homogenous landscapes throughout agricultural areas of the bobwhite range (Warner 1994). Urbanization and forest succession also have played important roles in determining the spatial distribution of bobwhites across the eastern U.S. (Veech 2006).

In response to the marked decline in bobwhite populations that was occurring by the 1920's, interested sportsmen called for research into the factors affecting bobwhite populations across their range. Stoddard (1931) and Leopold (1931) began their ground breaking work soon thereafter and published their research as the first formal, large-scale studies of wildlife and their habitats to be published in North America. These early works laid the groundwork for what would ultimately become professional wildlife management (Leopold 1933) and active bobwhite research continued throughout the 20th century (Scott 1985, Brennan 1999). The result of over 80 years of bobwhite research is a strong understanding of factors contributing to the decline and affecting population growth rates. Guthery (1997) reviewed this research and proposed a philosophy for bobwhite habitat management that focuses on increasing the amount of suitable habitat on a landscape scale (Williams et al. 2004). Similarly, demographic analyses capitalized on the wealth of published research and showed that populations are more sensitive to changes in survival than reproductive parameters (Folk et al. 2007, Sandercock et al. 2008), and that survival during the non-breeding season (October- March) contributes more to population growth rates than survival during the breeding season.

Despite the accumulated knowledge of factors affecting bobwhite populations across their range, conservation efforts targeting bobwhite populations have generally been unsuccessful at reversing population declines. The failure of these approaches has resulted from a variety of issues including continued changes in large-scale crop production practices (Klimstra 1982, Peterjohn 2003), declines in hunting participation (Burger et al. 1999), a potential disconnect between bobwhite research and management (Brennan 2002), changing resource management values within state agencies (Roseberry 1993, Dailey 2002), and changes in societal values toward land management (Burger et al. 1999, Askins 2001, Dailey 2002). Underlying the challenges facing bobwhite conservation is that historical bobwhite populations were a by-product of agricultural production (Leopold 1931, Dailey 2002), whereas contemporary land-management fails to provide abundant bobwhite habitat (Klimstra 1982). Therefore the primary challenge that remains for agencies interested in managing bobwhite populations in the Midwest is to determine how to incorporate effective conservation strategies into working agricultural landscapes, such that they maximize benefits for bobwhites and minimize impacts to agricultural production (Brennan 1991, Peterjohn 2003, Burger et al. 2006, Chapman et al. 2011).

As part of a larger project that sought to elucidate the factors affecting population growth rates of bobwhites in the core of their current range in Ohio, my research investigated survival and habitat use of bobwhites during the non-breeding season. Focusing on the non-breeding season allowed me to identify factors affecting habitat suitability and survival during the most important life-phase for bobwhites at the northern periphery of their range (Figure 1.1; Folk et al. 2007). The study was conducted on privately owned, unmanaged agricultural land that was representative of landscapes in which bobwhite occurred within Ohio. By focusing on private lands that received no active bobwhite management, I was able to identify factors affecting survival and habitat suitability in agricultural landscapes in order to make informed recommendations for management efforts in similar landscapes across Ohio.

STUDY DESIGN

Study Area

Site selection--The broader investigation sought to determine the influence of local habitat factors on survival and reproduction in unmanaged agricultural landscapes in the core of the bobwhite range in Ohio. Therefore, we developed a landscape level habitat suitability model to identify suitable landscapes that could potentially support bobwhite populations based on previously published research (e.g. Roseberry and Sudkamp 1998, Twedt et al. 2007, Riddle et al. 2008). We intersected a grid of 5 km^2

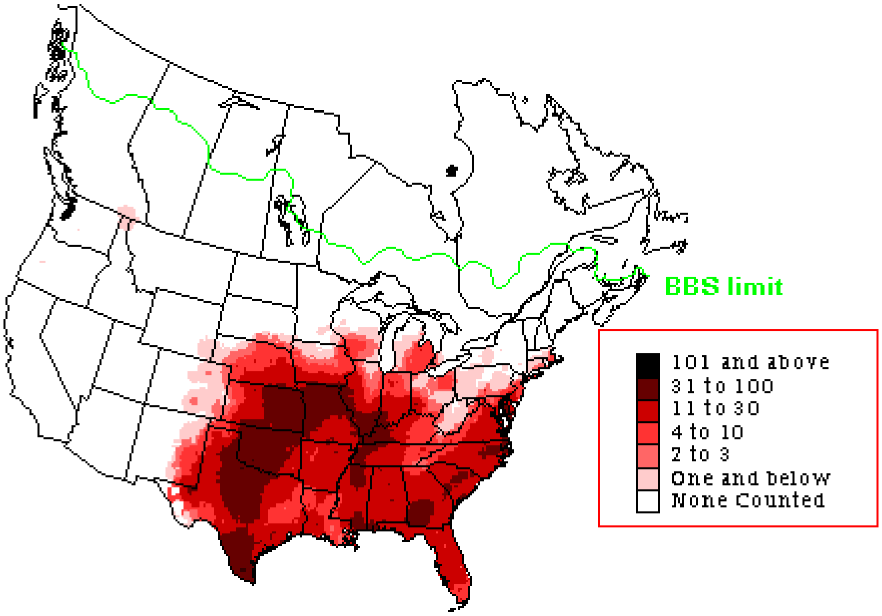

Figure 1.1. Geographic distribution and relative abundance of northern bobwhites detected during the 2009 Breeding Bird Survey throughout the United States (<http://137.227.242.23/bbs/htm96/map617/ra2890.html>, Accessed 18 November 2011)

hexagons with a spatial landscape coverage derived from the National Land Cover Dataset (NLCD; Homer et al. 2004) and parcels enrolled in the Conservation Reserve Program (CRP). We defined suitable hexagons as all those with < 50% forest cover and > 10% early successional vegetation (grassland, shrubland from NLCD and CRP). We classified suitable hexagons into 4 strata based on composition of adjacent hexagons; isolated agricultural, clustered agricultural, isolated mixed agriculture-forest, and clustered mixed agriculture-forest. We randomly selected sites from each of the 4 strata to pursue permission from landowners to search for bobwhites.

We received permission to work on ≥ 80% of the land within proposed site boundaries of 9 sites in Highland, Brown, and Adams County. We conducted fall covey call (Demaso et al. 1992) and spring whistle count (Terhune et al. 2009) surveys on each site during 2007-2009 to determine occupancy and relative abundance of bobwhites. Based on these surveys and landscape differences among sites, we choose 4 sites to conduct an intensive radio-telemetry study. We expanded study sites beyond the hexagon boundaries as we gained knowledge of the local distribution of bobwhites near each site.

Study area composition--The four sites were in Highland and Brown counties in the glaciated till plains physiographic region of Ohio (Ohio Division of Geologic Survey 1998) and the Eastern Tallgrass Prairie Bird Conservation Region (Palmer et al. 2011). The land area in Highland and Brown county was predominately rural (6.1% developed) and the primary land-use was agriculture (56.8%; Homer et al. 2004). Forests accounted for 33.3% of the area while early successional vegetation (grasslands and shrublands) accounted for 2.9% (Homer et al. 2004). Because the land was at the southern extent of the most recent glaciation event, the topography was gently rolling and therefore less amenable to modern large-scale agricultural production techniques typical of other regions in Ohio. This topography facilitated cropping and land use patterns that were more beneficial to bobwhites (e.g. small field sizes, diverse crops) rather than a landscape characterized by large row crop fields. The long-term mean annual temperature was 11.1˚ C and the long-term mean temperature during the non-breeding season (October-March) was 10.5 C (NCDC 2011). Mean annual precipitation was 110.2 cm. There was an average of 19.8 days with snow accumulation > 5 cm and mean annual snow accumulation was 67.5 cm (NCDC 2011).

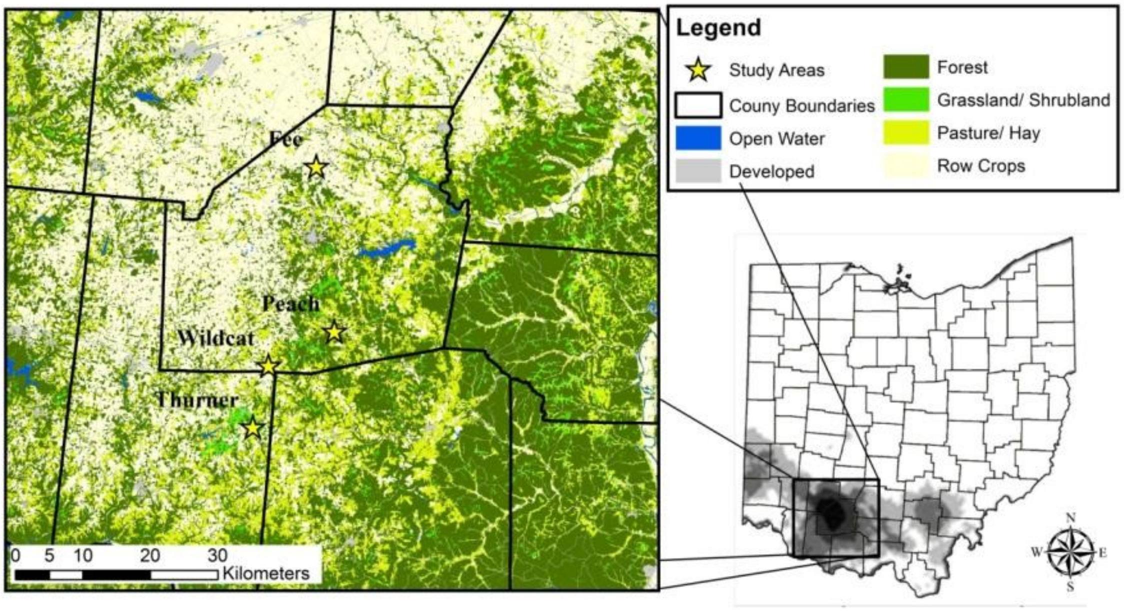

Figure 1.2. Location of 4 study sites where I studied non-breeding season (October - March) survival and habitat use of northern bobwhites in southwestern Ohio, 2009-2010. Inset map of Ohio shows the distribution of bobwhite populations in Ohio in 2002, based on Ohio Division of Wildlife call-count surveys (Spinola and Gates 2008).

The study sites represented a gradient from agricultural to forested landscapes and varied in local habitat composition (Figure 1.2; Table 1.1). Bobwhite density also varied among sites (Table 1.1). The primary land use was agriculture, including pasture and hay for livestock production and row crop production. Row crop fields were primarily soybeans (61.2%) and corn (35.3%). Other crops included winter wheat (2.5%) and tobacco (0.7%). No-till was the predominant tillage practice (96.5%).

I identified 3 categories of permanent natural cover; forests, early successional woody vegetation, and early successional herbaceous vegetation. Forest composition

	Fee	Peach	Thurner	Wildcat
Area (ha)	1284.4	397.7	738.8	838.3
Mean slope (%)	5.0	9.7	4.5	5.1
Mean covey density (coveys/ km^2)	0.59	0.45	0.72	1.47
Mean row crop field size (ha)	12.6	7.6	10.0	7.6
CRP Area (ha)	123.6	75.2	25.7	137.4
CRP Composition (%)[a]				
Cool Season Grasses	86.9	98.0	86.5	88.8
Warm Season Grasses	13.1	2.0	13.5	11.2
Landscape Composition (%)[b]				
Row Crop	61.6	17.6	31.8	34.9
Developed	6.4	4.1	6.3	5.2
Forest	20.7	50.0	28.1	32.0
Grassland/ Shrub	0.6	6.8	6.2	5.7
Pasture/ Hay	10.4	21.4	27.1	21.9
Other	0.3	0.1	0.6	0.2
Site Composition (%)[c]				
ES Herbaceous[d]	9.1	21.0	9.9	19.6
ES Woody[d]	3.1	4.7	6.5	4.2
Forest	8.4	28.6	16.1	10.4
Non Habitat	4.1	4.1	7.4	4.0
Pasture Hay	3.3	2.0	6.6	23.3
Row Crop	72.1	39.7	53.5	38.5

[a] Proportion of area of all CRP fields in respective category

[b] Proportion NLCD habitat cover within 10 km buffer around the centroid of each point

[c] Proportion of the maximum extent of the site boundaries from 2 years in each habitat type

[d] ES = early successional

Table 1.1. Physical and land-cover charecteristics of 4 study sites in southwestern Ohio on which I studied non-breeding season survival and habitat use of northern bobwhites during 2009-2011.

varied with topography, with distinct communities on dry ridges and depressional areas. Forests in dry upland ridges had an oak (*Quercus*) and hickory (*Carya*) overstory dominated by shagbark (*C. ovata*) and pignut hickory (*C. glabra*) and white (*Q. alba*) and red oak (*Q. rubra*). Forests in depressional areas were dominated by black walnut (*Juglans nigra*), green ash (*Fraxinus pennsylvanica*) and American elm (*Ulmus americana*). Some bottomland forests were dominated by pin oak (*Q. palustris*). The composition and structure of the forest understory appeared to be related to recent forest management practices and most forests had closed canopies with little vegetation in the understory during the dormant season. Forests with a history of grazing or timber extraction had more open canopies and dense understories consisting of blackberry (*Rubus allegheniensis*), black raspberry (*R. occidentalis*), and multiflora rose (*Rosa multiflora*).

Early successional woody vegetation was typically associated with linear habitat features (i.e. fencerow or ditches) or old fields with advancing secondary succession (3-20 years; Roseberry and Klimstra 1984). The dominant vegetation in this habitat category included black raspberry, blackberry, multiflora rose, and Japanese honeysuckle (*Lonicera japonica*). American hazel (*Corylus americana*), gray dogwood (*Cornus racemosa*), trumpet creeper (*Campsis radicans*), and poison ivy (*Toxicodendron radicans*) were present in high densities in some habitat patches but were absent in others. There was little Amur honeysuckle (*L. maackii*) on the sites.

Early successional herbaceous fields were typically whole fields enrolled in the general sign-up of the CRP or fallow fields. The composition of these fields varied with enrollment history and management but could be separated into 3 broad categories. The first category was characterized by cool season sod-forming grasses, typically fescue (*Festuca* spp.), and low forb diversity (goldenrod [*Solidago spp.*] and Queen Anne's lace [*Daucus carota*]). Fields in this category were typically enrolled in the CRP under the establishment of cool season grass conservation practice (CP-1) and had been established for ≥ 10 years. The second category of early successional grass fields was characterized by warm season bunch grasses planted under Conservation Practice 2 (establishment of warm season grasses) and Conservation Practice 4D (permanent wildlife cover) under the CRP. These fields were predominantly Indian grass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), switch grass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*). The relative abundance of forbs in these fields was related to planting age and post-establishment disturbance. Most fields had low abundances of partridge pea (*Chamaecrista fasciculata*), gray-headed cone flower (*Ratibida pinnata*) and goldenrod. Newer fields (< 5 years) had abundant forbs, particularly partridge pea and Illinois bundle flower (*Desmanthus illinoensis*). The final category of early successional grass fields were old fields not enrolled in the CRP. These fields were typically 5-20 years out of production (row crop or pasture) and dominated by a diversity of cool season grasses and forbs. Of the three systems identified, the old field category was consistently the most diverse and typically had woody vegetation (i.e. *Rubus* spp.) scattered throughout. Regulations require that producers suppress growth of woody vegetation in fields enrolled in the CRP, although a few fields had slight woody encroachment. One additional CRP practice, Conservation Practice 8A (grassed waterways), was abundant on each of the 4 sites, particularly in areas with high row crop production. Although these areas constituted 7% of total area enrolled in the CRP on the sites, I included them in the row crop category because they were planted in dense fescue and mowed annually. This management made waterways more structurally similar to harvested crop fields because they lacked cover offered by stands of permanent herbaceous habitat (e.g. CRP fields).

Radio-telemetry

I used radio-telemetry to study behavior and survival of bobwhites. Although the suitability of radio-telemetry techniques has been questioned in bobwhite studies (Guthery and Lusk 2004), traditional metrics of abundance and habitat use (e.g. Roseberry and Klimstra 1984) were unsuitable to study fine-scale habitat associations and their effect on non-breeding season survival. I attempted to minimize biases associated with radiotransmitters in survival analyses by using a post-capture exclusion period (Holt et al. 2009) and interpreted results in the context of potential biases. We used homing and triangulation from short distances (< 20 m) to collect fine-scale habitat use data (White and Garrott 1990). Although homing is generally more accurate than long-distance triangulation (White and Garrott 1990), potential inaccuracies may occur in habitat classification. Understanding these inaccuracies is essential to properly interpret classification-based habitat use studies (Aebischer et al. 1993, Conner et al. 2003).

I simulated the process of tracking with 4 observers in different habitats and measured accuracy of the resulting locations to quantify telemetry error in the study. I randomly selected 80 points from radiomarked bobwhites tracked during the 2009-2010 field season on two study areas. I randomly assigned 1 observer and a flushing threshold value of 3-15 m from each point. The flushing threshold value ensured that tracking observers (hereafter tracker) behaved similarly as if they were tracking a radiomarked bird. The range of 3-15 m represented a typical flushing distance for radiomarked bobwhites in natural situations. A second observer placed a transmitter at the location and recorded the habitat where the transmitter was placed. The transmitter was placed to simulate the posture and height of a transmitter on a bobwhite (Townsend et al. 2007). The tracker located the transmitter while the second observer followed to ensure the flushing threshold was not violated. If the threshold was crossed the trial was ended and recorded as failed. Once the tracker identified the location of the transmitter they recorded the habitat code and marked a point on a Global Positioning System (GPS) and then walked to the predicted location. The second observer recorded the Euclidian distance between the predicted location and the actual location of the transmitter (hereafter tracking error). The coordinates of the predicted location were recorded and the Euclidian distance between the point location and the true location was calculated (hereafter total error). The total error was the combination of the error associated with tracking and with the placement of the point on the GPS, whereas tracking error excluded error associated with the placement of the point on the GPS.

I tested for differences between tracking error and total error with a t-test. There was no difference between the two values ($P = 0.554$) indicating that errors in the data set resulted from tracking error and not from the approximation of points with the GPS. The mean distance between the actual transmitter location and the recorded transmitter location was 12.9 m (95% CI = 12.6, 13.3 m). The tracker correctly classified the habitat in 93.8% of trials. I tested for a difference in tracking accuracy between observers (n = 4) and among habitat types (n = 5) using analysis of variance. There was no difference in accuracy among observers (F = 0.739, P = 0.532) or between habitat types (F = 1.266, P = 0.292). Given the relatively low tracking error and consistency in errors among observers and habitat types, I concluded that the error in the data set was inconsequential to the results of the study.

THESIS CONTENT

The broad objective of my study was to characterize survival and habitat use patterns of bobwhites throughout the non-breeding season in Ohio. To address this topic, I prepared 4 research chapters that individually addressed survival, movements, habitat use, and the influence of habitat use on survival. I first investigated variability in survival within and among years to identify periods of low survival and the relationship between survival and winter weather. I then characterized the social behavior of individuals relative to covey affiliation and covey movement rates. Then, using coveys as the sampling unit, I analyzed habitat selection at multiple spatial scales. The final research chapter investigated the influence of habitat use on survival during the non-breeding season by comparing the relative influence of habitat composition at 4 spatial scales. Collectively, these 4 research chapters contribute to our understanding of the ecology and behavior of bobwhites throughout the non-breeding season in Ohio, with implications for management of private lands in Ohio and similar landscapes across the northern portion of the bobwhite range. In the final chapter I summarized the management implications from the research and made recommendations for strategies that may improve non-breeding season survival and habitat availability for bobwhites in Ohio. I prepared each chapter as a manuscript, generally formatted following the Journal of Wildlife Management format guidelines. Because I intend to submit each chapter for publication with coauthors, I have written chapters 2-5 using plural pronouns, although I take full responsibility for all content herein.

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CHAPTER 2: TEMPORAL VARIABILITY IN SURVIVAL OF NON-BREEDING NORTHERN BOBWHITES IN OHIO

ABSTRACT:

Non-breeding season survival is an important vital rate that affects population growth rates of northern bobwhites (*Colinus virginianus*). The influence of non-breeding season survival is particularly important in northern portions of bobwhite range where severe winter weather reduces survival rates. We radiomarked 311 bobwhites from 73 coveys to investigate non-breeding season survival of bobwhites on 4 private land study sites in southwestern Ohio during 1 October – 31 March 2008-2011. We used the bootstrapping feature in Program MARK to adjust for overdispersion caused by dependency in survival among individuals in the same covey. Temporal variation in survival was best modeled ($w_i = 0.935$) with weekly differences in survival rates that varied among years. We also examined 13 *a priori* models to investigate the influence of snow cover and temperature on daily survival rates. Non-breeding season survival was low ($\hat{S}_{2009\text{-}2010} = 0.05$, 95% CI = 0.03, 0.11, $\hat{S}_{2010\text{-}2011} = 0.12$, 95% CI = 0.07, 0.20) in the 2 years for which we had data for the entire season. Survival during 10 December-31 March varied among years ($\hat{S}_{2008\text{-}2009} = 0.45$, 95% CI = 0.29, 0.61, $\hat{S}_{2009\text{-}2010} = 0.11$, 95% CI = 0.05, 0.21, $\hat{S}_{2010\text{-}2011} = 0.25$, 95% CI = 0.17, 0.34). Survival was lowest during periods of prolonged snow cover in each year. Weather variables improved model fit and snow depth had a negative influence in the top 4 models (model averaged β = -0.134, 95% CI = -0.164, -0.103). The top model included an interaction term for snow and temperature (β = -0.011, 95% CI = -0.019, -0.003) that indicated survival was lower on days with higher temperatures and snow cover. Predation was the primary cause of mortality, and increased movements on warm days may increase individual vulnerability to predation during periods of snow cover. Management strategies to improve non-breeding season survival should focus on mitigating predation during periods of prolonged snow cover by providing protective woody cover near food resources.

INTRODUCTION

Life-history theory predicts that changes in reproduction are most important for short-lived species with high fecundity and low survival (Stahl and Oli 2006). However, survival generally has more influence on population growth rates of declining populations (Meats 1971). Demographic analyses support the relationship between survival and population growth rates of declining populations of northern bobwhites (*Colinus virginianus*; hereafter bobwhite) and have established that non-breeding season survival is the most influential vital rate (Folk et al. 2007b, Sandercock et al. 2008). Because variation in non-breeding season survival in northern populations strongly influences population viability (Guthery et al. 2000, Williams et al. 2003a) management strategies need spatially explicit estimates of survival rates on which to base conservation efforts (Brennan 1991, Cox et al. 2004).

Although low non-breeding season survival is characteristic of bobwhite populations in northern parts of their range, sources of mortality and seasonal variation in survival are less understood. Previous studies documented the influence of regionally variable factors such as hunter harvest (Williams et al. 2004b, Rolland et al. 2010, Pollock et al. 1989a) or seasonal variation in weather (Roseberry and Klimstra 1984, Robel and Kemp 1997). However, the influence of these and other factors that affect non-breeding season survival vary across the species' range and under different management scenarios (Williams et al. 2004a).

Seasonal and annual comparisons of survival require understanding of the precision of estimators through time. The precision of variance estimates in temporal survival analyses is affected by 2 factors; overdispersion and variability in sampling effort. Dependency among individuals in survival studies leads to overdispersion (Schmutz et al. 1995). Previous survival estimates reported for bobwhites from radio-telemetry studies have not explicitly addressed dependency in survival that arises from individuals in the same covey sharing resources and exposed to similar mortality factors (Williams et al. 2003b). Failure to address dependency between individuals in the analysis does not affect survival estimates, but does affect the precision of variance estimates (Schmutz et al. 1995). Similarly, variation in sampling effort throughout a study may reduce precision of variance estimates by confusing process and sampling variation (Burnham et al. 1987, Gould and Nichols 1998). Addressing overdispersion and variation in sampling effort in survival analyses can identify periods with the most variable survival on which to focus conservation efforts (Moynahan et al. 2006).
We investigated temporal patterns of variation in non-breeding season survival in a bobwhite population near the northern periphery of the species' range and exposed to

severe winter weather. We investigated temporal variation in survival throughout the non-breeding season and tested for independence in survival among radio-marked individuals. We also examined the influence of snow cover and temperature on non-breeding season survival in 2 years. Previous research on the influence of winter weather on bobwhite survival reported different effects of temperature and snow accumulation on survival (Roseberry and Klimstra 1984, Robel and Kemp 1997). We predicted that snow would contribute most substantially to survival and that cold temperatures would exacerbate the influence of snow cover.

STUDY AREA

Bobwhites were historically found throughout Ohio (Urban 1978) but their range has recently contracted to the southwestern portion of the state (Spinola and Gates 2008). We conducted our study in the core of current bobwhite range in Highland and Brown counties in southwestern Ohio. Highland and Brown counties are in the till plains physiographic region in the glaciated area of Ohio (Ohio Division of Geologic Survey 1998). Primary land use in the region was agriculture, including 39% row crops and 17% pasture/ hay (Homer et al. 2004). The region was mostly rural (6% developed). Forests and grasslands accounted for 33 and 3 % of the landscape, respectively.

We worked on 4 private land study sites (400-1200 ha) where bobwhites were consistently found during the non-breeding season (Oct. - Mar. 2008-2011). Mean annual covey densities on the sites ranged from 0.45 to 1.5 coveys/ km^2. Composition of the study areas was primarily row crop fields (55%) planted with soybeans and corn. Early successional vegetation, including fields enrolled in the Conservation Reserve

Program (CRP), old fields, fencerows, and agricultural drainage ditches, collectively accounted for 19% of the area of study sites. Early successional grass fields were dominated by fescue (*Festuca* spp.) or planted warm season grasses, primarily Indian grass (*Sorghastrum nutans*). Dominant forbs in grasslands were goldenrod (*Solidago* spp.), queen Anne's lace (*Daucus carota*), and partridge pea (*Chamaecrista fasciculate*). Early successional woody vegetation was primarily blackberry (*Rubus allegheniensis*) or black raspberry (*R. occidentalis*). Forests accounted for 13% of the study area. Upland forests were dominated by oaks (*Quercus* spp.) and hickory (*Carya* spp.) whereas forests in deppressional areas were characterized by ash (*Fraxinus* spp.) and black walnut (*Juglans nigra*).

Weather during the study was variable and generally more severe than long-term averages (Table 2.1). Timing and severity of weather varied among years. Weather was relatively mild in 2008-2009 with 2 short (7-12 days) periods of snow cover > 5 cm and total daily accumulation never exceeding 25 cm. Weather was mild during December-January 2009- 2010 but there was a prolonged period (22 days) of deep snow accumulation and cold temperatures during February 2010. Snow accumulation during this period exceeded 25 cm for 9 consecutive days. The last year (2010-2011) had consistent snow cover > 5 cm during December- January but little accumulation in February. Although the duration of snow cover was prolonged, snow depth never exceeded 25 cm.

There was a 23 day hunting season with a 4 bird bag limit during the last 3 weeks of November of each year. We did not restrict or otherwise influence hunter effort or

Winter	Temp (C)	Snow (cm)	Days ≥ 5 cm[a]
2008-2009	9.2	48.5	16
2009-2010	8.5	101.6	31
2010-2011	8.5	67.3	41
Long-term Average	10.5 (4.4)	67.5 (31.7)	19.8 (16.5)

[a] Number of days within season with ≥ 5 cm snow cover at the time of the observation

Table 2.1. Non-breeding season (Oct-Mar) weather summary from Dayton, Ohio, 90 km northwest of 4 private land study sites in southwestern Ohio (NCDC 2011).

access on any of the sites. We distributed log books to hunters and landowners on each site to monitor hunting effort. We asked respondents to record the approximate size of each covey encountered and the number of individuals harvested on each hunt.

METHODS

Field techniques

We captured bobwhites with baited funnel traps (Stoddard 1931) and targeted mist-netting (Wiley et al. *in prep*) during October- March 2008-2011. We attached an aluminum leg band and recorded age, sex, and body mass of each bird (Rosene 1969). We fitted a subsample of individuals weighing >165 g with a 6.6 g (≤ 4% body mass) necklace style radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Transmitters were equipped with an 8 hr mortality sensor. All birds were released at the capture site within 30 min of capture. Trapping, handling, and marking protocols used in this study were reviewed and approved by the Animal Care and Use Committee at Ohio State University (protocol number 2007A0228).

We tracked all radio-marked birds ≥6 days/week by homing and triangulation from short distances (<25 m; White and Garrott 1990). We immediately located the transmitter after detecting a mortality signal and determined the fate of the individual from field signs at the recovery site (Einarsen 1956) and condition of the transmitter. We recorded the cause of mortality as avian, mammalian, or undetermined predation, harvest, investigator-caused (e.g. transmitter entanglement, trap mortality), other (e.g. vehicle collision), weather, or unknown.

Statistical Analyses

We used the known-fates model in Program MARK to estimate temporal and weather-related effects on survival (White and Burnham 1999). The known-fates model uses a binomial model to obtain maximum likelihood estimates of survival for competing models. The maximum likelihood approach allows comparisons of models with different parameters to estimate effects on survival (Murray 2006). We generated encounter histories with daily intervals for all birds that survived a 7-day post-capture exclusion period to control for the short-term acute effects of capture and radio marking (Guthery and Lusk 2004, Holt et al. 2009). We excluded data from the first year of the study in the primary survival analyses because there were few birds radio-marked during 1 October - 9 December. The analyses described hereafter were conducted with individuals radio-marked during 1 October -31 March 2009-2011.

Survival analyses proceeded in 3 stages to identify the best temporal model, test for dependence in survival, and to investigate the influence of weather covariates on survival. We first compared *a priori* models to determine the appropriate temporal scale for seasonal variation in survival rates (i.e. weekly, bi-weekly, monthly, annual). Each model included a constant intercept term and collapsed daily intervals into time intervals.

Temporal models tested for weekly, bi-weekly, monthly and constant variation in survival throughout the season. We also compared 2 models with linear and quadratic trends. Because we had no *a priori* prediction about the influence of year on survival, we added an additive and interaction year term to each candidate model (excluding the null model) to test a total of 17 temporal models. We used the information theoretic approach to compare support for each model, based on Akaike Information Criterion adjusted for small sample sizes (AIC_C; Anderson and Burnham 2002). We considered models with $\Delta AIC_C \leq 2.0$ as having equivalent support (Anderson and Burnham 2002). We added additional parameters to the best fitting temporal model to test for differences in age and gender.

We calculated survival of individuals captured during the first year of the study during 10 December- 31 March with the best fitting temporal model. We also estimated survival for the same interval in each of the 2 full years with a shortened encounter history to compare December-March survival for all 3 years. We extrapolated from the 112 day interval to approximate survival for the entire non-breeding season (October-March 182 day interval) following Sandercock et al. (2008: 972) to compare estimates of non-breeding season survival for all 3 study years.

We used an intercept only, random effects model to estimate process variance with the variance components analysis in Program MARK (Burnham et al. 1987, Gould and Nichols 1998, White et al. 2001). We compared the ratio of sampling variance and process variance for the two years and reported the estimate of process variance. Sampling variance is an estimate of variability in the parameter estimate that includes variation in sampling effort and true, process variation. Process variance removes the sampling variability form the original estimate to provide a more concise estimate of variation in the population parameter.

Overdispersion parameters, or variance inflation factors (c), are used to adjust log-likelihoods and variance estimates to more correctly model overdispersed data (Schmutz et al. 1995, Anderson and Burnham 2002). The general approach for estimating c is to divide the goodness of fit statistic (χ^2) of the model with the most parameters by the degrees of freedom of that model (Anderson and Burnham 2002). However, this approach is sensitive to sample sizes and fails to explicitly consider the cause of overdispersion.

Bootstrapping can be used to estimate c when the source of dependency is known (Bishop et al. 2008). A common example of known sources of dependency is siblings, where ≥ 2 individuals in the survival analysis have the same maternal resources and are exposed to similar environments and mortality sources. The bootstrapping procedure resamples from known groups in the data (e.g. siblings or coveys), rather than by individual encounter histories to generate survival estimates. The estimate of the overdispersion parameter ($\hat{c}$) is then calculated as

$$\hat{c} = SD(\hat{S})^2 / SE(\hat{S})^2$$

where $SD(\hat{S})$ is the standard deviation of bootstrapped survival estimates and $SE(\hat{S})$ is the standard error of the survival estimate from the maximum likelihood analysis (Bishop et al. 2008).

We used the bootstrap procedure in Program MARK to test for dependency in survival among covey members. We generated 10,000 estimates of $\hat{S}$ with the most parsimonious temporal model ($\Delta AIC_c<2$ and fewest parameters). Using the best fitting temporal model removes variability in the data that could be misinterpreted as overdispersed data. The procedure removes individuals associated with randomly selected coveys from the data and estimates $\hat{S}$ for the subset data (Bishop et al. 2008). The total sample size of each data set depends on the number of unique encounter histories (radio-marked individuals) for each covey in the sample. Covey affiliation was specified as an individual covariate in the encounter history. We used the median $\hat{c}$ estimate from the 2 years in the bootstrapping analysis to improve model selection with Quasi-AIC (QAICc; Anderson and Burnham 2002) .

A covey was defined as ≥ 2 individuals that were together for ≥ 7 consecutive days. Although some investigators have reported dynamic covey affiliation among individuals through the non-breeding season (Yoho and Dimmick 1972, Williams et al. 2004b), individuals rarely changed covey affiliations in our study (Chapter 3). When 2 formerly unique coveys combined we identified the resulting group as a unique covey in the analysis. The covey affiliation variable to structure the bootstrap for each individual was the final covey that the individual was associated with before death or censoring.

We developed a candidate model set with time-varying covariates that represented duration and depth of snow cover and temperature to investigate the influence of winter weather on survival. We used data from the last 2 years and included a year effect in each weather model (Anthony and Willis 2009). Snow depth was recorded daily for each site in 6 categories ranging from 0 - ≥ 25 cm. We classified snow depth based on average depth across the site given the horizontal variation in snow cover caused by drifting. Because we did not measure snow depth at specific locations used by bobwhites the categories provided a relative metric to represent the variation in snow depth among days, rather than actual snow depth realized by individuals. We used the mean depth reading from all sites as the snow depth estimate for each day because we did not visit each site everyday throughout the season. Temperature data were obtained from an Ohio Agricultural Research and Development Center research station ~60 km east of the study sites in Piketon, Ohio, USA. The station was near the same latitude and elevation of each study site and had complete records of daily temperatures throughout the study. The snow depth (*SNOW*) and temperature (*TEMP*) values were used to create additional survival covariates. Snow day (*SNDAY*) was a binomial variable for any day when snow depth was ≥ 5 cm. Snow duration (*DURATION*) was a cumulative variable that increased with each consecutive day of snow ≥ 5 cm. Freezing day (*FRZDAY*) was a binomial variable for any day when the mean temperature was ≤ 0˚ C.

We fit each model in Program MARK with the known-fate model using a logit link function. We used the difference between $QAIC_c$ from the best model and all other models ($\Delta QAIC_c$) and Akaike weight (w_i) to determine the relative support for each candidate model. We model-averaged β estimates from all models with $w_i \geq 0.001$ (Anderson and Burnham 2002). The statistical significance of each parameter (β_i) was interpreted from 95% confidence intervals of model-averaged coefficients.

We calculated a cumulative incidence function (CIF) to estimate cause-specific mortality related to hunter harvest to measure the contribution of hunter harvest to annual survival rates (Heisey and Patterson 2006). The cumulative incidence function calculates the relative influence of a specific mortality factor on survival in a population exposed to multiple risk factors (in addition to the factor(s) of interest, i.e. harvest.). The approach uses the staggered entry design of the Kaplan Meier estimator (Pollock et al. 1989b) to generate survival estimates and cause-specific mortality rates that are sensitive to problems of staggered entry (individuals that die early are not available for capture later in the study and differential survival rates through the season with variable sample sizes). The CIF approach also respects the property of "conservation of mortality" raised by the existence of multiple mortality sources (Heisey and Patterson 2006: 1545). We used the *wild1* package in R to calculate the CIF for harvest with the data from all individuals surviving the 7 day exclusion period between the last 2 years of the study (Sargeant 2011).

We tested the relationship between snow depth and body mass of captured birds to further investigate causes of winter mortality. We compared models that included a year effect and a year by snow depth interaction term. We also included capture technique to control for potential differences in body masses of birds captured with baited traps versus targeted netting, and a continuous variable for day within season. We compared the candidate model set using AIC and then interpreted the significance of the terms based on β values and 95% confidence intervals.

RESULTS

We included 311 bobwhites in survival analyses (55 in 2008-2009, 130 in 2009-2010 and 126 in 2010-2011). The sample comprised 75% juveniles with nearly equal representation of males (54%) and females (46%). Five of 311 birds were censored due to investigator-caused mortalities and 27 were censored due to transmitter failure. We included 256 individuals from the last 2 years in the temporal and weather effects analysis. All daily intervals in the analysis had ≥ 3 radiomarked birds and the mean number of radiomarked individuals per daily interval was 31 (range 3-60, SD =11.1).

We identified 73 coveys (15 in 2008-2009, 27 in 2009-2010, and 31 in 2010-2011). Two coveys joined and were identified as a new covey on 2 occasions in 2009-2010 and 4 occasions in 2010-2011. The mean number of radiomarked individuals in each covey was 4.6 (SD = 2.3) and ranged from 1 to 12. The mean number of radio-marked individuals/ covey/ day was 2.3 (SD = 0.8).

The best fitting temporal model included weekly effects and the interaction of week with year (Table 2.2). There was little support for other temporal models, but the high ranking of heterogeneous models (biweekly and monthly models) with the annual interaction term indicated that there was substantial inter and intra-annual variation in survival. Additional covariates for sex and age did not improve model fit and were therefore not included in the final model. There was no significant difference in survival between genders ($\beta_{\text{Female}} = 0.044$, 95% CI = -0.278, 0.367). Adults generally had higher survival than juveniles ($\beta_{\text{Adult}} = 0.286$, 95% CI = -0.093, 0.665) although confidence intervals contained 0. The ratio of the standard error of process variance to observed

Model	AIC_c[b]	ΔAIC_c[b]	w_i[b]	K[b]
Week + Year + Week x Year	1585.479	0.000	0.935	52
BiWeek + Year + BiWeek x Year	1590.822	5.343	0.065	26
Month + Year + Month x Year	1617.168	31.689	0.000	12
Week	1654.372	68.894	0.000	26
Week + Year	1655.735	70.256	0.000	27
BiWeek	1674.825	89.347	0.000	13
BiWeek + Year	1676.236	90.757	0.000	14
Month	1678.458	92.979	0.000	6
Month + Year	1680.189	94.711	0.000	7
T + Year + TT x Year	1680.235	94.757	0.000	6
T + Year + T x Year	1692.596	107.118	0.000	4
TT	1693.162	107.683	0.000	3
TT + Year	1694.938	109.459	0.000	4
Constant	1697.542	112.064	0.000	1
Constant + Year	1698.906	113.428	0.000	2
T	1699.384	113.906	0.000	2
T + Year	1700.785	115.307	0.000	3

[a] Temporal effects modeled as constant through year, linear time trend (T), quadratic time trend (TT), and weekly, bi-weekly, and monthly periods.
[b] AIC_c= Akaike's Information Criterion adjusted for small sample sizes, ΔAIC_c= difference between AIC_c of best fitting and current model, w_i= Akaike's weight, K= number of parameters in model.

Table 2.2. Model selection results for a candidate model set to explain inter and intra-seasonal temporal variation observed in non-breeding season survival of northern bobwhites in southwestern Ohio during 1 October – 31 March 2009-2011.

variance in weekly survival intervals was 1, indicating that the observed variation in survival was not attributable to differential sampling effort across weeks (Burnham et al. 1987). The bootstrapping analysis revealed that there was slight overdispersion in the data due to dependency between covey mates (Table 2.3; $\hat{c}$ =1.54).

Non-breeding season survival was low each year ($\hat{S}_{2009\text{-}2010}$ = 0.055, 95% CI = 0.026, 0.113, $\hat{S}_{2010\text{-}2011}$ = 0.121, 95% CI = 0.069, 0.203). Survival rates during 10

	Maximum Likelihood		Bootstrap		
Year	$\hat{S}$	SE($\hat{S}$)	$\bar{\hat{S}}$	SD($\bar{\hat{S}}$)	$\hat{c}$ [a]
2009-2010	0.055	0.021	0.057	0.028	1.83
2010-2011	0.121	0.034	0.122	0.038	1.25

[a] variance inflation factor; estimated by $SD(\hat{S})^2 / SE(\hat{S})^2$

Table 2.3. Survival estimates from maximum likelihood and bootstrapping procedures in the known-fates model of Program MARK for radio-marked northern bobwhites during the non-breeding season during 1 October -31 March 2009-2011.

December- 31 March varied among years ($\hat{S}_{2008\text{-}2009}$ = 0.449, 95% CI = 0.295, 0.613, $\hat{S}_{2009\text{-}2010}$ = 0.114, 95% CI = 0.059, 0.217, $\hat{S}_{2010\text{-}2011}$ = 0.247, 95% CI = 0.170, 0.345). Estimated non-breeding season survival for the 182 day interval for 2008-2009 was 0.272, following Sandercock et al. (2008: 972). The estimation procedure from the 112 day interval to the entire 182 day interval closely approximated survival from the third year (estimated $\hat{S}_{2010\text{-}2011}$ = 0.103) but underestimated survival for the second year (estimated $\hat{S}_{2009\text{-}2010}$ = 0.029) suggesting that the approach was more accurate in years with higher winter survival, as was the case in the first and last year of this study. Daily survival rates consistently decreased throughout the non-breeding season and lowest survival coincided with periods of snow cover during December-February (Figure 2.1). Fall survival (October- November) was lower than other snow-free periods.

Predation was the primary cause of mortality (78.5%), and avian predators were implicated in a majority of predation events (Table 2.4). Avian predators were also suspected in a majority of mortality cases recorded as unclassified predation, although evidence at the recovery site was deemed insufficient to directly implicate avian predators. We confirmed predation by foxes (red [*Vulpes vulpes*] or gray [*Urocyon*

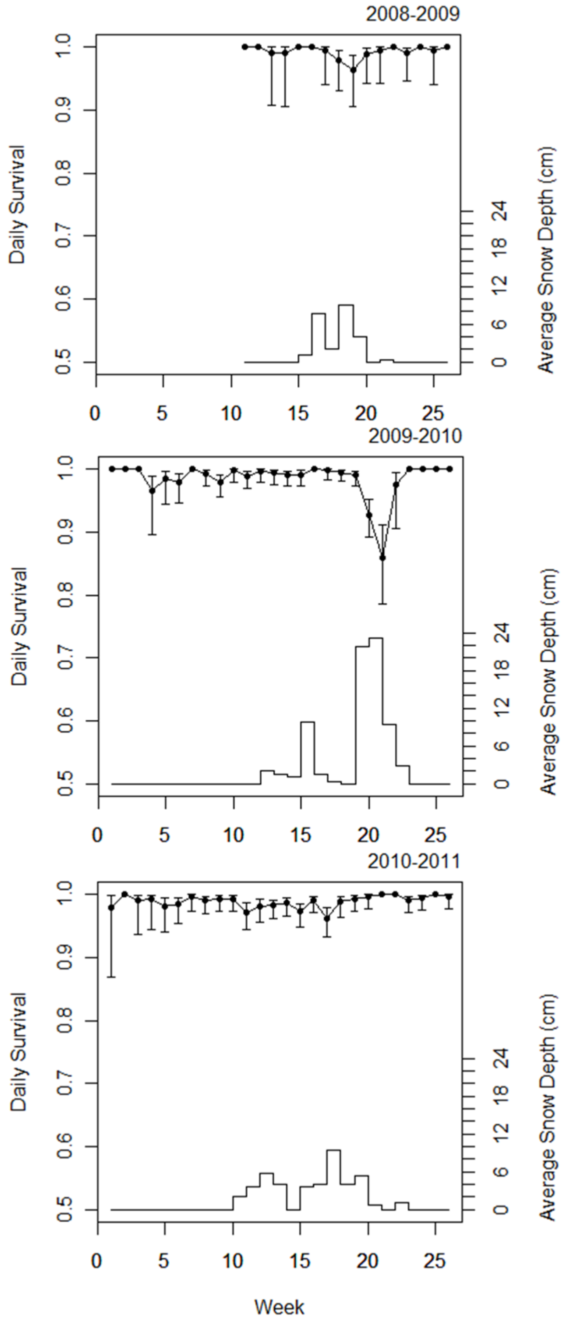

Figure 2.1. Daily survival estimates (Ŝ) and 95% CI for northern bobwhites over weekly intervals of the non-breeding season on 4 private lands sites in southwestern Ohio during 1 October – 31 March 2008-2011. The lower line represents mean snow depth (cm), from a weather station in Dayton, Ohio (90 km northwest of the sites), for each weekly interval (NCDC 2011).

Mortality Cause	%
Harvest	5.4
Investigator[a]	2.7
Other	1.1
Predation	
Avian	23.7
Mammalian	16.1
Unclassified	38.7
Unknown	10.2
Weather	2.2

[a] capture or transmitter related mortality

Table 2.4. Inferred mortality causes from evidence at recovery locations of radiomarked northern bobwhites (*n* = 186) during the non-breeding season in southwestern Ohio 1 October – 31 March 2008-2011.

cinereoargenteus]), mink (*Neovision vision*), feral cats (*Felis catus*), Cooper's (*Accipiter cooperii*) and sharp-shinned (*A. striatus*) hawks. We documented 13 hunting parties on the sites during 2009-2011 with hunter log books and observations in the field. Only 8 (6 in 2009-10, 2 in 2010-11) of 105 radiomarked bobwhites during the season were harvested during the 2 years. The CIF for harvest related mortality was 0.068 (95%CI = 0.012, 0.123).

Winter weather covariates improved the overall fit of candidate survival models over the baseline temporal model (Table 2.5). Snow depth had a negative influence on daily survival rates (model averaged β = -0.134, 95% CI = -0.164,-0.103). Confidence intervals of model averaged β estimates for temperature (β = 0.008) contained 0, indicating that this variable alone had little influence on survival (95% CI = -0.030, 0.047). The best supported model (w_i = 0.860) included snow depth, temperature, and a

Model[a]	QAIC_c[b]	$\Delta\mathrm{QAIC}_c$[b]	w_i[b]	K[b]
Year + SNOW + TEMP + TEMP x SNOW	1026.885	0.000	0.860	5
Year + SNOW	1031.768	4.883	0.075	3
Year + SNOW + TEMP	1033.139	6.254	0.038	4
Year + SNOW + Year x SNOW	1033.763	6.879	0.028	4
Year + DURATION + DURATION^2	1047.530	20.645	0.000	4
Year + SNDAY	1057.501	30.617	0.000	3
Year + SNDAY + FRZDAY	1059.417	32.532	0.000	4
Year + DURATION	1065.763	38.878	0.000	3
Year + DURATION + TEMP + DURATION x TEMP	1065.984	39.100	0.000	5
Year + FRZDAY	1092.313	65.428	0.000	3
Year + TEMP	1094.699	67.814	0.000	3
Year	1104.519	77.635	0.000	2
Year + SNDAY + FRZDAY + SNDAY x FRZDAY	1423.530	396.645	0.000	5

[a] All models included additive effect of the year of the study (Year). SNOW was daily snow depth averaged across all sites, TEMP was the daily regional ambient temperature, DURATION is an additive term for the number of consecutive days with ≥ 5 cm of snow (SNDAY). FRZDAY represents all days with sub-zero temperatures.

[b] QAIC_c= Quasi Akaike's Information Criterion adjusted for small sample sizes, $\Delta\mathrm{QAIC}_c$= difference between QAIC_c of best fitting and current model, w_i= Akaike's weight, K= number of parameters in model.

Table 2.5. Model selection results for a candidate model set examining the relationship between winter weather variables and daily survival rates of non-breeding northern bobwhites in southwestern Ohio during 1 October-31 March 2009-2011.

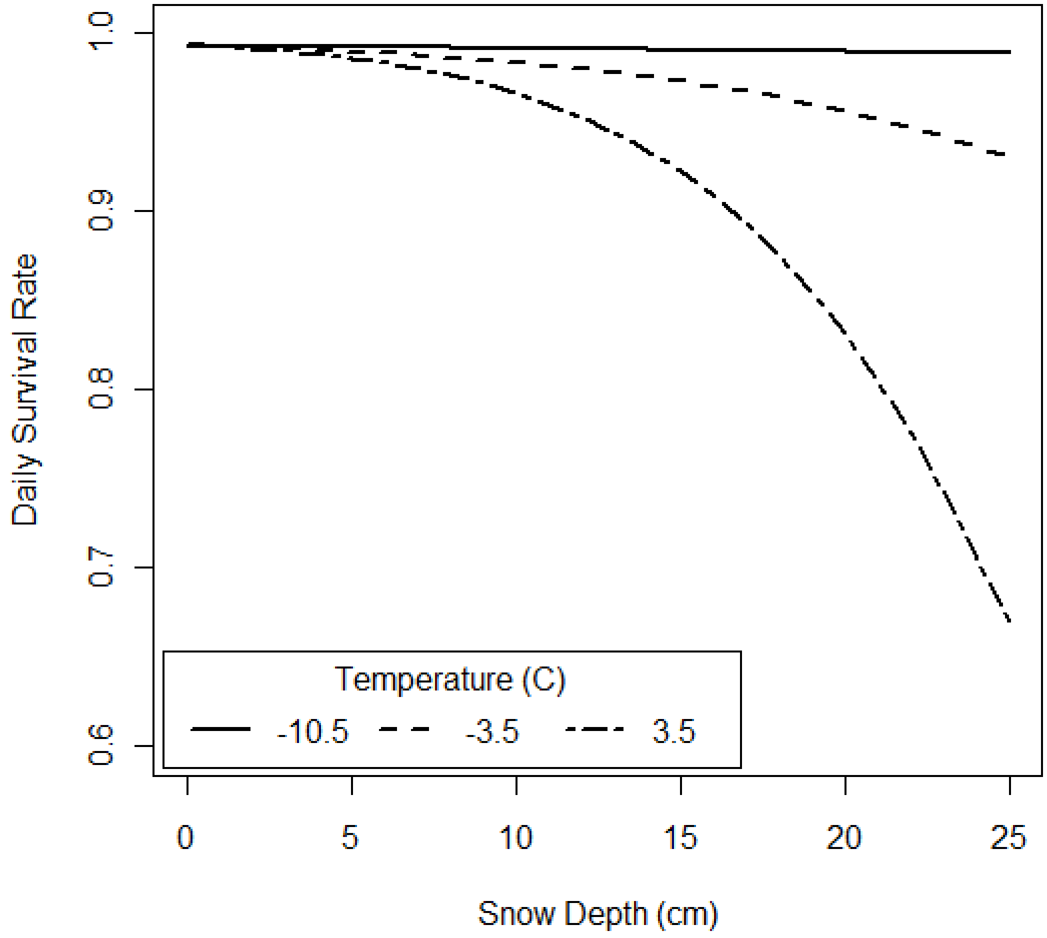

Figure 2.2. Relationship between snow depth, temperature, and daily survival rates for northern bobwhites during the non-breeding season in southwestern Ohio during 1 October- 31 March 2009-2011. Estimates are from the best fitting model with weather covariates that included parameters for temperature, snow depth and their interaction. Temperature lines represent mean (-3.5) and ± 2 SD (3.5) of mean temperature on days with ≥ 5 cm of snow. Data are shown during the first year of the study (2009-2010) when snow depths were most variable (0-30.5 cm).

temperature by snow depth interaction term. The interaction term indicated that daily survival decreased as temperature and snow depth increased (β = -0.011, 95% CI = -0.019,-0.003; Figure 2.2).

The best fitting model (w_i = 0.999) describing time and weather effects on body mass, included a term for snow depth, year, and their interaction (Appendix A). There was no main effect of year on body mass (*P* = 0.723, β = 0.712, 95% CI=-3.217, 4.640). Body mass declined with snow depth (*P* < 0.001, β = -0.525, 95% CI=-0.807, -0.243) but the effect differed between years with the interaction (*P* < 0.001, β = 1.870, 95% CI=1.420, 2.321). We observed a negative relationship between snow depth and body mass in the first year and a positive relationship in the second year (Figure 2.3).

DISCUSSION

The high ranking of the most heterogeneous temporal models with different annual slope terms demonstrated a high degree of inter and intra-seasonal variability in non-breeding season survival of bobwhites in our study. Our estimated survival rates varied among years and were generally lower than previously reported estimates. The 2009-10 estimate was among the lowest reported in the literature (Sandercock et al. 2008). Lohr et al. (2011) conducted a comparable study on a declining population in New Jersey and reported higher non-breeding season survival ($\hat{S}$=0.23) during 2 mild winters (Lohr 2009). The estimate from Lohr et al. (2011) was close to the estimated seasonal survival from the mildest winter in our study (2008-2009). Burger et al. (1995) reported a more intermediate estimate ($\hat{S}$=0.159) from their three-year study in northern Missouri. The estimates from this study were within the range of known-fate survival estimates reported during 1 November -30 April in Oklahoma ($\hat{S}$ range= 0.00-0.385; Cox et al. 2004). Variation in survival rates from the 3 years of this study were consistent with that reported over 11 years by Cox et al. (2004), illustrating the propensity of bobwhite populations to have variable seasonal survival among years.

Cox et al. (2004) also discussed the potential for biased survival estimates caused by radio-transmitters. There is conflicting evidence regarding the influence of radio-transmitters on survival of bobwhites across their range. Guthery and Lusk (2004) conducted a meta-analysis of published survival estimates from telemetry studies and concluded that > 80% of the estimates were biased low (but see Folk et al. 2007a). In contrast, Palmer and Wellendorf (2007) concluded that there was little evidence for a radio-transmitter influence in a large-scale mark-recapture study in Florida. The absence of a chronic effect of transmitters has been further supported with mark recapture studies (Terhune et al. 2007, Sisson et al. 2009) and controlled experiments (Hernandez et al. 2004). Osborne et al. (1997) reported that transmitters may influence metabolic processes. Hernandez et al. (2004) also reported a metabolic influence of transmitters, although the increased energy demands were easily met in their study. However, the influence of transmitters may vary with the energy demands of a population in different habitat types (Terhune 2007) and with natural physiological changes (Roseberry and Klimstra 1971).

Energy demands are higher in northern populations during periods of snow cover and cold temperatures (Guthery 1999, Hiller and Guthery 2004). Increased energy demands and decreased food availability during periods of snow cover may reduce body mass (Robel and Linderman 1966, Roseberry and Klimstra 1971), which would increase the weight of the transmitter relative to body mass. Proportionally larger transmitters have been shown to negatively affect survival in other ground-dwelling gamebirds (Johnson and Berner 1980, Burger et al. 1991) and therefore systematic changes in body mass throughout the season could have biased our inferences on temporal variation in survival. However, our analysis of body mass showed inconsistent responses to snow depth among years, suggesting that body mass is not consistently negatively influenced by snow cover. Therefore inferences from radio-marked birds during periods with snow cover were likely not biased relative to snow-free periods within the season or among years in the study. Despite the potential for a systematic bias in survival caused by transmitters, comparisons among intervals in this study and with previous radiotelemetry studies are still valid.

Mortality during the non-breeding season is largely caused by hunter harvest (Pollock et al. 1989a, Williams et al. 2004b), predation (Errington 1934, Rollins and Carroll 2001), and weather (Roseberry and Klimstra 1984, Robel and Kemp 1997) in northern populations of bobwhite. The contribution of these mortality sources varies through the non-breeding season and is influenced by quality and availability of habitat (i.e. carrying capacity; Errington 1934). Errington and Hamerstrom (1935) identified two primary mortality periods in bobwhite populations. The first coincided with senescence of herbaceous vegetation and harvest of standing crops in fall. The second was coincident with severe winter weather. We observed low survival during both periods in our study.

The first period of low survival (mid-October –November) coincided with crop harvest and hunting season (last 3 weeks of November). The co-incidence of these factors limited our ability to discern the separate influences of each. A high proportion of the study sites were corn and soybeans that were harvested during mid to late fall. Because bobwhites, particularly broods, use crop fields through the summer (M. Liberati unpublished data, Potter et al. 2011), crop harvest causes a rapid loss of usable habitat (Guthery 1997) thereby reducing carrying capacity (Errington 1934). Cause-specific mortality rates for harvest mortality in this study were lower than previously estimates in populations exposed to more hunting pressure (Burger et al. 1995, Cox et al. 2004). Hunting has been identified as a primary factor affecting non-breeding season survival of bobwhites in Missouri (Burger et al. 1995), Oklahoma (Cox et al. 2004) and Florida (Rolland et al. 2010) and likely contributed to lower survival during fall in our study. Collectively, the loss of usable habitat and hunter harvest resulted in low fall survival, although the influence of low fall survival is negligible compared to that observed during periods of snow cover.

Earlier studies provided anecdotal evidence of the influence of winter weather on daily survival (Errington 1936, Leopold 1937) and the relationship between annual snow accumulation and seasonal survival (Roseberry and Klimstra 1984, Robel and Kemp 1997). However, no studies have directly assessed the influence of winter weather on daily survival rates. Our analyses revealed that snow depth was the best predictor of daily survival through the season, rather than temperature variables alone or variables representing duration of snow cover. The relationship between temperature and daily survival was inconsistent with our prediction that the energetically demanding period of high snow and low temperatures (Case and Robel 1974) would result in the lowest survival. Rather, periods with high snow and low temperatures had relatively high daily survival. Contrary to our study, Robel and Kemp (1997) found that the number of days below sub-zero temperatures were the most influential weather parameter in their long-term data set.

Field observations of bobwhites during the winter from this study and others indicate that food availability during periods of prolonged snow coverage influences survival (Errington and Hamerstrom 1936, Roseberry 1964). We documented only 4 cases where the cause of mortality appeared to be a direct physiological effect of weather or snow cover and all other mortalities during periods with snow cover were attributed to predation. Therefore, it appears that the influence of snow cover was not a direct physiological effect of decreased food availability (i.e. starvation) as has been previously reported (e.g. Leopold 1937, Trautman et al. 1939) but rather was more related to increased vulnerability of bobwhites to predation during these periods. We observed cases where radiomarked coveys moved large distances between successive telemetry locations during periods with deep snow. We suspect that these movements were a behavioral response to increased energy demands characteristic of periods with prolonged snow cover and cold temperatures (Case 1973, Case and Robel 1974) and the lack of available food sources. Analyses of movement data from our study revealed that there was a significant positive relationship between temperature and mean daily covey movement rates on days with ≥ 5 cm snow ($F_{1,59} = 4.433$, $P = 0.039$, A. Janke, unpublished data) showing that bobwhites were more active on warm days with snow cover compared to cold days with snow cover.

The tendency for increased movements among bobwhites in search of food during periods of snow cover has been previously reported to influence movements and survival (Errington and Hamerstrom 1936, Roseberry 1964, Roseberry and Klimstra 1984). Although we did not directly assess the influence of habitat on survival during periods of snow cover, it is arguable that individuals using areas woody cover near appropriate food sources made fewer movements and therefore had higher survival than those where woody cover and food were further apart. Therefore, management strategies that focus on providing suitable winter cover near quality food sources may minimize predation during periods of prolonged snow cover and improve non-breeding season survival.

MANAGEMENT IMPLICATIONS

Providing woody cover adjacent to quality food sources is the best strategy to minimize vulnerability of bobwhites to predation during periods of snow cover. Although the severity and timing of severe weather cannot be controlled, efforts that provide appropriate habitat to mitigate predation losses during winter have potential to be most influential on non-breeding season survival (Flanders- Wanner et al. 2004). The importance of survival during periods of severe winter weather may also increase as the frequency of severe winter storm events (i.e. snow accumulation) increases with climate change (Hayhoe et al. 2010). Because of the disproportional influence of non-breeding season survival on population growth rates (Folk et al. 2007b, Sandercock et al. 2008), bobwhite management strategies should focus on improving winter survival in Ohio before focusing on alternative, less influential population vital rates (e.g. nest success, summer survival).

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CHAPTER 3: MOVEMENTS AND COVEY DYNAMICS OF NORTHERN BOBWHITES IN OHIO

ABSTRACT

Understanding species' behavior across their geographic range can provide insight into factors affecting variation in population dynamics. Covey behavior varies among northern bobwhite (*Colinus virginianus*) populations across the eastern US, with potentially important implications for non-breeding season survival. We investigated changes in covey affiliation by banded and radiomarked individuals during 1 October - 31 March 2009-2011 on 4 agricultural study areas in southwestern Ohio. We also examined movement rates of radiomarked coveys and the influence of weather and habitat on point-specific residency time. We documented no cases of banded individuals changing covey affiliations (*n* = 413) and only 1 case of a radiomarked individual (*n* = 307) changing covey affiliations (*n* = 57 coveys). Despite a marked decline in covey size throughout the season, 2 formerly unique coveys combined to form a larger covey on only 6 occasions. Mean minimum daily movement rate was 139.2 m (95% CI =135.2, 143.2) and was greatest during fall covey formation. Temperature was the most influential variable explaining variation in residency time. Residency increased as temperatures decreased (β = -0.0359, 95% CI = -0.0449, -0.0267). Woody edge density was included in the top model but had only marginal effects on residency time (β =

0.00084, 95% CI = 0.0029, 0.0014). The tendency for individuals to remain in the same covey throughout the season rather than to join other coveys to maintain optimal size may represent a population level Allee Effect in our low density population. Such an effect likely contributed to low survival rates previously reported in this population. Management strategies that increase local densities will enhance opportunity for interchange among coveys, which could increase non-breeding season survival.

INTRODUCTION

Northern bobwhites (*Colinus virginianus*; hereafter bobwhite) form tight social groups called coveys during the non-breeding season (Johnsgard 1973). Coveys serve multiple functions related to thermodynamics (Case 1973), foraging efficiency, and predator avoidance and have an important influence on individual survival (Williams et al. 2003). The season that bobwhites are in coveys coincides with the period of highest annual mortality in northern populations of bobwhites (Roseberry and Klimstra 1984), and survival during this period is an important determinant of population growth rates (Folk et al. 2007, Sandercock et al. 2008). Understanding the ecology and behavior of bobwhites during this period is therefore important to inform management strategies that aim to increase non-breeding season survival and population growth rates.

Although much is known about ecology and habitat needs of bobwhites across their range, few contemporary studies have reported on the dynamics of covey affiliation and behavior. Some authors have reported that covey composition (individual affiliation) is dynamic (e.g. Yoho and Dimmick 1972), with individuals moving between groups on a regular basis, while others have reported stable covey affiliations among individuals (e.g.

Robel and Kemp 1997). Understanding covey dynamics and what factors contribute to its variation is important because of the influence of covey size on non-breeding season survival (Williams et al. 2003). Conflicting evidence from different studies across the bobwhite range suggests that local populations may behave differently, perhaps in response to density, habitat conditions, weather, or a combination of these factors.

Movements play an important role in determining covey behavior and interactions among individuals. Coveys establish somewhat territorial home ranges in fall and remain relatively sedentary through the winter (Murphy and Baskett 1952). Although movement rates are comparatively low throughout the non-breeding season, increased movements have been shown to negatively influence non-breeding season survival (Williams et al. 2000, Folk 2006). Understanding behavioral and environmental factors that affect movements could help identify landscapes that facilitate decreased movements.

Recent advances in telemetry have spurred development of analytical techniques to characterize movement behavior of animals (Schick et al. 2008). Although most of these techniques were developed for location data collected at fine temporal scales (i.e. hourly locations), they have potential applications with coarse resolution data as long as the limitations of the procedures are recognized. One such technique is the concept of first passage time (Fauchald and Tveraa 2003). The technique calculates residency time by combining 2 movement observations to approximate the time an individual remained within a certain distance of a given point. By combining 2 observations to characterize movement rates around a point, we can investigate the influence of point-specific environmental factors (i.e. weather and habitat) on residency time (Le Corre et al. 2008).

We investigated covey dynamics and movement behavior of bobwhites in a population near the northern extent of the species' range. We used capture histories and radiotelemetry to investigate changes in covey affiliation by individual bobwhites during the non-breeding season. We also investigated covey movements and factors that affected movement rates using the first passage time technique. Specifically, we compared models with covariates for the influence of habitat composition and weather on residency time. Based on previous research, we predicted that weather, particularly snow depth, and the availability of woody cover would have the greatest influence on movement rates (Roseberry 1964).

STUDY AREA

We captured and radio-marked bobwhites on 4 private land study sites in Highland and Brown Counties in southwestern Ohio. The sites varied in area (400-1200 ha) and mean annual covey densities (0.45 to 1.5 coveys/ km^2). Forested habitat had primarily mature oak (*Quercus* spp.) and hickory (*Carya* spp.) overstories with sparse understory vegetation. Forest cover on the sites varied from 8 to 29%. Grasslands accounted for 9-20% of the sites. Most grass fields were cool season (90%) consisting of either fescue (*Festuca* spp.) monocultures or cool season bunch grasses such as timothy (*Phleum pretense*) and orchard grass (*Dactylis glomerata*). A few (10%) grasslands planted in warm season grasses were predominantly Indian grass (*Sorghastrum nutans*) and big (*Andropogon gerardii*) and little bluestem (*Schizachyrium scoparium*). Goldenrod (*Solidago* spp.) was the most abundant forb in grasslands. The most abundant shrub species along forest edges, fencerows, or drainage ditches were blackberry (*Rubus allegheniensis*), black raspberry (*R. occidentalis*), and multi-flora rose (*Rosa multiflora*).

The long-term (30 year) mean temperature during October- March was 10.5 C and mean annual snow accumulation was 67.5 cm (NCDC 2011). The winters during the study were above or near the long-term mean snow accumulation with 101.6 cm and 67.3 cm in 2009-10 and 2010-11, respectively.

METHODS

We captured bobwhites on each site with baited funnel traps (Stoddard 1931) and targeted mist-netting (Wiley et al. *in prep*) during 1 October – 31 March 2009-2011. We attached an aluminum leg band to each individual and recorded its age, gender, and covey affiliation. A subset of individuals that weighed ≥ 165 g were fitted with a 6.6 g necklace style radiotransmitter (Advanced Telemetry Systems, Isanti, MN USA). Capture, handling, and marking protocols used in this study were reviewed and approved by the Animal Care and Use Committee at Ohio State University (protocol number 2007A0228).

We located each radiomarked individual once daily ≥ 6 times/ week by homing and triangulation from short distances (≤ 20 m; White and Garrott 1990). We determined direction and approximate distance to radiomarked individuals and recorded the location on a Global Positioning System (GPS; Garmin GPS Map 76, Garmin International, Inc. Olathe, KS, USA). Birds were located at various times throughout the day to capture a full range of diurnal activity patterns. After locating each individual we recorded whether all radio-marked individuals in the covey were together or separated by

≥ 30 m. We attempted to maintain a sufficient distance from individuals to avoid regular flushing. We recorded the number of individuals in the covey when a covey was flushed.

We reported the frequency of locations for which radio-marked birds in the covey were separated by ≥ 30 m. We only included days where ≥ 2 radiomarked individuals were in the covey to calculate the frequency of separation. We only included coveys that had ≥2 individuals radiomarked for ≥ 30 days in the analysis to ensure a representative sample of covey behavior. We estimated monthly covey size of each radiomarked covey as the mean of all flush counts in each month. We took the mean size of all coveys to summarize the population-level trends in covey size. Estimates of covey size through the season may have been biased high because coveys where all individuals died are not included in estimates after we stopped following them, and most coveys did not enter the analysis prior to any mortalities occurred.

We approximated the minimum daily movement (MDM) rate of coveys by calculating the Euclidean distance between telemetry locations on successive days where all individuals were together (hereafter covey points). We scaled the distance between the 2 locations by the time that elapsed between them, and excluded locations that were not taken on successive days. We only included coveys that had ≥ 30 covey locations in the analysis. We tested for differences in the MDM rates among months and years with analysis of variance (ANOVA) in R (R Development Core Team 2009). To measure the distance between adjacent coveys, we calculated the centroid of locations for each covey and then measured the Euclidean distance to the nearest covey on the same site. We tested for differences among covey distances by site and year with ANOVA. One covey was excluded from the analysis because it was the only covey present on 1 site during 1 year.

A habitat coverage shapefile was digitized for each study site over high spatial resolution (0.3 m) orthophotographs (OSIP 2008) in ArcGIS (version 9.3, ESRI Redlands, CA, USA). We distinguished 6 cover types; early successional herbaceous, early successional woody, forest, non-habitat, pasture/ hay fields, and row crop fields. The early successional herbaceous category included grass fields enrolled in the Conservation Reserve Program (CRP) or fallow fields. The early successional woody category comprised fencerows and drainage ditches that were ≤ 50 m wide and patches of woody vegetation (>500 m^2) within grass fields. The pasture/ hay category included all fields that were mowed or grazed during the preceding growing season.

We calculated residency time for each covey location using the concept of first passage time (Fauchald and Tveraa 2003). This technique used movement rates of animals to estimate the amount of time the animal stayed within a circular radius (*r*) around a point. We used the mean MDM from all coveys in the study as the *r* value in our analysis and calculated residency time (*q*) for the point on day *i* as:

$$q_i = \frac{r}{MDM_{\ i-1,i}} + \frac{r}{MDM_{\ i,i+1}}$$

A high residency time represents a point where movement rates to and from the point were low, indicating that bobwhites stayed within the area for a long period of time.

We generated 11 habitat and weather covariates to test their influence on residency time (Table 3.1). We also included a covariate for year and a linearly increasing covariate for day within season. We buffered each location with radius = *r*

Variable	Description
Time	
Day	Linear trend from 1 October (1) to 31 March (182)
Year	Year of the study
Weather	
Temp	Mean temperature from 3 day moving average[a]
Snow	Mean snow depth from 3 day moving average[a]
Duration	Number of consecutive days with snow cover >5 cm on location day
SnowDay	Binomial variable for mean snow depth >5 cm
FreezeDay	Binomial variable for mean temperature <0 C
Habitat	
FOR	% Forest within buffer
RCR	% Row crop fields within buffer
ESW	% Early successional woody vegetation (e.g. fencerows, ditches)
ESH	% Early successional herbaceous vegetation (e.g. grasslands)
Edge	Woody edge (forests and ESW) density within buffer (meters/ ha)
Diversity	Shannon diversity index[b] of habitat types within buffer

[a] 3 day moving average for day *i* is *i*-1 through *i*+1

[b] sum of p_i*ln(p_i) for each, where p_i is the proportion habitat *i* within the buffer

Table 3.1. Covariates used in *a priori* models to explain variation in residency time of non-breeding northern bobwhites in southwestern Ohio during 1 October – 31 March 2009-2011.

and intersected each buffer with the habitat coverage shapefile. We calculated the percent of the 6 habitat categories in each buffer and used the Shannon Diversity Index to represent the diversity of habitat types within each buffer. We also calculated the density of woody edge within each buffer by intersecting the buffer with a line feature with edges of early successional woody and forest habitat patches.

We calculated weather variables for each point by averaging observations from the three days over which residency time was calculated (*i*-1 to *i*+1). We recorded the mean snow depth on the sites in 6 categories ranging from 0 - ≥ 25 cm. Because we did not measure snow depth at specific locations used by bobwhites the categories provided a relative metric to represent the variation in snow depth among days, rather than actual snow depth realized by individuals. We used the mean depth from all sites as the snow depth estimate for each day because we did not visit each site everyday throughout the season. We created a binomial variable to represent the presence or absence of snow > 5 cm deep (snow days) and a continuous variable for the number of consecutive days before the location day with > 5 cm snow cover (duration). Daily temperatures were recorded at an Ohio Agricultural Research and Development Center research station ~60 km east of the study sites in Piketon, Ohio, USA. The station was near the same latitude and elevation of each study site and had complete records of daily temperatures throughout the study. We created a binomial variable for points recorded on days with mean temperatures above and below freezing (freezing days).

We constructed 37 *a priori* models with various combinations and interactions of weather and habitat variables hypothesized to influence movement rates. We tested for correlations among independent variables and did not include variables with correlations > 0.6 in the same model. Residency time was right-skewed so we log-transformed the variable. We used Akaike's Information Criteria corrected for small sample sizes (AICc) to compare the fit of each model and used model averaging to estimate coefficients for the most important variables. We considered all models with ΔAICc ≤ 2.0 as having equivalent support and included estimates from all models with $w_i > 0.001$ to calculate model averaged parameter coefficients (Anderson and Burnham 2002).

RESULTS

We captured and leg-banded 413 unique individuals from 57 coveys during 2009-10 ($n = 211$) and 2010-11 ($n = 202$). We recaptured 142 banded individuals and documented 0 cases where individuals changed covey affiliation. We radiomarked 307 individuals and recorded 1 instance where a radio-marked individual changed covey affiliation. That individual joined a second covey for 14 days then returned to its former covey. One radiomarked bobwhite that was thought to be the only remaining individual in its covey joined a nearby covey on 1 occasion. We observed 6 instances where 2 formerly unique coveys merged to form a single covey. Two combinations occurred in early fall whereas the other 4 covey combinations occurred during January-February.

Forty-six of 57 coveys (81%) had ≥ 2 radiomarked individuals for ≥ 30 days ($\bar{x} = 81$ days, SE = 5.2) and were used to estimate the frequency that covey members were together. All radiomarked birds were within 30 m of each other on 95.1% of daily locations ($n = 3751$; 95% CI = 93.6, 96.5). Mean distance between radiomarked individuals when coveys were split was 177.4 m (95% CI = 160.0, 194.7 m). The mean number of flush counts/ covey/ month was 4.2 (SE = 0.9). Mean October covey size was 11.9 individuals and decreased throughout the season in both years (Figure 3.1).

There were 48 coveys with ≥ 30 covey locations ($\bar{x} = 86$ SE = 5.3) included in the movement analysis. The mean MDM rate was 139.2 m (95% CI = 135.2, 143.2). Movement rates differed among months ($F_{5,\,3749} = 35.584$, $P < 0.001$) but not years ($F_{1,\,3753} = 0.700$, $P = 0.409$). Movements were greatest during fall (October- November) and decreased through the winter (Figure 3.2). The mean distance from the centroid of one

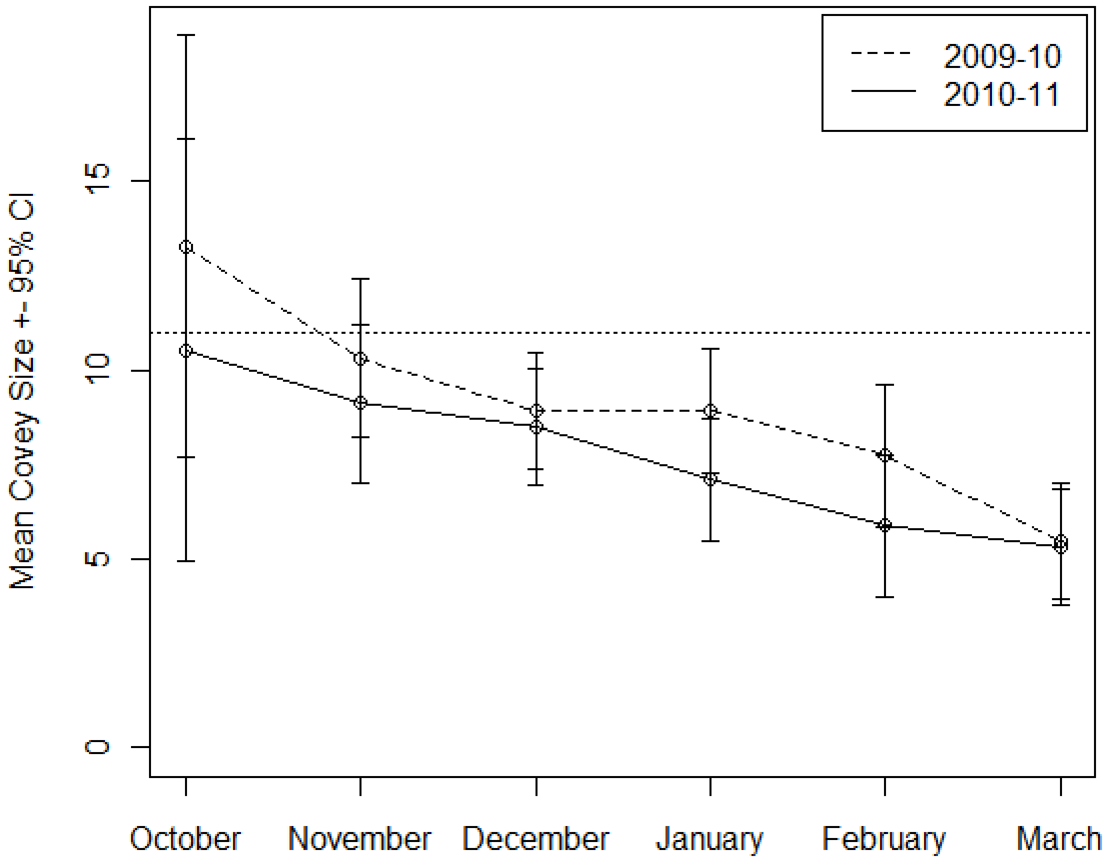

Figure 3.1. Mean monthly covey size and 95% confidence intervals for 57 radiomarked coveys on 4 private land sites in southwestern Ohio during 1 October – 31 March 2009-2011. The dashed horizontal line represents optimal covey size (*n* = 11) identified by Williams et al. (2003).

covey to the centroid of the nearest covey was 787.0 m (95% CI = 661.4, 912.5 m) and differed among sites ($F_{3,\ 43} = 8.0$, $P < 0.001$) but not years ($F_{1,\ 45} = 0.2$, $P = 0.691$).

The total area buffered around each point for the residency time analysis was 6.1 ha. Mean residency time at a point was 7.2 days (95% CI = 6.8, 7.7). The best fitting model predicting log-residency time had additive effects of woody edge density, temperature, and snow depth (Table 3.2; Appendix B). Woody edge density (model

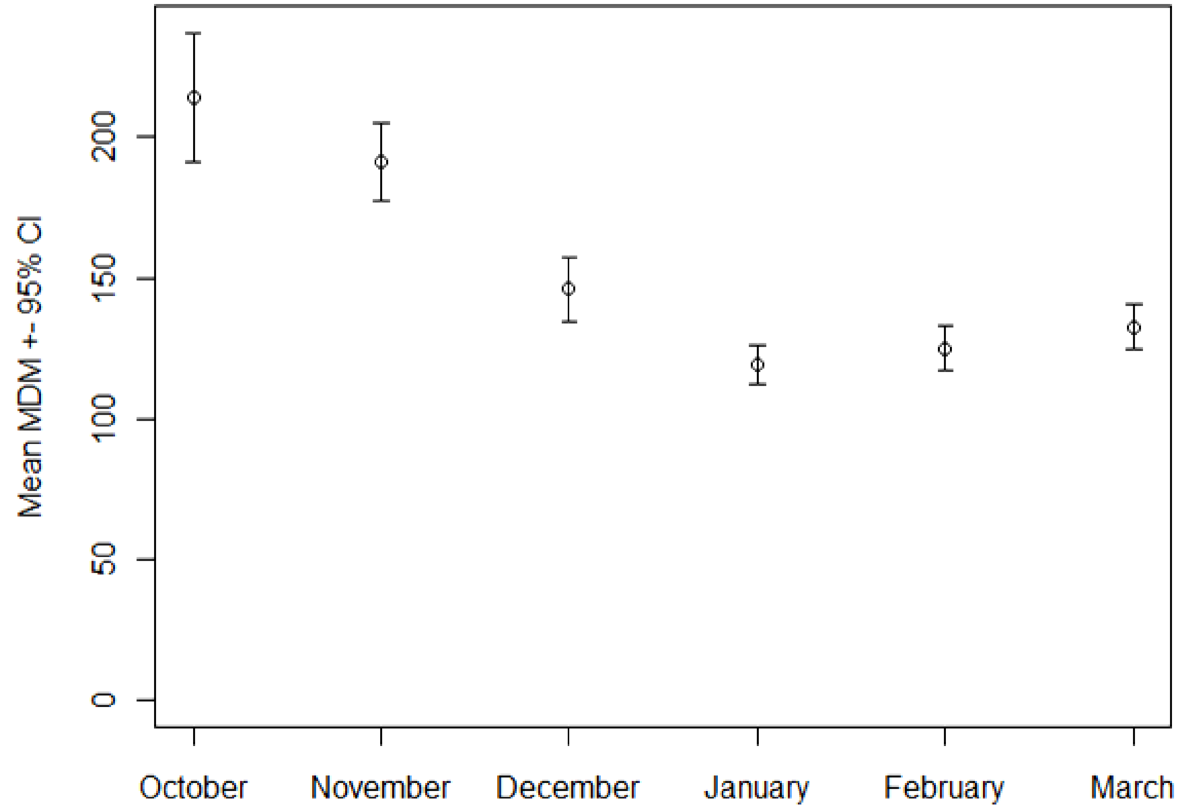

Figure 3.2. Mean monthly minimum daily movement rates (MDM) of northern bobwhite coveys ($n = 48$) in southwestern Ohio during 1 October – 31 March 2009-2011.

averaged $\beta = 0.0009$, % CI = 0.0029, 0.0014; Figure 3.3) and temperature (model averaged $\beta = -0.0358$, 95% CI = -0.0449, -0.0267; Figure 3.3) had significant ($P < 0.001$) effects in the top 3 models ($\Delta AIC_c < 2.0$). Models with temperature ranked highest among all other models. Snow and temperature by woody edge interaction terms in the top models were not significant ($P = 0.065$, $P = 0.072$, respectively) and had little influence on residency time (*Snow* model averaged $\beta = 0.0077$, 95% , CI = -0.0009, 0.0163, *Edge* interaction $\beta = 0.0001$, 95% CI = -0.0000, 0.0002).

Model [a]	k^b	AIC_C^b	ΔAIC_C^b	w_i^b
Edge + *Temp* + *Snow*	4	9414.674	0.000	0.361
Edge + *Temp* + *Edge* x *Temp*	4	9414.841	0.167	0.332
Edge + *Temp*	3	9415.711	1.037	0.215
Day + *ESH* + *ESH* x *Day*	4	9418.289	3.615	0.059
ESW + *Temp* + *Snow*	4	9421.120	6.446	0.014
ESW + *Temp*	3	9422.748	8.073	0.006
Snow + *Temp*	3	9423.327	8.653	0.005
Temp	2	9424.717	10.043	0.002
ESW + *Temp* + *ESW* x *Temp*	4	9424.807	10.132	0.002
Snow + *Temp* + *Snow* x *Temp*	4	9425.613	10.938	0.002

[a] *Edge* = woody edge density (m/ ha); *Temp* = average daily temperature (C); *Snow* = average snow depth (cm); *ESH*= % early successional herbaceous vegetation; *ESW*= % early successional woody vegetation

[b] k= number of parameters; AIC_c= AIC corrected for small sample sizes; ΔAIC_c= Difference between AIC_c for best model and model i; w_i=Akaike weight

Table 3.2. Highest ranked models ($w_i > 0.001$) from a 37 *a priori* model candidate set tested to explain variation in residency time of non-breeding northern bobwhites in southwestern Ohio during 1 October - 31 March 2009-2011.

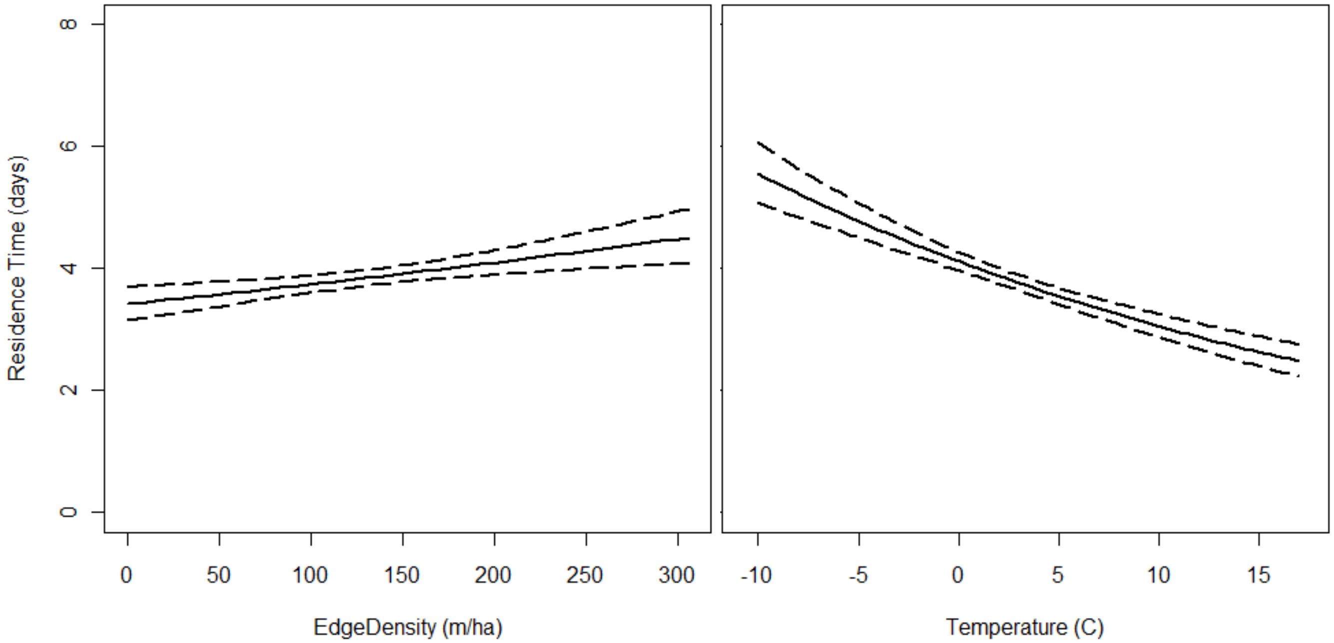

Figure 3.3. Influence of woody edge density (m/ ha) and temperature (C) on residency time of northern bobwhites on private land in southwestern Ohio during 1 October- 31 March 2009-2010. High residency time represents low movement rates. Relationship plotted from the best fitting model (Edge + Temp + Snow) with all other covariates held at their mean.

DISCUSSION

Covey dynamics and movements play a potentially important role in management of bobwhite populations but are often overlooked (Williams et al. 2004a, Williams et al. 2004b, Hardin et al. 2005). Despite the tendency for covey sizes to decline during the non-breeding season, we documented few cases where individuals changed covey affiliations or 2 formerly unique coveys merged. The lack of changes in covey affiliation may have important implications for non-breeding season survival (Williams et al. 2003) and help explain low observed survival rates previously reported for this population (Chapter 2).

Our observation of strong covey affiliations and few individuals changing coveys was consistent with previous studies in Missouri (Murphy and Baskett 1952, Janvrin et al. 1991) and Kansas (Robel and Kemp 1997). However, Williams et al. (2004b) and Yoho and Dimmick (1972) reported frequent interchange of individuals between coveys in their studies. Switching of individuals among coveys therefore seems to vary on a region or site-by-site basis. The specific mechanisms driving the different behaviors of individuals across sites are unclear but may relate to covey densities or the nature of the habitat occupied by different bobwhite populations (Ellis et al. 1969, Yoho and Dimmick 1972). These factors also likely affect the tendency for coveys to join to form larger coveys, which has been documented across the range (Stoddard 1931, Errington and Hamerstrom 1936, Roseberry and Klimstra 1984, Williams et al. 2004b).

Changes in covey affiliation by individuals through intergroup movements and joining of adjacent coveys increases individual survival and group persistence by maintaining optimal size for foraging efficiency, thermoregulation, and predator avoidance (Williams et al. 2003). Additionally, individual movement from coveys occupying poor habitat to coveys occupying good habitat may enhance individual survival (Roseberry and Klimstra 1984). If individual bobwhites were distributed among coveys in an ideal-free manner (*sensu* Fretwell and Lucas 1970) we would predict that individuals would change covey affiliations throughout the season to maintain optimal group size and occupy the best habitat. However, it appears that changes in covey affiliation depend on interactions among adjacent coveys (Yoho and Dimmick 1972) and that density may limit the ability of individuals to distribute in an ideal free manner throughout the non-breeding season.

Our study was conducted on relatively large study areas, 3 of which had low covey densities (0.45 – 0.72 coveys/ km^2). Three of the 4 winter covey combinations occurred on the site with the highest covey densities (1.5 coveys/ km^2) and lowest mean distance between covey centroids (536 m). The other winter combination occurred on 1 of the few areas where covey ranges overlapped on the lower density sites. As shown by the high inter-covey distances relative to mean MDM, coveys were generally not in close contact in our study. Therefore individuals may have not had the opportunity to change affiliation or combine. Covey distribution is primarily influenced by distribution and availability of suitable habitat across a landscape (Ellis et al. 1969). On sites with more suitable habitat, we would expect higher covey densities and more interaction among coveys, which could afford more opportunities for interchange. Allee effects, where individual fitness decreases in response to low population size or density (Stephens et al.

1999), may play an important role in bobwhite survival during the non-breeding season at a population level. Coveys in low density and fragmented populations may not maintain optimal group size because of decreased interactions with adjacent coveys, thereby reducing the ability of the population to sustain high mortality within seasons (Guthery et al. 2000).

Increased movement rates could potentially compensate for lower densities, if individuals in lower density populations could move to interact with adjacent individuals. However, our estimate of MDM rate (139 m/ day) was lower than previous estimates of covey movements from radiotelemetry studies in New Jersey (160 m/ day, Lohr et al. 2011) and Kansas (195-227 m/ day, Madison et al. 2000; 228-275 m/ day Williams et al. 2000). The importance of low movement rates in this population is unclear, particularly given that home range estimates were relatively large (26 ha; Chapter 4). Additionally, lower movement rates generally coincide with increased survival (Williams et al. 2000, Folk 2006) whereas survival in our study was low (Chapter 2).

There were consistent temporal trends in movement rates across the 2 years of the study. Movements were high in fall and decreased through winter. High movement rates in the fall coincided with the fall shuffle; the period when individuals form coveys and establish winter ranges (Rosene 1969). The specific mechanisms of covey formation and winter range establishment in bobwhites are generally unknown. Covey calling and increased movements are thought to allow contact with adjacent coveys as they establish range boundaries (Stokes 1967, Urban 1972). The period of highest movement documented in this study also coincided with the period of highest calling activity on the sites (A. Janke unpublished data) indicating that covey formation was likely ongoing throughout October. Movement then decreased as the non-breeding season progressed and covey home ranges were established. This too is consistent with other studies that investigated temporal variation in movements through fall and winter (Murphy and Baskett 1952).

Although natural temporal variation in movements likely plays an important role in residency time of coveys during the non-breeding season, we postulated that habitat and weather would also play an important role, and that weather variables would be the most important determinants of residency time. Models with weather variables ranked high among candidate models but the only variable with a significant effect on residency time was mean daily temperature. Because temperatures varied widely from fall to winter, temperature in this model may reflect seasonal changes in movement rates that occurred throughout the season, rather than a direct influence of temperature on movements. Snow depth was included in the top model, but had only a slight effect and the parameter confidence interval contained 0. This was inconsistent with our original hypothesis that movements would decrease during periods of snow cover. Although bobwhites tend to move less in short term responses to snow cover (Roseberry 1964), substantial movements during periods of snow cover have been reported (Roseberry and Klimstra 1984, Errington and Hamerstrom 1936) and were observed during this study (A. Janke personal observation). Such movements, apparently in search of more suitable food or cover, may have diminished the influence of snow cover on movements detected in the analysis. Increased or even average movement rates during periods of snow cover also explain the low survival observed during these periods (Chapter 2), as it could increase susceptibility to predation or energy metabolism during an energetically demanding period (Roseberry 1964, Swanson and Weinacht 1997, Guthery 1999).

In Chapter 4, we showed that bobwhites selected early successional woody vegetation within home ranges. As a result, we predicted that the abundance of woody cover around a point would influence residency time. The high ranking of woody edge density showed the potential importance of this cover type to movement rates, but effect sizes were marginal. One potential explanation for our failure to detect an influence of habitat composition on residency time is our choice of buffer radius. The radius should represent the scale at which bobwhites perceived the landscape and our radius may have overestimated the scale (Barraquand and Benhamou 2008, Le Corre et al. 2008). Another potential explanation for the minimal influence of habitat on residence time is that bobwhites may not decrease movements in suitable habitats within home ranges (Anderson et al. 2008). Rather they may use suitable areas within their home range uniformly. This pattern of space use would still result in preference for the habitat types shown in Chapter 4, but also explain why we failed to detect significant relationships between movements and habitat use. Systematic movements between areas of suitable cover within the home range, as opposed to higher residency times in such areas, could serve to decrease bobwhite predictability by predators in specific locations within home ranges (Anderson et al. 2008).

MANAGEMENT IMPLICATIONS

That individuals and coveys maintained stable covey affiliations throughout the non-breeding season despite the tendency for sub-optimal group sizes (Williams et al. 2003) could have important implications for survival and population growth rates. It appears that covey combinations are more likely to occur on sites with higher covey densities. Therefore, management strategies that focus on attaining high local densities of bobwhites may be more advantageous than more widely dispersed efforts that create small, isolated populations. Such a landscape approach has been previously recommended in the light of potential Allee effects in bobwhite populations (Williams et al. 2004a) and may be worthy of further investigation and experimentation.

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CHAPTER 4: HOME RANGE AND HABITAT SELECTION OF NORTHERN BOBWHITE COVEYS IN AN AGRICULTURAL LANDSCAPE

ABSTRACT

Although changes in agricultural practices are the primary factor implicated in long-term population declines of northern bobwhites (*Colinus virginianus*), agricultural landscapes offer the only opportunity to improve bobwhite populations throughout the Midwest. Because of the influence of non-breeding season survival on bobwhite population growth rates, understanding habitat needs of bobwhites in agricultural landscapes during the non-breeding season is important for conservation efforts that aim to slow population declines. We used compositional analysis to investigate hierarchical habitat selection by radiomarked coveys on 4 private land study areas in southwestern Ohio. Mean covey home range size was 26.1 ± 2.2 ha (*n* = 48). Early successional woody vegetation (e.g. fencerows and ditches) was the most important habitat type at all scales. Home ranges were established in areas with more grassland cover, but selection for grassland cover decreased at the third order scale. Grassland selection also varied among sites and was strongest on sites with more row crop cover. Scale and site-dependent selection suggested a diminishing return of increasing grassland cover in agricultural landscapes. Forest habitat was avoided at the second order scale, but selected within home ranges. Management strategies aimed at increasing availability of non-

breeding season habitat on agricultural lands in Ohio should focus on providing early successional woody cover adjacent to food sources, such as row crop or grass fields.

INTRODUCTION

Changes in crop production practices since the mid 1900's have altered the distribution and availability farmland wildlife habitat in North America (Matson et al. 1997, Peterjohn 2003). Changes in the Midwest were characterized by conversion of small diverse crop fields into large monocultures (Warner 1994), elimination of fencerows (Demers et al. 1995), and unchecked forest succession (Trani et al. 2001). Collectively, these factors have fragmented or eliminated suitable habitat for northern bobwhites (*Colinus virginianus*; hereafter bobwhites) across a considerable portion of the Midwest (Roseberry et al. 1979, Klimstra 1982), contributing to range-wide population declines over the last century (Brennan 1991). Urbanization and forest succession have also played important roles in changing the distribution of bobwhite habitat throughout the Midwest (Veech 2006). Unlike agricultural landscapes however, urbanization and increased forest cover generally causes extirpation of bobwhite populations (Veech 2006). Bobwhites have traditionally been dependent on agricultural landscapes in the Midwest (Leopold 1931) and managing habitat in such landscapes is the only viable strategy for restoring bobwhite populations across the Midwest (Chapman et al. 2011).

Management strategies aimed at reversing population declines should focus on demographic parameters that most strongly influence population growth rates (Bradbury et al. 2001). Survival is generally an important vital rate in declining populations (Meats 1971) and demographic analyses of bobwhites have supported this relationship (Folk et al. 2007, Sandercock et al. 2008). Specifically, non-breeding season survival is the most influential vital rate of bobwhite populations (Sandercock et al. 2008) and is particularly important in northern latitudes where severe winter weather negatively influences survival (Guthery et al. 2000, Folk et al. 2007, Chapter 2). As such, conservation efforts that focus on improving non-breeding season survival should be most effective in reversing bobwhite population declines.

Conservation efforts in agricultural landscapes such as the Conservation Reserve Program (CRP) generally focus on planting entire fields to grassland habitat. Although favorable bobwhite demographic responses to grassland cover have been documented during the breeding season (Best et al. 1997, Riffell et al. 2008, Collins et al. 2009), such efforts have largely been ineffective in stemming the long-term bobwhite decline (Ryan et al. 1998), which suggests that increasing grassland cover alone is inefficient at improving population growth rates. The lack of a significant population response may relate to inability of current conservation efforts to increase suitable cover during the most limiting time of the year (Guthery 1997). In bobwhite populations near the northern periphery of their range the most habitat-limited period is during the non-breeding season, following the senescence of herbaceous vegetation and diminished quality of cover resulting from snow accumulation (Leopold 1931, Roseberry and Klimstra 1984). Habitat selection studies can be useful in identifying important cover types on which to focus conservation efforts during such habitat-limited periods.

We investigated habitat selection by bobwhite coveys in Ohio to understand the hierarchical factors affecting habitat suitability in agricultural landscapes (Orians and

Wittenberger 1991, McClean et al. 1998). Because of the differences in demographics and habitat use on managed and unmanaged sites (Hughes et al. 2005, Potter et al. 2011), we focused exclusively on privately owned, unmanaged land in the core of the current distribution of bobwhites in Ohio. We compared selection at Johnson's (1980) second and third order scales, defining third order use 2 ways (Porter and Church 1987). This approach allowed us to identify habitat factors that influenced home range establishment, positioning of core use areas within home ranges, and specific habitat types used. We also compared selection among 4 study sites that differed in habitat composition, which allowed us to elucidate factors that affected resource selection under different levels of habitat availability.

STUDY AREA

We worked on 4 private land sites in Highland and Brown counties in southwestern Ohio, USA. The counties were in the glaciated till plains physiographic region (Ohio Division of Geologic Survey 1998) and were located in a region that supported the highest densities of bobwhites in Ohio (Spinola and Gates 2008). Long-term (30 year) mean temperature in the region was 1.7 C during November-March (NCDC 2011). Mean annual snow accumulation for the same period was 57.9 cm (NCDC 2011).

Study sites were selected to represent a range of landscapes where bobwhites occur on unmanaged agricultural land in the region. The size of the 4 sites varied from 400 to 1200 ha. Sites were distributed across a landscape gradient from forested (20-50% forested within 10 km) to agricultural (39-72% cropland and pasture within 10 km). Site-

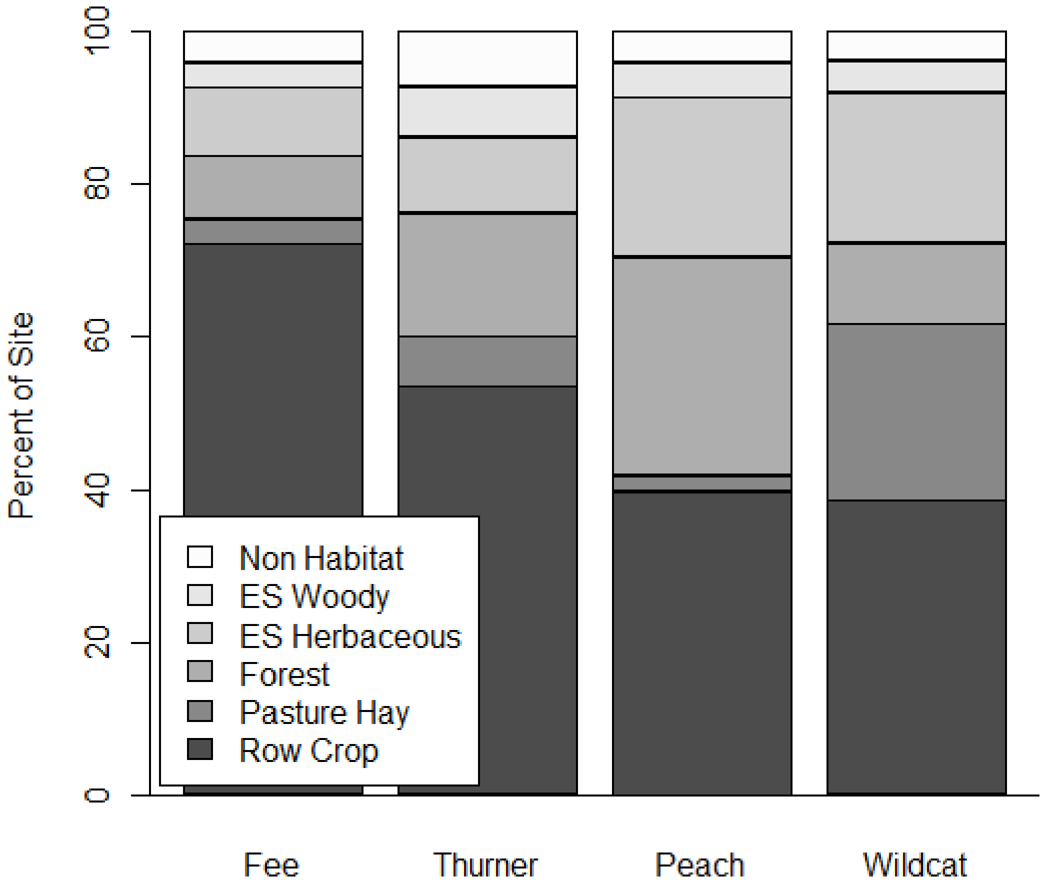

Figure 4.1. Habitat composition of four study sites where bobwhite coveys were captured and radiomarked in southwestern Ohio, USA during 1 November- 31March 2009-2011. Early successional (ES) herbaceous category primarily included grasslands. Early successional woody cover was primarily fencerows and drainage ditches with a dominant understory shrub layer. Non-habitat included water, residential areas, and roads.

specific habitat compositions were distributed along a similar gradient; forest cover ranged from 8 to 29%, agricultural cover ranged from 41 to 75%, and grassland cover ranged from 9 to 20% (Figure 4.1).

Most grasslands were whole fields enrolled in the CRP and were planted to either warm (10%) or cool season grasses (90%). Warm season grass fields were predominately Indian grass (*Sorghastrum nutans*), big (*Andropogon gerardii*), and little bluestem (*Schizachyrium scoparium*) with few forbs, primarily partridge pea (*Chamaecrista fasciculata*). Cool season grass fields were dominated by fescue (*Festuca* spp.) and bluegrass (*Poa* spp.) with abundant goldenrod (*Solidago* spp.) and Queen Anne's lace (*Daucus carota*). Some fields classified as cool season grasses were predominately bunch grasses, such as timothy (*Phleum pratense*), orchard grass (*Dactylis glomerata*) and broomsedge (*Andropogon virginicus*). These fields provided more structure and forb diversity than sod-forming grass fields. Early successional woody vegetation was generally found in linear habitat features such as fencerows and drainage ditches. Dominant woody cover was blackberry (*Rubus allegheniensis*), black raspberry (*R. occidentalis*), and multi-flora rose (*Rosa multiflora*). Upland forests were mostly mature oaks (*Quercus* spp.) and hickories (*Carya* spp.) with little understory vegetation. Bottomland forests were dominated by green ash (*Fraxinus pennsylvanica*), elms (*Ulmus* spp.), and black walnut (*Juglans nigra*). Row crop fields were predominantly corn (35%) or soybeans (61%), but also included some tobacco (1%) and winter wheat fields (2%). No-till practices were used on 97% of row crop fields.

METHODS

We studied habitat use of bobwhite coveys during 1 November-31 March 2009-2011. October is generally included in the non-breeding season for bobwhites but we excluded October from analyses because covey formation was ongoing and home ranges were not yet established. Additionally, unharvested crops provided an abundant cover type that was generally not available after crop harvest in October. Because individual covey affiliation was strong during this study (Chapter 3) habitat use patterns of individual radiomarked bobwhites were not independent among covey members. Consequently, we used coveys as the sampling unit in all analyses. We defined a covey as ≥ 2 individuals that were located together for ≥ 7 days. When 2 unique coveys joined to form a larger covey and were together for ≥ 7 days, we classified the larger covey as a new unique covey (Williams et al. 2003).

We used covey call surveys (Demaso et al. 1992) and systematic searches to identify all coveys within the boundaries of each site. Covey call surveys were conducted with trained observers listening for calling coveys at randomly selected points from 45 minutes before sunrise to sunrise, during October and November (Demaso et al. 1992). Systematic searches with pointing dogs were subsequently conducted throughout the season on each site and targeted areas where calling coveys were heard (Kellogg et al. 1982, Gutzwiller 1990). We also searched the sites throughout the season to locate remaining coveys, especially during periods of snow cover when bobwhite tracks could be detected in the snow.

We focused capture efforts in areas known to be occupied by coveys. Baited funnel traps (Stoddard 1931) and targeted mist netting (Wiley et al. *in prep*) were used to capture bobwhites and to maintain ≥ 2 radiomarked individuals/ covey. We fitted a 6.6 g necklace style radiotransmitter (Advanced Telemetry Systems, Isanti, MN USA) to individuals weighing ≥ 165 g (<4% body mass). Capture, handling, and marking protocols used in this study were reviewed and approved by the Animal Care and Use Committee at Ohio State University (protocol number 2007A0228).

We located each radiomarked individual once daily ≥ 6 times/ week by homing and triangulation from short distances (≤ 20 m; White and Garrott 1990). We located coveys at different times on subsequent days to capture a range of diurnal activity patterns. We approximated the distance and direction of the radiomarked individuals and recorded the location on a Global Positioning System (GPS; Garmin GPS Map 76, Garmin International, Inc. Olathe, KS, USA). The habitat in which individuals were located was assigned to 1 of 21 habitat classification codes. We attempted to maintain a sufficient distance from individuals to avoid regular flushing. We recorded whether all radiomarked individuals in the covey were together or separated at each location. We termed locations where all radiomarked individuals in the covey were together covey locations and excluded all other points from the final analyses. All individuals were together on > 95% of all daily locations (Chapter 3).

We evaluated the accuracy of tracking and field habitat classification protocols by comparing point estimates from known transmitter locations with multiple observers and in different habitat types (Chapter 1). The tracking points were within 12.9 m (95% CI = 12.6, 13.3 m) of the true transmitter location and habitat classification was 94% accurate and did not differ among observers or by habitat type. Therefore we treated the location data as error free in subsequent analyses.

Study area boundaries were defined as the area that was thoroughly searched each year and therefore varied slightly among years. We digitized habitat composition of each site for each year in ArcGIS (version 9.3, ESRI Redlands, CA, USA) over high spatial resolution (0.305 m) orthophotographs (Ohio Statewide Imagery Program 2008). We identified 13 habitat types in the baseline coverage and collapsed those categories into 6 more general categories; early successional herbaceous vegetation, early successional woody vegetation, forest, pasture and hay fields, row crop fields, and non-habitat. Early successional herbaceous vegetation was predominately grass fields enrolled in the CRP or old fields that were dominated by grasses and forbs. Early successional woody vegetation included fencerows, ditches, and portions of CRP or old-fields that were dominated by woody shrubs (patch size ≥ 500 m^2). Grasslands with sparse trees or shrubs (generally Eastern red cedar [*Juniperus virginiana*] or autumn olive [*Elaeagnus umbellata*]) were not classified as early successional woody. Riparian areas < 50 m wide generally had dense understory vegetation and were classified as early successional woody vegetation. Habitat patches with mature overstory trees and > 50 m wide were classified as forests. Pasture and hay fields were defined as any grass field that was mowed or grazed during the preceding growing season. In some cases this included fields enrolled in the CRP that were annually mowed. Non-habitat included all residential and commercial properties, cemeteries, roads, roadside ditches, and water.

We used a fixed kernel density estimator to calculate covey home ranges (Worton 1989, White and Garrott 1990). Kernel home ranges are a nonparametric probabilistic estimate of home range based on the distribution and concentration of locations. The probabilistic nature of the estimator makes it more appropriate for estimating home range than data-driven estimates such as minimum or local convex hull estimators (Lichti and Swihart 2011). Although their use is widespread, estimation of home ranges with kernel techniques have some shortcomings that mostly arise from selecting a smoothing parameter or bandwidth (Gitzen et al. 2006, Downs and Horner 2008). To identify the best bandwidth for our study we qualitatively compared home range estimates from coveys with different point patterns (e.g. clumped vs. evenly dispersed) using 3 bandwidth estimators; least squares cross validation (LSCV; Seaman and Powell 1996), reference bandwidth (Worton 1989), and likelihood cross validation (LCV; Horne and Garton 2006). The LCV procedure fit the data the best across point patterns and sample sizes.

We used the LCV procedure in the Animal Space Use software (Version 1.3 Horne and Garrot 2009) to calculate the bandwidth for each covey with ≥ 30 locations (Seaman et al. 1999). We then estimated home ranges (95% Utilization distribution [UD]) and core use areas (50% UD) for each covey (White and Garrott 1990) with the specified bandwidth using the *kernelUD* function in the ADEHABITAT package in R (Calenge 2006, R Development Core Team 2009). We compared area estimates of each home range with sample sizes using linear regression to ensure home range estimates were independent of sample size. We used analysis of variance (ANOVA) to test for differences in home range area among sites and years.

We used compositional analysis (Johnson 1980, Aebischer et al. 1993) to test for non-random habitat use at three spatial scales (Porter and Church 1987). Compositional analysis uses individuals (i.e. coveys) as the sampling unit to examine proportional habitat use, rather than individual locations pooled from the entire population. This approach ensures that the technique is robust to varying sample sizes among individuals, given appropriate sampling effort. Compositional analysis also facilitates the study of hierarchical selection by defining use and availability for sampling units at different spatial scales.

Because compositional analysis assumes that all individuals used all habitat types, zero values for use must be replaced with a small number such that the log-ratio can be calculated. Aebischer et al. (1993) recommended replacing zero values with 0.01%. However Bingham and Brennan (2004) found that selection of the replacement value influences probability of making Type 1 errors, where the test statistic incorrectly shows non-random habitat use. They showed that larger replacement values (0.3 - 0.7%) than suggested by Aebischer et al. (1993) reduced the probability of making a Type 1 error. Therefore, we replaced all zero values with 0.3%.

We tested for second-order habitat selection (Johnson 1980) by defining availability as the composition of the study area and use as the composition of the home range for each covey. We examined third order selection by defining home ranges as available and the composition of the core areas (hereafter third core) and specific radio-locations (hereafter third point) as used habitat (Johnson 1980, Porter and Church 1987). Comparing two definitions of use at the third order scale allowed us to compare where coveys focused activities (core area) and what specific habitats they used within the home range. We used Wilks' Lambda (Λ) as a global test of habitat selection across all coveys at each scale (α=0.05) and tested for differences among sites and years with multivariate analysis of variation (MANOVA). We used t-tests to form a ranking matrix of preferred habitat types (Aebischer et al. 1993). Aebischer (1993) recommended that the number of sample units in the analysis should be greater than the number of habitat types.

Therefore, we only reported selection for groups (site or year combinations) containing > 5 coveys.

Following Alldredge and Griswold (2006: 337) we defined selection as disproportional habitat use relative to availability. We called selection significant when t-tests revealed that selection or avoidance of 1 habitat type deviated from random use ($\alpha=0.05$; Aebischer et al. 1993) . We used preference to describe the relative ranking of each habitat type, where higher ranked habitats were preferred over lower ranked habitats.

We calculated standardized selection ratios to graphically characterize habitat preference among sites and scales following Manly et al. (2002:51). The standardized selection ratio is calculated by dividing the geometric mean of the selection ratios in each habitat type by the sum of all selection ratios for that scale. The selection ratio is calculated as the proportion of the habitat type used relative to habitat available to each covey. Taking the geometric mean of the ratios across coveys makes the approach correspond with the ranking matrix from compositional analysis based on log-ratios of selection (Pendleton et al. 1998). We replaced 0 values in the used fields with 0.3% and excluded observations with 0 as availability for any habitat category from the mean selection ratio calculations. We compared standardized selection ratios with the inverse of the number of habitat types in the analysis (i.e. 1/5=0.2) where greater values indicate selection and lower values indicate avoidance.

RESULTS

We identified and radiomarked 56 coveys, 48 of which had ≥ 30 locations and were included in the analysis (n = 23 in 2009-2010 and n = 25 in 2010-2011). Three sites had > 5 coveys and were included in site-specific analyses (Fee n = 13, Peach n = 3, Thurner n = 9, Wildcat n = 23). We recorded a mean of 86 locations/ covey (range = 30 - 139, SD = 32). Two formerly unique coveys joined to form a new covey on 2 occasions in each year (Chapter 3). In each case a shift in the former ranges of each covey was evident as the new covey used areas from each of the original covey's apparent winter range (A. Janke, personal observation).

Mean home range size was 26.1 ha (95% CI = 21.6, 30.5) and mean core use area was 4.7 ha (95% CI=3.9, 5.5; Table 4.1). Sample size did not influence home range (P = 0.7131, r^2 = 0.003) or core use (P = 0.5295, r^2 = 0.009) area estimates. There was no difference in home range size among study sites ($F_{4,43}$ = 0.209, P = 0.084) or years ($F_{1,46}$ = 0.3941, P = 0.533). Row crop was the most abundant habitat type within home ranges and core use areas (Table 4.1). Early successional herbaceous vegetation was the next most abundant habitat type in home ranges (25.6%) and core use areas (27.5%) after row crop fields (Table 4.1).

Habitat use was non-random at all three spatial scales (second order Λ = 0.320, P < 0.001; third order core Λ = 0.599, P = 0.002; third order point Λ = 0.058, P = 0.002). Selection differed among sites at second order (P = 0.027) and third order point scales (P = 0.012), but not at the third order core scale (P = 0.545). Manly selection ratios were consistent with the ranking matrices for all sites with > 5 coveys (Figure 4.2). Early

		Home Range[a]		Core Area[a]	
Site	*n*	x̄	SE	x̄	SE
Fee	13	23.27	4.57	4.30	0.81
Peach	3	9.91	4.49	1.53	0.56
Thurner	9	35.51	3.83	6.37	0.69
Wildcat	23	26.02	2.94	4.73	0.56
Total	48	26.05	2.16	4.72	0.40

[a] Home range = 95% kernel utilization distribution, Core area = 50% kernel UD

Table 4.1. Home range and core use areas of northern bobwhite coveys on private land in southwestern Ohio during 1 November-31 March 2009-2011.

	Home Range[a]		Core Area[a]		Locations	
Parameter	x̄	SE	x̄	SE	x̄	SE
% ES Herbaceous	25.65	2.65	27.49	3.53	20.86	2.41
% ES Woody	11.49	1.14	16.83	2.25	48.92	2.99
% Forest	10.85	1.27	14.68	2.43	21.30	2.83
% Non Habitat	4.01	0.64	3.73	0.91	0.40	0.14
% Pasture Hay	9.77	1.41	8.55	2.08	2.96	1.05
% Row Crop	38.23	2.46	28.71	2.68	5.55	1.46

[a] Home range = 95% kernel utilization distribution, Core area = 50% kernel UD

[b] ES=early successional

Table 4.2. Habitat composition of home ranges, core use areas, and telemetry locations of bobwhite coveys on private land in southwestern Ohio during 1 November-31 March 2009-2011.

		Cover type [a, b]				
Cover type [a]	Rank	ES Herbaceous	ES Woody	Forest	Pasture Hay	Row Crop
Fee (*n*= 13)						
ES Woody	1	+	.	+++	+++	+++
ES Herbaceous	2	.	-	+	+	+
Forest	3	-	---	.	+++	+
Row Crop	4	-	---	-	+++	.
Pasture Hay	5	-	---	---	.	---
Thurner (*n*= 9)						
ES Woody	1	+++	.	+++	+++	+++
ES Herbaceous	2	.	---	+++	+++	+
Forest	3	---	---	.	+	+
Row Crop	4	-	---	-	+	.
Pasture Hay	5	---	---	-	.	-
Wildcat (*n*= 23)						
ES Woody	1	+++	.	+++	+++	+++
Row Crop	2	+	---	+	+++	.
ES Herbaceous	3	.	---	+	+	-
Forest	4	-	---	.	+	-
Pasture Hay	5	-	---	-	.	---

[a] ES = Early successional

[b] (+) indicates row habitat type is preferred over column habitat type; (-) indicates column habitat type is preferred over row habitat type; sign is tripled (e.g. +++) if relationship is significant (α=0.05).

Table 4.3. Ranking matrix for second order (availability = study area, use = home range) habitat selection by northern bobwhite coveys from 3 sites in southwestern Ohio during 1 November – 31 March 2009-2011.

		Cover type [a, b]				
Cover type [a]	Rank	ES Herbaceous	ES Woody	Forest	Pasture Hay	Row Crop
ES Woody	1	+	.	+++	+++	+++
ES Herbaceous	2	.	-	+	+++	+++
Forest	3	-	---	.	+++	+
Row Crop	4	---	---	-	+++	.
Pasture Hay	5	---	---	---	.	---

[a] ES = Early successional

[b] (+) indicates row habitat type is preferred over column habitat type; (-) indicates column habitat type is preferred over row habitat type; sign is tripled (e.g. +++) if relationship is significant ($\alpha=0.05$).

Table 4.4. Ranking matrix for third order core (availability = core use area, use = home range) habitat selection by northern bobwhite coveys pooled across 4 sites in southwestern Ohio during 1 November – 31 March 2009-2011.

		Cover type[a, b]				
Cover type[a]	Rank	ES Herbaceous	ES Woody	Forest	Pasture Hay	Row Crop
Fee (n= 13)						
ES Woody	1	+++	.	+	+++	+++
Forest	2	+	-	.	+++	+++
ES Herbaceous	3	.	---	-	+	+++
Pasture Hay	4	-	---	---	.	+
Row Crop	5	---	---	---	-	.
Thurner (n= 9)						
ES Woody	1	+++	.	+	+++	+++
Forest	2	+++	-	.	+++	+++
ES Herbaceous	3	.	---	---	+++	+++
Pasture Hay	4	---	---	---	.	+++
Row Crop	5	---	---	---	---	.
Wildcat (n= 23)						
ES Woody	1	+++	.	+++	+++	+++
Forest	2	+++	---	.	+++	+++
ES Herbaceous	3	.	---	---	+++	+++
Pasture Hay	4	---	---	---	.	+++
Row Crop	5	---	---	---	---	.

[a] ES = Early successional

[b] (+) indicates row habitat type is preferred over column habitat type; (-) indicates column habitat type is preferred over row habitat type; sign is tripled (e.g. +++) if relationship is significant (α=0.05).

Table 4.5. Ranking matrix for third order point (availability = telemetry location habitat, use = home range) habitat selection for northern bobwhite coveys from 3 sites in southwestern Ohio during 1 November – 31 March 2009-2011.

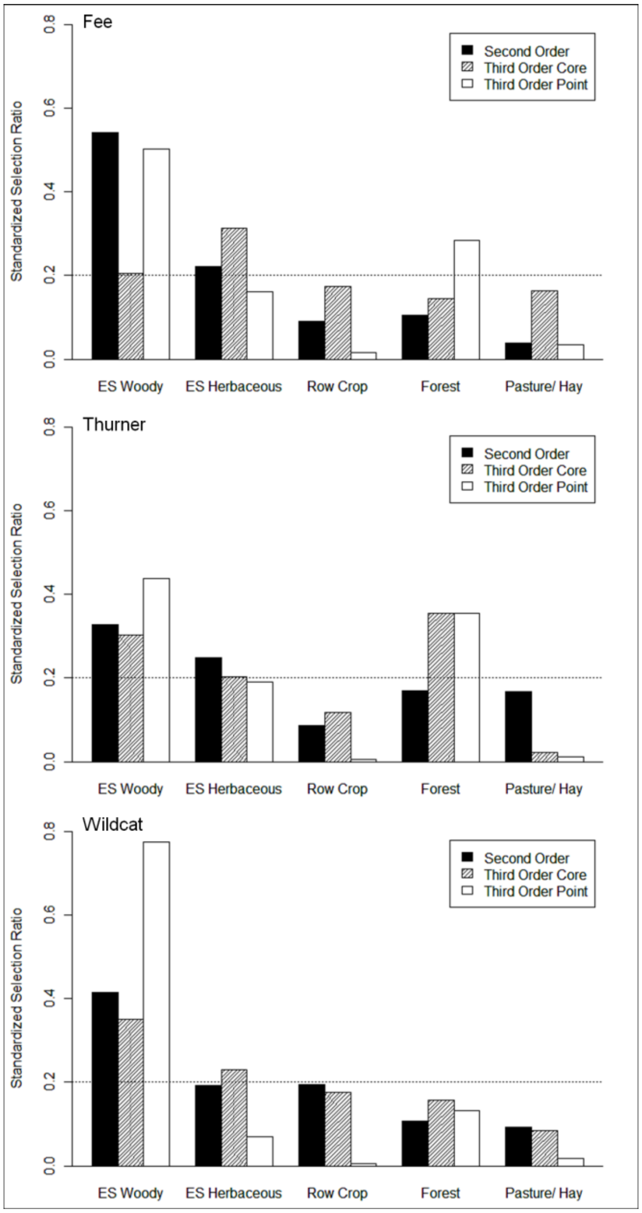

Figure 4.2. Standardized selection ratios calculated as the geometric mean of Manly's selection ratios for each habitat type at three spatial scales from three sites with ≥ 5 northern bobwhite coveys (Manly et al. 2002). Dashed line represents the inverse number of resources compared (*n*= 5) where values greater than that line indicate selection. Data collected from radio-marked coveys on private land in southwest Ohio during 1 November – 31 March 2009-2011.

successional woody vegetation was selected over all habitat categories at each scale (Tables 4.3- 4.5, Figure 4.2). Bobwhites selected grasslands at the second order at 2 sites (Fee and Thurner) where row crop habitat was most abundant. Row crop habitat ranked higher than early successional herbaceous vegetation at the second order on the study area with more grassland cover (Wildcat; Table 4.3; Figure 4.2). Forest habitat ranked above agriculture (row crops and pasture/ hay) but was generally not selected for over other permanent cover types at the second order (Table 4.3).

Permanent cover categories (early successional woody and herbaceous and forest) ranked highest at third order core scale, although their use did not significantly deviate from random within the home range (Table 4.4). Although row crop habitat was avoided at all scales, it was relatively more preferred at the third order core scale (Figure 4.2). The ranking matrix for third order point scale was identical among the 3 sites (Table 4.5). Habitat categories with woody cover (early successional woody and forest) ranked highest. Early successional woody cover was selected over all other categories at each site. Forest cover was selected over other categories at the Thurner and Wildcat sites, but not at the Fee site.

DISCUSSION

Our hierarchical analysis of habitat selection revealed that bobwhites used habitat non-randomly at all 3 levels of selection and that habitat preferences differed among sites. The primary difference among sites was the rank of row crops and early successional herbaceous vegetation, which varied in availability among sites and comprised most of the area within covey home ranges. Habitat composition within home ranges was diverse and home ranges were established in areas with more early successional woody and herbaceous vegetation. The high ranking of early successional woody, early successional herbaceous, and forest habitats at the third order core scale showed that bobwhites focused their activities within home ranges on areas with permanent cover. Manly selection ratios revealed that row crops were selected more at third order core scale than at the other 2 scales. Preference for row crop and early successional herbaceous vegetation at this scale suggests that use within the home range focused on areas where woody cover (early successional woody or forests) and food (early successional herbaceous or row crops) were in close proximity. Third order point scale revealed strong selection for woody cover from early successional woody and forest habitats.

Early successional woody vegetation was the most selected habitat type in this study. Forty-nine percent of covey locations were in early successional woody cover, although the category accounted for 11% of the habitat composition of home ranges and 4% of study sites. Many previous studies have established the importance of woody cover for bobwhites during the non-breeding season throughout their range (Yoho and Dimmick 1972, Roseberry and Klimstra 1984, Williams et al. 2000, Hiller et al. 2007). Woody cover is particularly important for bobwhites exposed to severe winter weather in the northern portion of their range (Errington and Hamerstrom 1936, Roseberry 1964) because is it thermodynamically advantageous (Guthery et al. 2005) and maintains structure during periods of snow cover. Early successional woody vegetation was primarily fencerows and drainage ditches, which had thick shrubby vegetation in the understory. Such habitat types are known to provide good habitat for bobwhites and other wintering songbirds (Best 1983, Best et al. 1990) but have been eliminated from many modern agricultural landscapes (Demers et al. 1995). Therefore, conservation efforts that focus on maintaining such cover or providing functionally comparable edge types would be advantageous (e.g. shrubby forest edges; Hanson and Miller 1961).

Forest selection differed substantially among the three scales. Forest were avoided at the second order but preference increased from third order core to third order point. Avoidance of forests at the landscape scale was consistent with previous studies that have shown that forests are avoided because closed canopies result in open understories with insufficient cover that limits dispersal (Yoho and Dimmick 1972, Roseberry and Klimstra 1984, Riddle et al. 2008). Most forests in this study were characterized by mature overstories with sparse understory vegetation. However, forests with open canopies that allowed growth of woody vegetation in the understory were used more (M. J. Wiley, unpublished data). Such understory vegetation differences facilitated forest use by bobwhite during the non-breeding season in Illinois (Roseberry and Klimstra 1984) and Tennessee (Yoho and Dimmick 1972). Further, Lohr et al. (2011) found that coveys preferred forested habitat over shrubland habitat with second order selection in New Jersey. That forests were avoided at the landscape scale, but used at smaller scales in this study suggests that home ranges may be established in areas where forests had suitable understory vegetation that was functionally equivalent to woody cover in the early successional woody category. Active forest management, to increase suitable woody cover in forest understories may increase preference for the category at in the establishment of home ranges and increase usable space at a site scale (Guthery 1997).

Although woody cover was the most important habitat type in the study, forest and early successional woody vegetation generally only contributed a small proportion of the total area of the home ranges in the study. Home ranges in our study were large relative to previous home range estimates from the core of the bobwhite range (Dixon et al. 1996). Home range size in bobwhites and other upland game birds is often related to availability and distribution of suitable habitat (Gatti et al. 1989, Sisson et al. 2000, Guthery et al. 2004, Singh et al. 2011). The 2 primary habitat requirements of bobwhites are food sources and refuge cover (i.e. loafing and escape cover; Stoddard 1931, Guthery and Bingham 1992). Food is available from 2 primary sources in unmanaged agricultural landscapes --forbs in grasslands or along field edges and waste grain in crop fields (Baumgras 1943)-- and is generally abundant throughout the non-breeding season. Woody cover however, is more limiting and likely led to larger home range sizes that were necessary to exploit heterogeneously distributed patches of suitable woody cover near food sources.

The most abundant cover types within home ranges were early successional herbaceous and row crop. Bobwhites preferred these 2 cover types differently among sites; early successional herbaceous vegetation was preferred over row crops at the agricultural sites (Fee and Thurner) but rankings switched on the site with the most grassland cover (Wildcat). The different response to grassland and row crop habitat under varying levels of availability was shown previously with bobwhites in Kansas

(Williams et al. 2000) and may represent a functional response to grassland and row crop habitat in agricultural systems. Functional responses occur when the value of a habitat type decreases as that habitat type becomes more abundant on the landscape (Mysterud and Ims 1998, Beyer et al. 2010).

Guthery and Bingham (1992: 342) showed that resource cover (e.g. grasslands or row crop fields) is only suitable within a certain distance of refuge cover (e.g. woody cover), a condition defined as the "radius of full use." Therefore, as the area of a certain cover type increases, the area near woody cover (i.e. within the radius of full use) decreases, making a larger proportion of the cover type unsuitable and therefore unused (Best et al. 1990). As field sizes increased, bobwhites used a smaller proportion of the cover type than was available (i.e. interior portions). Although grasslands and row crops were important habitat types (particularly as food sources) their over-abundance on the landscape led to avoidance in our analysis at third order point scale. Efforts that minimize the edge to interior ratio of these two categories would therefore be effective in providing bobwhites with additional suitable habitat on a landscape scale (i.e. increase usable space; Guthery 1997).

Another factor contributing to avoidance of grassland cover in this study may relate to the quality of that habitat on our study sites. Most grass fields in the study were enrolled in the CRP for a long period ($\geq$ 20 years), which led to decreased vegetation diversity (Negus et al. 2010) and resulted in a dominance of low quality sod-forming grasses (Barnes et al. 1995, Washburn et al. 2000). Newer fields with bunch grasses generally had greater forb diversity and were used more (A. Janke personal observation).

Treating different grassland types as functional homologues, by including them in the same habitat category in the analyses, may have obscured different use or selection related to contract age or habitat composition (McCoy et al. 2001, Riffell et al. 2010). While these differences may be important for conservation planning, the abundance of sod-forming grass fields in this study is representative of a more abundant habitat type available to bobwhites throughout their range in Ohio (Swanson et al. 1999).

Although apparently low quality grasslands in this study were not selected, they still contributed a large share of the total home range, which suggested some relationship between grassland cover and home range establishment. The spatial distribution of bobwhites before covey formation is likely an important determinant of where home ranges are ultimately established (Agee 1957). Because reproduction in agricultural landscape occurs almost exclusively in grasslands (Taylor et al. 1999, Collins et al. 2009, M. R. Liberati, unpublished data) a majority of the population is near grassland cover before the fall shuffle and covey formation at the end of the breeding season (Rosene 1969). Although movement rates increase during this period (Townsend et al. 2003, Chapter 3) we observed a tendency for post-breeding adults and broods to stay near their natal grounds (typically grasslands; M. R. Liberati, unpublished data). The tendency for bobwhites to establish winter ranges near breeding habitat might result in otherwise suitable habitat being unoccupied if far from grasslands. Therefore, the spatial distribution of breeding season habitat may be an important determinant of non-breeding season habitat utilization and bobwhite distribution in landscapes with varying amounts of grassland cover. As such, management strategies should consider establishing or managing woody cover in landscapes with suitable breeding season habitat.

MANAGEMENT IMPLICATIONS

Our analyses showed that bobwhites needed a diversity of habitat types within their home range to meet their needs throughout the non-breeding season. Management strategies aimed at increasing suitable habitat through the non-breeding season in Ohio should focus on providing woody cover adjacent to food sources (agricultural or grassland fields) in landscapes that are capable of supporting bobwhites throughout the year. Grasslands are an important component of winter ranges, but should be small so as to maximize the edge to interior ratio. Quality of grassland cover may also be important and bunch grasses appear to be more suitable than sod-forming grasses. Riparian and fragmented forests may provide an opportunity area to increase suitable woody cover in agricultural landscapes by implementing forest management practices such as edge feathering. Woody edge-focused conservation efforts would marginally impact existing agricultural practices (Barbour et al. 2007) and improve the suitability of agricultural landscapes during the most cover-limited time of the year for bobwhites and other early successional wildlife species in Ohio.

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CHAPTER 5: EVIDENCE FOR SCALE-DEPENDENT INFLUENCE OF HABITAT USE ON SURVIVAL: NORTHERN BOBWHITES DURING THE NON-BREEDING SEASON

ABSTRACT

Habitat influences survival through direct (e.g. food availability) and indirect (e.g. predator activity) effects that are manifest at multiple spatial scales. Understanding the influence of habitat on individual fitness metrics across spatial scales can explain habitat use patterns and inform management strategies. Although much is known about scale-dependent influences of habitat on reproductive vital rates, few investigations have focused on non-breeding season survival, an important vital rate in some populations. Northern bobwhites (*Colinus virginianus*) are an appropriate species to address such questions because of the diversity of landscapes in which they occur, their sedentary nature during the non-breeding season, and their vulnerability to a diversity of generalist predators. We used radio-telemetry to understand the influence of habitat use on bobwhite survival in Ohio during October- March 2009-2011. We compared 37 *a priori* models for influence of habitat at 4 spatial scales; 1) study site-specific, 2) a 78.5 ha circular landscape around the center of an individual's locations, 3) the composition of individual home ranges, 4) and microhabitat use. Models with positive edge effects within home ranges were best supported (n = 3, w_i = 0.841), and the highest ranking

model included an effect of early successional woody edge density (β = 0.026, 95% CI = 0.009, 0.042). At the landscape scale, survival was negatively influenced by the proportion of the buffer in pasture or hay fields (β = -0.022, 95% CI = -0.040, -0.003) and early successional herbaceous vegetation (β = -0.013, 95% CI = -0.026, 0.001). Models with terms for microhabitat use and site effects ranked below the null model and had no support. Within home ranges increased edge density provided more escape cover for bobwhites to avoid predation, whereas at the landscape scale survival was influenced by factors that influence predator distribution in agricultural landscapes. Such differential survival responses to habitat among scales showed that fitness consequences of habitat use varied among scales and that the advantage of specific habitat features were scale-dependent.

INTRODUCTION

The assumption that habitat use is adaptive cuts across traditional habitat use studies (Jones 2001, Johnson 2007). However, failure to support this assumption by investigating the influence of habitat use on fitness metrics may produce recommendations that are ineffective at improving population vital rates (Van Horne 1983, Jones 2001, Aldridge and Boyce 2007).

Habitat influences individual fitness through direct (e.g. habitat availability) and indirect (e.g. predator activity) effects on reproduction and survival. Habitat influences vary among spatial scales at which predator and prey species differentially respond to habitat availability and landscape configuration (Brown and Litvaitis 1995). Prey species make adaptive responses to minimize predation by avoiding landscapes with high predator densities (Rodewald and Yahner 2001), avoiding patches with greater predator activity (Brown and Litvaitis 1995, Marzluff et al. 2007), or by making small-scale behavioral changes in microhabitat use to minimize predation risk (Lima 1990, Watts 1991, Brown and Litvaitis 1995, Marzluff et al. 2007). Predator distribution is influenced by patch-specific factors, such as prey density (Andersson and Erlinge 1977), and large-scale processes, such as habitat fragmentation (Gehring and Swihart 2003, Klug et al. 2009). Individuals or nests in habitats that support higher predator activity may experience higher predation (Angelstam 1986, Redpath and Thirgood 1999).

Given the responses of predators and prey to habitat at multiple spatial scales, Brown and Litvaitis (1995) defined 4 scales at which habitat may influence individual fitness; 1) landscape, 2) multiple patches, 3) patch, and 4) site. At the largest scale (landscape), landscape level factors such as availability or proximity of suitable habitat patches influence predator and prey distribution and abundance (Dunning et al. 1992). Progressively smaller scales represent neighborhoods where prey species are influenced by predator habitat use patterns, alternate prey densities, and small-scale individual predator avoidance behaviors (Addicott et al. 1987, Brown and Litvaitis 1995). Because habitat use is a hierarchical process for predators and prey, investigations that aim to characterize the influence of habitat use on fitness metrics should investigate influences of habitat variables on survival that are representative of multiple spatial scales (Orians and Wittenberger 1991, Chalfoun and Martin 2007).

Many investigations have used a hierarchical approach to characterize the relationship between habitat and reproductive fitness metrics in birds (e,g, Clark et al.

1999, Bergin et al. 2000, Stephens et al. 2005). Such studies are complicated, however, by the multiplicity of reproductive vital rates that influence fitness during the breeding season (Chalfoun and Martin 2007). For example, Chalfoun and Martin (2007) found that birds selected nesting habitat that resulted in lower nest survival, suggesting a maladapted behavior. However, when they examined additional fitness-related variables (e.g. nesting attempts, nestling size) they found that preferred habitats were associated with increased net reproductive success (i.e. fledged offspring), illustrating the complexity of habitat-mediated trade-offs in habitat use by birds throughout the breeding season. The non-breeding season may provide a more simple system with which to study habitat-mediated trade-offs in habitat use and fitness metrics because survival is the only major fitness component (McNamara and Houston 1986) and is influenced by habitat use (Grubb and Greenwald 1982).

Using northern bobwhite (*Colinus virginianus*; hereafter bobwhite) as our model, we investigated the influence of habitat use on non-breeding season survival at multiple spatial scales. Bobwhites are well suited to address questions related to habitat influences on survival during the non-breeding season because their sedentary nature allows for comparisons between survival and characteristics of discrete home ranges and the landscapes in which they occurred (Seckinger et al. 2008). Low density bobwhite populations have little influence on the spatial distribution of predators (Roseberry and Klimstra 1984), although low non-breeding season survival results from predation (Chapter 2) and bobwhites contribute a small portion of the diet to many predator species (Rosene 1969, Rollins and Carroll 2001). Bobwhites may respond to habitat suitability at multiple spatial scales to minimize predation by the diverse guild of generalist predators in agricultural landscapes.

We identified habitat factors that influence non-breeding season survival of bobwhites on agricultural study sites in Ohio. Previous analyses established that non-breeding season survival in our population was low (Chapter 2) and that bobwhites used habitat non-randomly within study sites and home ranges (Chapter 4). We developed a candidate model set that represented bobwhite and predator habitat suitability at 4 spatial scales starting at the study sites (site) and progressively smaller; a 78.5 ha landscape around individual locations, home ranges, and microhabitat use. We identified the most important scale that influenced bobwhite survival and the most important factors at each scale. We discuss the findings of our hierarchical approach in the context of current knowledge of bobwhite habitat and predator responses to landscape composition in agricultural landscapes.

STUDY AREA

We focused on 4 private land study sites in Highland and Brown counties in the glaciated till plains physiographic region in southwestern Ohio (Ohio Division of Geologic Survey 1998). The sites varied in size (400 -1200 ha) and were distributed along a gradient from agricultural (39-72% cropland and pasture within 10 km) to forested (20-50% forested within 10 km) landscapes. Habitat composition on the study sites spanned a similar gradient with forest cover ranging from 8-29% and agricultural cover ranging from 41-75%. Grasslands were present on all sites and grassland cover ranged from 9-20%.

Row crops fields were the primary land use on each site and were generally planted in corn (35%) or soybeans (61%). Upland forests were dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.) and had closed canopies with little understory vegetation. Riparian and bottomland forests also had closed canopies and were dominated by black walnut (*Juglans nigra*), elms (*Ulmus* spp.), and green ash (*Fraxinus pennsylvanica*). Areas classified as grasslands were fields enrolled in the Conservation Reserve Program (CRP) or old fields dominated by herbaceous vegetation. Most grasslands (90%) were cool season grasses, primarily fescue (*Festuca* spp.) or cool season bunch grasses such as timothy (*Phleum pretense*) or orchard grass (*Dactylis glomerata*). Other grasslands were planted in warm season grasses, primarily Indian grass (*Sorghastrum nutans*). Fencerows and drainage ditches contributed a small proportion (3%) of the area on the study sites but were used extensively by bobwhites. Blackberry (*Rubus allegheniensis*), black raspberry (*R. occidentalis*) and multi-flora rose (*Rosa multiflora*) were the most abundant species in fencerows and ditches.

Long-term (30-year) mean temperature in the region was 10.5 C during October-March (NCDC 2011). Mean annual snow accumulation for the same period was 67.5 cm and there was an average of 20 days with snow depth > 5 cm (NCDC 2011). The 2 winters during the study were more severe than the long term averages, with above-average snow accumulation during 2009-10 (101.6 cm, 31 days with snow > 5 cm) and more days with snow accumulation > 5 cm during 2010-11 (67.3 cm, 41 days with snow > 5 cm).

METHODS

Site selection

To investigate the influence of habitat use on survival, we conducted our study on sites with a diversity of habitat compositions that supported bobwhites throughout the non-breeding season. We identified sites in the core of the current bobwhite range in Ohio (Spinola and Gates 2008) with a landscape level habitat suitability model derived from published habitat use studies (e.g. Roseberry and Klimstra 1984, Roseberry and Sudkamp 1998, Riddle et al. 2008). We determined habitat composition of 5 km^2 hexagon grids based on the National Land Cover Dataset (Homer et al. 2004) and a layer of parcels enrolled in the CRP. We compared the ratio of cover types within each hexagon and excluded hexagons with > 50% forest cover or < 10% early successional vegetation (grassland, shrubland , or CRP). Remaining hexagons were classified as potentially suitable and grouped into 4 strata based on habitat composition and proximity to adjacent suitable hexagons. The strata were isolated agricultural, clustered agricultural, isolated mixed agriculture-forest, and clustered mixed agriculture-forest. We randomly selected sites from each of the 4 strata where access permission was sought from landowners. We obtained permission on 9 sites and conducted covey call surveys to determine if sites were occupied during the non-breeding season (Demaso et al. 1992). We selected 4 sites with sufficient numbers of bobwhite coveys to conduct radio-telemetry studies. We acquired additional permission from surrounding landowners as needed so final site sizes varied (400 -1200 ha). Although we did not replicate site types, our approach to site selection ensured that we gained a representative sample of landscapes occupied by bobwhites during the non-breeding season in the core of their current range in Ohio.

Data collection

We captured bobwhites using baited funnel traps (Stoddard 1931) and targeted mist netting (Wiley et al. *in prep*) during October-March 2009-2011. We attached an aluminum leg band to each individual and recorded its age, gender, and covey affiliation. A subset of individuals in each covey weighing >165 g were fit with a 6.6 g. (≤ 4% body mass) mortality sensing necklace style radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). We released all birds at the capture site within 30 min of capture. Trapping, handling, and marking protocols used in this study were reviewed and approved by the Animal Care and Use Committee at Ohio State University (protocol number 2007A0228).

We located all radiomarked individuals once daily ≥ 6 times/ week by homing and triangulation from short distances (≤ 20 m; White and Garrott 1990). We recorded locations at different times on subsequent days to capture a range of diurnal activity patterns. We approximated the distance and direction of radiomarked individuals and recorded the location on a Global Positioning System (GPS; Garmin GPS Map 76, Garmin International, Inc. Olathe, KS, USA). We maintained a sufficient distance from individuals to avoid regular flushing. After locating each individual we recorded whether all radiomarked individuals in the covey were together or separated to distinguish individual locations from covey locations. We also recorded the habitat in which the individual was located using 1 of 21 habitat classification codes. We immediately located transmitters after detecting mortality signals and determined the fate of individuals from field signs at recovery sites (Einarsen 1956) and condition of transmitters.

Previous analyses that related bobwhite habitat use to survival used covey home ranges to represent individual habitat use (e.g. Williams et al. 2000, Seckinger et al. 2008, Holt et al. 2009a). However, such an approach may misrepresent individual habitat use because it includes locations that were recorded after individual's death. To overcome this, we created habitat use histories for each individual by combining individual locations with all covey locations from the first location for that covey through the initial capture of the individual, such that locations after death or censoring were excluded. We assumed that all individuals were with the radiomarked covey from the start of the study until death or censoring. This assumption was supported by previous analyses that showed that changes in covey affiliation in our study were rare, and that individuals were closely associated with covey members > 95% of the time (Chapter 3). Our approach increased the number of locations used for each individual habitat use history to provide a more accurate approximation of the landscape where that individual occurred throughout the non-breeding season. Because of generally short individual exposure times, using only locations from time of capture through death or censoring would have misrepresented individual habitat use history and decreased accuracy of habitat use covariates used in the survival analysis (Seaman et al. 1999).

We digitized the composition of 13 habitat types on each site in ArcGIS (version 9.3 ESRI Redlands, CA, USA) over high spatial resolution (0.305 m) orthophotographs (Ohio Statewide Imagery Program 2008). We digitized the coverage of each site for each year, to capture small-scale changes in cover among years. We collapsed the digitized site cover and specific telemetry location habitat classifications into 6 general habitat categories; early successional herbaceous, early successional woody, forest, pasture and hay fields, row crop fields, and non-habitat. Early successional herbaceous included all fields enrolled in the CRP and old fields that were dominated by herbaceous vegetation. Early successional woody was primarily fencerows and ditches that were characterized by high amounts of early successional woody vegetation in the understory. The category also included patches of woody cover in grass fields that were ≥ 500 m^2. The forest category included all riparian and upland forests that were > 50 m wide with overstory trees. Pasture and hay fields were all grass fields that were mowed or grazed during the preceding growing season. Non-habitat included all residential and commercial properties in addition to roads and water bodies.

Survival analyses

We excluded the first 7 days of each individual encounter history to control for short-term acute effects of capture and radio-marking (Guthery and Lusk 2004, Holt et al. 2009b). We used the known-fates model with a logit link function in Program MARK to estimate the influence of habitat use on survival (White and Burnham 1999). Known fate models use the binomial model to obtain maximum likelihood estimates of survival and to competitively rank models with different parameters in an information theoretic framework (Murray 2006). The analysis proceeded in 2 steps. First, we compared 6 *a priori* models to explain variation related to temporal trends within and among the 2 study years. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to select the most parsimonious temporal model ($\Delta AIC_c < 2$, fewest parameters; Anderson and Burnham 2002), which became the baseline model in subsequent analyses. We used the bootstrapping procedure in Program MARK to estimate a variance inflation factor to improve model selection with Quasi- AIC ($QAIC_c$). The bootstrapping procedure approximated a variance inflation factor for the data by explicitly examining the source of dependency among individuals that results in overdispersion (Bishop et al. 2008, Chapter 2). We structured the bootstrap by covey members, because the source of dependency in survival between individuals in our study was thought to result from covey mates sharing common resources (Williams et al. 2003). We generated 10,000 replicate survival estimates in the bootstrapping procedure.

We examined the influence of habitat use and landscape composition on survival at 4 spatial scales; site, landscape, home range, and microhabitat. The site scale was a dummy-coded variable for the 4 sites in the analysis that represented large-scale factors that influenced predator occupancy (Dunning et al. 1992) or other site-specific factors that may influence bobwhite survival (e.g. bobwhite density, local plant communities).

For the landscape scale we used a 78.5 ha circular buffer (500 m radius) around the centroid of all radio-locations for each individual as an independent measure of the landscape in which the individual was located. The buffer radius was selected to minimize overlap with adjacent coveys to avoid pseudo replication at the site level while still capturing variability in landscapes where individuals occurred. The 500 m radius was approximately half the mean maximum distance between any 2 telemetry locations for a single individual in the analysis (907 m). Within each buffer we calculated the proportion of each of the 6 habitat types, Shannon diversity index of habitat types, total edge density, edge density of each habitat type, number of patches of each habitat type that intersected the buffer, and mean patch size by habitat type.

For the home range scale we considered the composition of individual home ranges that were calculated to represent the area that an individual was immediately familiar with (i.e. actively used; Addicott et al. 1987). We generated adaptive nearest neighbor convex hull (NNCH) home ranges (Getz and Wilmers 2004) for each individual with the *NNCH* function in *ADEHABITAT* in the R Statistical Program (Calenge 2006). We used NNCH to represent the area we knew the individual used, rather than a probabilistic home range estimator (e.g. kernel home range; Worton 1989) that is more likely to include unused areas in the home range estimate (Lichti and Swihart 2011). Following Getz et al. (2007) we set the adaptive neighborhood selector (*a*) to the maximum distance between any 2 relocations for an individual in the dataset. We determined the proportion of the home range in each of the 6 habitat types, Shannon diversity index of habitat types, total edge density, and edge density of each habitat type within the home range. Variables at the microhabitat scale were proportions of individual locations in each habitat type.

We developed 37 *a priori* models from combinations of scale-specific variables. We excluded correlated ($r > 0.6$) variables from scale-specific models, but retained variables that were correlated among scales. Model development was based on previous research conducted on bobwhites habitat needs and demographic responses to habitat at varying spatial and temporal scales. Specifically, we developed models thought to represent habitat quality for bobwhites and generalist predators that influence bobwhite survival. We predicted that edge density at home range and landscape scales may improve survival by providing habitat interspersion (Leopold 1933) or potentially negatively affect survival by increasing predator activity near edges (Thompson et al. 2002, Seckinger et al. 2008). We also tested for quadratic relationships between edge density and survival to test for a diminishing return of edge habitat that has been previously shown in landscape-scale studies of bobwhite habitat suitability (Guthery et al. 2001, Duren et al. 2011). We tested models with forest and grassland cover effects within the home range and at the landscape scale and postulated that increases in permanent cover types might increase predator activity and decrease survival (Andersson and Erlinge 1977). We also tested for the potential influence of patch size or patch diversity at the landscape scale (Roseberry and Sudkamp 1998). We tested for an influence of use of specific habitat types at the microhabitat scale because use of specific habitat types has been shown to improve survival (Lohr et al. 2011).

Rather than comparing support for each scale-specific model set in individual analyses, we analyzed all models in a single information theoretic framework. Such an approach allowed us to identify the scale(s) that most significantly influenced survival in our dataset. However, our approach may have resulted in undervaluing processes that occurred at alternative scales not represented in competitive models (ΔQAIC ≤ 2.00).

Therefore, in addition to interpreting the most competitive models, we interpreted models from each scale that ranked above the null model based on parameter coefficients and confidence intervals to understand scale-dependent influences and their relative contribution to bobwhite survival during the non-breeding season.

RESULTS

We included 196 radiomarked individuals from 50 coveys in the analysis. The mean number of locations for each individual was 81 (SD = 35.6). The best fitting temporal model included a quadratic relationship with days within the season (Table 5.1). The same model with a year effect had similar support, ranking within 2 ΔAIC units of the top model. The model without year effect was the most parsimonious model and was therefore used as the baseline model in bootstrapping and habitat use analyses. The bootstrapping analysis revealed slight overdispersion in the temporal model set ($\hat{c}$ = 1.10).

Total edge density, row crop edge density, and early successional woody edge density were highly correlated ($r > 0.6$). Therefore, we removed row crop edge density and total edge density from the candidate model set at the home range and landscape scales. The best supported models ($n = 3$, $w_i = 0.826$) contained woody edge effects at the home range scale (Table 5.2, Appendix C). Coefficient estimates for all edge parameters in the competitive models were positive, indicating that survival was higher for individuals in home ranges with more edge density.

The coefficient for early successional woody edge density within home ranges was β = 0.026 (95% CI = 0.009, 0.042; Figure 5.1) in the best supported model

Model	k	AIC_c	ΔAIC_c	w_i
Time + Time^2	3	1151.47	0.000	0.669
Year + Time + Time2	4	1152.87	1.407	0.331
Time	2	1178.25	26.786	0.000
Year + Time	3	1178.61	27.143	0.000
Null	1	1184.38	32.917	0.000
Year	2	1185.36	33.889	0.000

Table 5.1. Ranking of temporal models used to explain baseline variability in survival of northern bobwhites in southwestern Ohio during 1 October – 31 March 2009-2011.

Scale[a]	Model[b,c]	k	QAIC_c	ΔQAIC_c	w_i
HR	Time + ESW Edge	4	1039.39	0.000	0.428
HR	Time + ESW Edge + ESW Edge ^2	5	1040.77	1.380	0.214
HR	Time + FOR Edge + ESW Edge	5	1040.92	1.528	0.199
LA	Time + %ESH + %PHA	5	1044.87	5.480	0.028
LA	Time + %RCR	4	1046.99	7.600	0.010
--	Time	3	1047.33	7.945	0.008
HR	Time + FOR Edge	4	1047.44	8.055	0.008
HR	Time + %ESH	4	1047.79	8.400	0.006
Site	Time + Site	6	1047.86	8.468	0.006
LA	Time + %ESH	4	1048.09	8.703	0.006
HR	Time + %FOR	4	1048.22	8.831	0.005
MI	Time + %ESH	4	1048.29	8.897	0.005
MI	Time + %ESW	4	1048.33	8.937	0.005
MI	Time + %ESH + %ESW	5	1048.35	8.959	0.005
MI	Time + %RCR	4	1048.63	9.237	0.004

[a] HR= home range scale model; LA= landscape scale model; MI = microhabitat scale model; ES = early successional

[b] ESW = early successional woody; ESH = early successional herbaceous; FOR = forest; RCR = row crop; EDGE = edge density

[c] Time = baseline temporal model (Null)

Table 5.2. Highest ranking models out of 37 *a priori* models (Appendix C) used to examine the influence of habitat use on survival of northern bobwhites in southwestern Ohio during 1 October- 31 March 2009-2011.

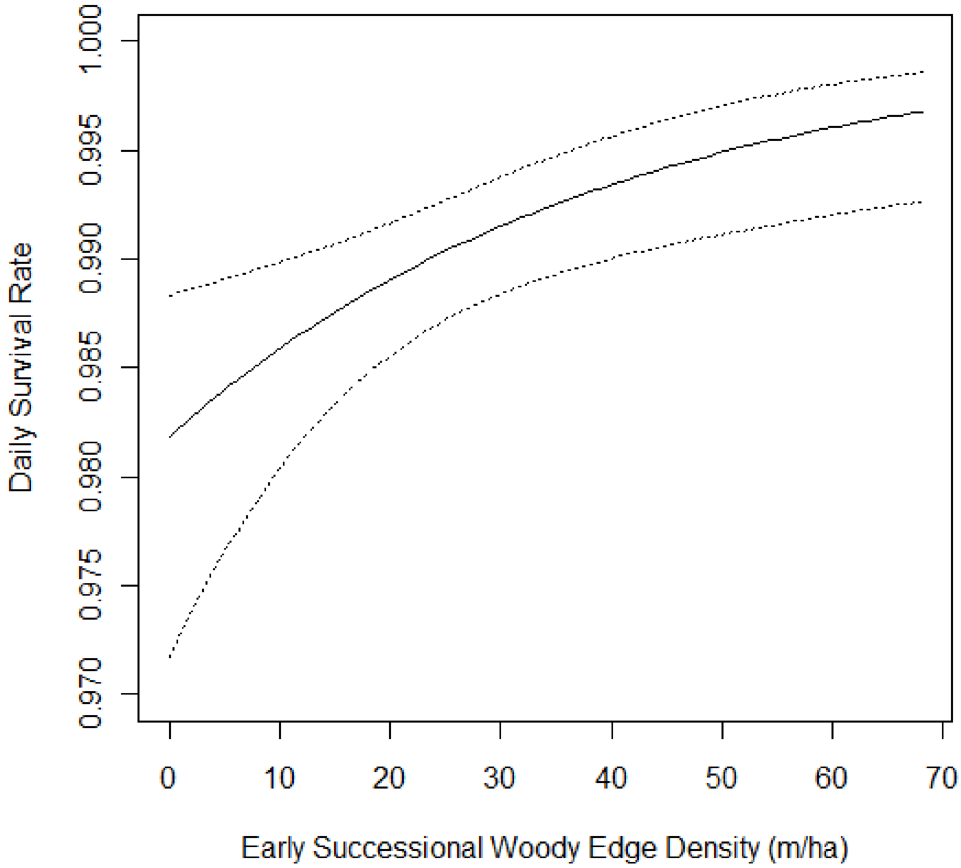

Figure 5.1. Influence of woody edge density within individual home ranges from the most competitive model explaining non-breeding season survival of northern bobwhites in southwestern Ohio during 1 October – 31 March 2009-2011.

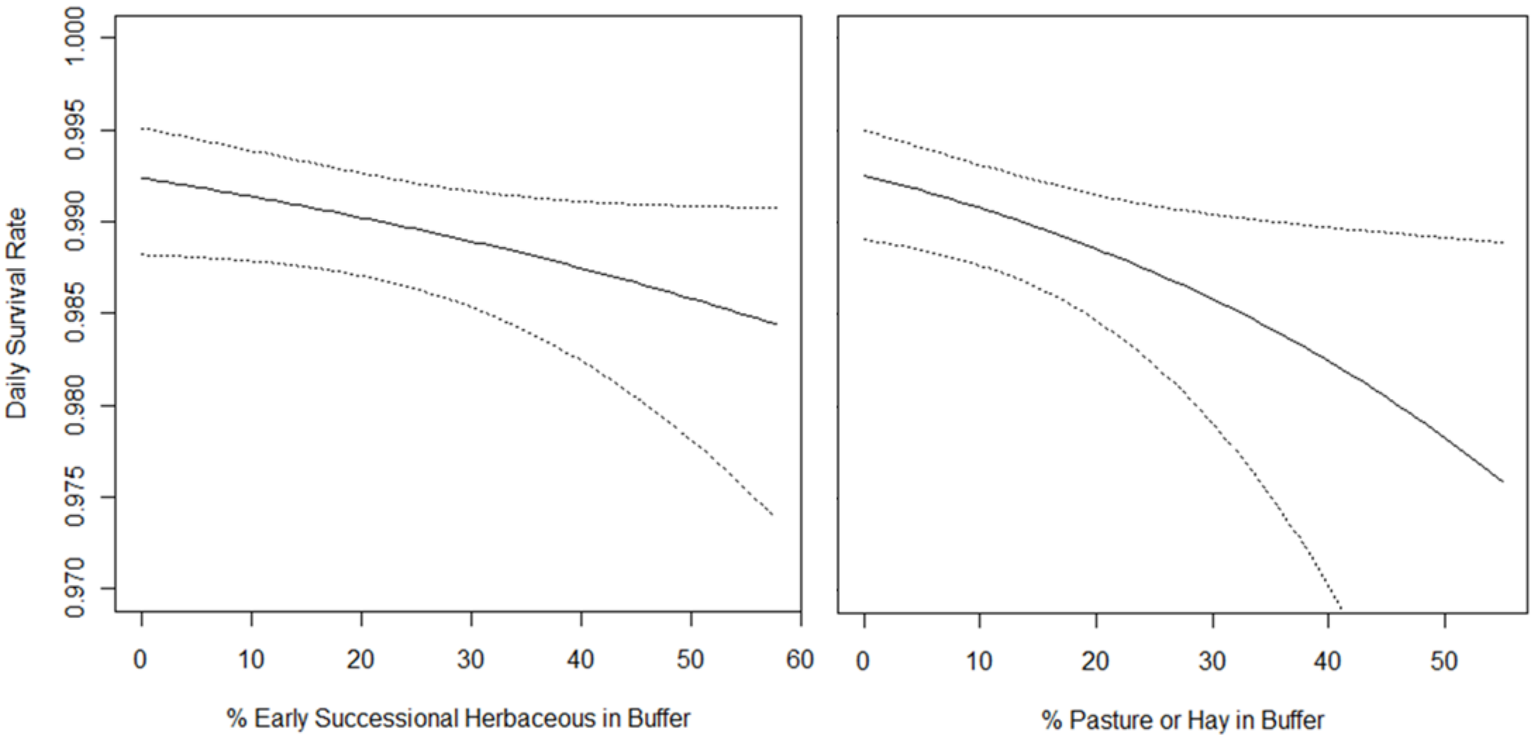

Figure 5.2. Influence of the percent of the landscape surrounding individuals in early successional herbaceous vegetation and pasture/ hay fields from model for bobwhite survival in southwestern Ohio during 1 October- 31 March 2009-2011. Landscape was defined as a 500 m radius buffer from the centroid of all the individual's telemetry locations.

(w_i = 0.428). The next best supported model (w_i = 0.214) included an effect for early successional woody edge within home ranges (β = 0.044, 95% CI = -0.003, 0.090) with a weak quadratic effect (β = -0.000, 95% CI = -0.001, 0.000). A third model with strong support (w_i = 0.199) had an early successional woody edge effect (β = 0.024, 95% CI = 0.007, 0.041) and a positive influence of forest edge density (β = 0.013, 95% CI = -0.024, 0.050) within home ranges, although confidence intervals contained 0.

The best supported model (w_i = 0.028) at the landscape scale showed a negative relationship between the proportion of the buffer in perennial herbaceous cover (early successional herbaceous and pasture/ hay). Parameter values were negative for early successional herbaceous vegetation (β = -0.013 , 95% CI = -0.026, 0.001; Figure 5.2) and pasture and hay fields (β = -0.022, 95% CI = -0.040, -0.003), although the early successional herbaceous confidence interval slightly contained 0. The next best supported landscape scale model differed from the best supported landscape model by 2.12 $QAIC_c$. The model (w_i = 0.010) included a positive term for the proportion of the buffer in row crop habitat (β = 0.002, 95% CI = -0.008, 0.012) though the confidence interval contained 0. Models with microhabitat use terms and the site term ranked below the null model and therefore had no support.

DISCUSSION

Fitness consequences of non-breeding season habitat use varied among scales at which bobwhites and generalist predators respond to habitat suitability. Survival was primarily influenced by edge density within individual home ranges. Despite the influence of edge density within home ranges, models with edge density at the landscape scale were not competitive. Similarly, grassland habitat at the landscape scale influenced survival, but models with grassland effects at smaller scales were not competitive. The variable influence of specific habitat variables (e.g. edge density, grassland cover) on survival across scales showed that habitat effects were scale-dependent.

Woody edge density within home ranges had the greatest influence on survival suggesting that factors that influence habitat suitability where individuals are located has the greatest effect on survival. The strong support for models with home range effects were consistent with Roseberry and Klimstra (1984: 71) who reported winter mortality in bobwhites was primarily influenced by the "security of the range it occupies." Woody cover associated with field and forest edges is the primary habitat used by bobwhites in agricultural landscapes during the non-breeding season (Leopold 1933, Roseberry and Klimstra 1984, Chapter 4). Distribution and availability of woody cover in these landscapes determines the suitability of adjacent cover types; areas near woody cover are suitable, whereas areas farther from woody cover are not (Guthery and Bingham 1992, Guthery 1999). Guthery (1997) described this spatial dependence of cover type suitability as usable space and later implied that usable space should maximize fitness (Guthery et al. 2005). That edge density within home ranges improved survival in our study supports the relationship between increased usable space (a product of higher edge density) and fitness in bobwhites. Demographic responses to localized variability in usable space have been previously documented in bobwhite populations. Roseberry et al. (1979) documented the negative influence of landscape changes in usable space over a 9-

year period in Southern Illinois, where the resulting reduction in habitat quality and availability for bobwhites caused a decline in population vital rates, including winter survival. Also, Seckinger et al. (2008) showed that changes in forest understory vegetation that increased usable space for bobwhites had a positive effect on non-breeding season survival.

Positive demographic responses to edge habitat types have been shown in wintering birds that preferentially forage in areas near escape cover (Grubb and Greenwald 1982, Best et al. 1990, Lima 1990, Watts 1991). Such habitat use patterns positively influence survival by reducing individual vulnerability to avian predators while foraging (Roth et al. 2006). Because avian predators are the largest source of bobwhite predation during the non-breeding season (Chapter 2, Stoddard 1931, Seckinger et al. 2008, Sisson et al. 2009) selection of home ranges with more woody edge (i.e. more usable space) is likely a comparable adaptive behavior that minimizes exposure to predation or reduces predator success (Brown and Litvaitis 1995). In previous analyses we showed that movements were lower in areas with higher edge density (Chapter 3), which may also reduce individual vulnerability to predators (Williams et al. 2000, Folk 2006).

Although home range edge density models were best supported, high ranking models at the landscape scale had significant effect sizes and offered insights into additional factors that influenced survival. The best supported landscape scale model showed that survival decreased with higher proportions of perennial cover (grasslands and pasture/ hay fields) in the landscape. Similar models at the home range scale were not supported, which suggests that landscape-scale influences of perennial cover had more influence on survival than perennial cover at smaller scales. The next best supported landscape-scale model showed a positive influence of row crop habitat on survival. Home ranges in the study areas were generally established in either grassland or row crop dominated landscapes (Chapter 4) and the inverse effect of these landscapes on survival suggests a fitness-tradeoff among them. Differences in survival among the 2 landscapes likely related to the influence of habitat composition on distribution of predators in agricultural landscapes. In these systems, predators respond to habitat composition (Gehring and Swihart 2003, Wilson et al. 2010) and abundance of primary prey species (i.e. small mammals or passerines: Preston 1990) in different cover types and habitat patches. Previous research on mammalian and avian predators in agricultural landscapes has shown that they are more likely to occur in landscapes with grassland cover than landscapes dominated by row crop fields (Kuehl and Clark 2002, Gehring and Swihart 2003, Roth et al. 2008, Wilson et al. 2010). Because generalist predators depend on a diversity of prey species in such landscapes (Andersson and Erlinge 1977), opportunistic predation on bobwhites may be greater in areas where increased perennial cover supports higher prey populations and therefore facilitates increased predator activity (Brown and Litvaitis 1995, Redpath and Thirgood 1999). Although do not have empirical evidence to support the relationship between predator distribution and landscape composition within sites, we found that avian predators were more abundant on sites with more grassland cover (A. Janke unpublished data).

The relationship between predator distribution and survival in natural systems is well established in avian nest survival studies (Angelstam 1986, Zanette and Jenkins 2000, Phillips et al. 2003, Pieron and Rohwer 2010) and has been previously documented with gallinaceous birds (Redpath and Thirgood 1999, Seckinger et al. 2008, Robinson et al. 2009). Redpath and Thirgood (1999) reported that red grouse (*Lagopus lagopus*) survival in Scotland was lower on moors where higher prey densities supported higher densities of hen harriers (*Circus cyaneus*), a primary predator of grouse in their study. Similarly, Taylor et al. (1999) postulated that increased survival of bobwhites as distances from grassland cover increased in Kansas resulted from landscape-scale processes that influenced predator distribution relative to grassland cover on their study sites.

Landscapes with abundant perennial cover on our study sites had larger grass field sizes and little woody cover. Large interior portions of grass fields that are generally not used by bobwhites attract more avian predators than large crop fields (Wilson et al. 2010). Under Guthery's (1997) definition of bobwhite habitat-- any point on a landscape is either fully usable or not, based on the distribution of adjacent cover types-- interior portions of crop and grass fields are functionally identical for bobwhites during the non-breeding season (i.e. not usable), but the latter may indirectly influence bobwhite survival in nearby habitat. Flock (2006) found that grassland cover (CRP fields) had a negative influence on bobwhite survival in Kansas, and suggested that the relationship resulted from the absence of woody vegetation in CRP fields. The consistency between our results suggests that landscapes with high amounts of perennial cover and little woody cover may decrease bobwhite survival rates during the non-breeding season by providing less suitable habitat (woody cover) and influencing spatial distribution of predators. Arguably, such landscapes may offset non-breeding season losses by supporting reproduction during the breeding season (Roseberry and Klimstra 1984, Collins et al. 2009, Lohr et al. 2011) but population growth rates in bobwhites are less sensitive to changes in reproduction than to changes in non-breeding season survival (Sandercock et al. 2008).

MANAGEMENT IMPLICATIONS

More than 80 years of bobwhite research has led to a firm understanding of factors affecting population growth rates (Sandercock et al. 2008, Demaso et al. 2011) and habitat suitability for bobwhites in a variety of landscapes (Guthery 1997). Despite this knowledge, bobwhite populations have consistently declined across most of their range in the last century (Church et al. 1993). The decline is generally attributed to changes in land-use practices (Brennan 1991) and the influence of those changes on bobwhite habitat availability and quality at multiple spatial scales (Williams et al. 2004). Increased landscape heterogeneity (Warner 1994) and fragmentation of agricultural landscapes throughout the bobwhite range has changed predator communities (Andren 1994). Changes in habitat availability and quality, coupled with changes in predator communities in agricultural landscapes, may interact to influence individual fitness (Evans 2004, Whittingham and Evans 2004) and potentially influence population declines in agricultural landscapes (Evans 2004) or at least suppress local populations (Rollins and Carroll 2001, Cresswell 2011).

Conservation efforts aimed at improving population growth rates should focus on the most influential vital rates (Bradbury et al. 2001). Survival is the most important vital rate (Sandercock et al. 2008) in bobwhites, and non-breeding season survival is more important than breeding season survival for northern populations (Guthery et al. 2000, Folk et al. 2007). Therefore, our analysis of the influence of habitat on survival during this period in a northern population should help in developing effective conservation efforts to increase survival by reducing predation. Our results show that the availability of usable habitat within the home range (as determined by woody edge density) is the most important determinant of survival in this population. Therefore management strategies that increase woody cover near food sources (e.g. row crop or grassland fields) will have the greatest impact. Because of the landscape scale influences we observed, such efforts should focus on landscapes with intermediate amounts of perennial cover that may support lower predator populations while still providing appropriate habitat types for bobwhites throughout their life-cycle.

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CHAPTER 6: MANAGEMENT IMPLICATIONS

> *"One of the characters common to the entire range of quail in the north central region is that every farm has good quail cover from May to December, but that most farms have deficient winter cover or often none at all" Leopold (1931:70)*

In Game Survey of the North Central States, Leopold (1931) began the technical portion of his report with a detailed account of the present status of northern bobwhites (*Colinus virginianus*; hereafter bobwhite) in the North Central states, including Ohio. Therein, he identified winter cover as the primary factor affecting suitability of farms in the region and described the factors leading to loss of suitable woody cover. Arguably, continued lack of appropriate winter cover during periods of snow cover is the most important factor determining the ability of modern farms to support bobwhite populations in agricultural landscapes in Ohio. Although my research only investigated ecology of Ohio bobwhites during the non-breeding season, low observed survival rates, and the disproportionate effect of that vital rate on population growth rates (Folk et al. 2007, Sandercock et al. 2008), supports this assertion. The importance of winter cover may also increase as the frequency of severe winter storm events (i.e. snow accumulation) increases with climate change (Hayhoe et al. 2010). Without sufficient winter cover, breeding season gains may be negated and populations will continue to decline.

Non-breeding season habitat for bobwhites in agricultural landscapes in Ohio comprises 3 habitat types; row crops, grasslands, and woody cover. As any site becomes dominated by 1 cover type, a commensurate decrease in habitat suitability for bobwhites can be expected. Such a relationship has been shown in agricultural landscapes in relation to forest cover (Riddle et al. 2008), and my analyses suggested the same relationship with grasslands and row crops. Thus, management strategies that focus exclusively on providing a single cover type will be less effective than strategies that focus on providing more balanced amounts of several cover types.

Of the 3 necessary habitat types for bobwhites, woody cover is the most important. I supported this relationship by showing that woody cover was selected for in the establishment of home ranges, in the positioning of the core use area within home ranges, and in point-specific locations throughout the season. I also showed a fitness-related benefit of woody edge density, which supports the importance of woody cover to habitat suitability and non-breeding season survival. Field observations and third-order point compositional analysis suggested that woody cover was available from 2 cover types; woody fencerows or ditches or in forest understories. With the challenges of maintaining woody cover in fencerows or along ditches in agricultural landscapes (Best 1983, Demers et al. 1995), forests may represent an opportunity area for active management to provide woody cover in such landscapes (Chapman et al. 2011). Any active forest management practice that opens the overstory and stimulates growth of early successional woody vegetation is likely to benefit bobwhites (e.g. timber harvesting, cutting firewood). However, a focus on reducing canopy coverage along forest edges through edge feathering may be the most effective practice for bobwhite habitat management on private lands. Edge feathering provides early successional woody vegetation along forest edges by felling trees into the forests, felling trees into adjacent fields, or by planting woody shrubs along forest edges. Such an edge-focused habitat management approach is unlikely to have significant effects on crop production, and will increase usable space for bobwhites during the non-breeding season.

Distribution of woody cover influences the suitability of row crop and grassland habitat; areas near woody cover are usable whereas areas away from woody cover are not (Guthery and Bingham 1992, Guthery 1999). The primary value of row crop and grass cover during the non-breeding season is as a food source (Errington and Hamerstrom 1936). Row crop fields are often undervalued in bobwhite management because they are generally overabundant. However, my analyses and others have shown that row crop fields are an important component of bobwhite habitat (Williams et al. 2000, but see Guthery et al. 2001) and deserve consideration in comprehensive management plans. One simple management strategy that may improve the contribution of row crop habitat to bobwhites during the non-breeding season is to leave rows of unharvested crops along field edges adjacent to woody cover. By leaving standing crops, bobwhites can access food close to escape cover during periods of snow cover, which could reduce predation (Errington and Hamerstrom 1936, Roseberry 1964).

Grassland habitat influenced the spatial distribution of coveys throughout the non-breeding season. The importance of grasslands results from their influence on the distribution of bobwhites during covey formation (Agee 1957) resulting from their use during the breeding season (Roseberry and Klimstra 1984, Taylor et al. 1999, Collins et al. 2009). However, selection for grassland cover decreased as the proportion of an area in grassland cover increased. Additionally, landscapes with more perennial cover (grasslands or pasture/ hay fields) were associated with lower survival. Such a relationship between grassland cover and bobwhite survival and habitat suitability suggests that efforts to provide small areas of usable grassland cover may be more effective than focusing on establishment of large areas of grassland cover.

Grasslands may be more valuable for bobwhites if they are managed to provide a diversity of forbs, grasses, and woody cover. Regulations on land enrolled in the CRP generally prohibit growth of woody cover, which resulted in large fields in my study being unsuitable habitat. However, fields that had abundant forbs (e.g. Partridge pea [*Chamaecrista fasciculata*] or Illinois bundle flower [*Desmanthus illinoensis*]) or woody vegetation were used throughout the winter. Herbaceous field borders (i.e. CP-33 under the CRP), which provide grassland cover near crop field edges, may also be an effective way of improving the suitability of lands enrolled in the CRP for bobwhites in Ohio (Burger et al. 2006). Such strategies have been shown to increase bobwhite populations in the southern portion of their range (Palmer et al. 2005, Riddle et al. 2008) but have not been thoroughly evaluated in the north. Because of the importance of food near woody cover for bobwhites however, field border programs should focus on establishing forbs and allowing woody growth that is resilient to snow accumulation. If such practices provide only grassland cover, they may serve as a barrier between woody vegetation and food sources in row crop fields during periods of snow cover, which may negatively affect bobwhite survival.

Grasslands are an important and necessary component of bobwhite habitat in Ohio and across the bobwhite range. Replacement of native grasses (e.g. warm season bunch grasses) with tame grasses (cool season sod-forming grass) on modern farms has undoubtedly contributed to bobwhite population declines, and landscapes devoid of suitable grassland cover are unlikely to support bobwhite populations. However, classifying bobwhites as grassland birds and using that status to promote the establishment of grasses has become dogma in bobwhite management. Such a narrow focus in the northern portion of the bobwhite range is unlikely to improve population growth rates because of the limiting nature of winter cover (Leopold 1931) and disproportionate influence of winter survival on population growth rates (Folk et al. 2007, Sandercock et al. 2008). In focusing exclusively on grassland establishment for bobwhite conservation in Ohio, we have arguably ‘lost the forest for the trees,’ as grasslands are only 1 of the necessary elements of bobwhite habitat. Traditional practices under the CRP that focus on establishing large-tracts of grassland cover will continue to be ineffective at improving bobwhite habitat suitability on a large scale in Ohio. Evidence for the inability of grass-focused conservation practices to reverse population declines alone is in the 76% population decline that occurred in Ohio during 1984-2004 (Spinola and Gates 2008); the first 19 years of the CRP following the passage of the Food Security

Act of 1985. The suitability of large herbaceous CRP fields for bobwhites during the non-breeding season is entirely contingent on adjacent cover types (i.e. presence or absence of woody cover). In landscapes devoid of woody cover, such practices will not improve bobwhite habitat suitability. Conservation efforts targeting bobwhites should shift focus from large field enrollment to increasing usable space (Williams et al. 2004). Increased usable space in Ohio will be realized by increasing availability and distribution of early successional woody cover in association with grassland cover in agricultural landscapes.

Some conservation practices under the CRP have provisions that facilitate establishment or maintenance of woody cover in Ohio (CP-33, CP-42, CP-4D, CP-3A, Ohio Pheasant SAFE CP-38E) and thus could be used to compensate producers for providing woody cover along with grassland cover. Additional incentives to use woody cover and a refined focus among professionals on usable space, rather than exclusively grasslands, may promote inclusion of woody cover in new contracts. Additionally, many state agencies have developed State Acres for Wildlife Enhancement (SAFE) programs under the CRP that focus specifically on bobwhite habitat. Such a practice may be effective in Ohio if the focus is on providing diverse forbs and early successional woody cover in the core of the bobwhite range in the state. Conservation efforts should initially be narrowly focused in priority regions with bobwhite populations so as to increase local densities to guard against population level Allee Effects. As local gains are made, efforts can be expanded to increasingly larger landscapes (Terhune et al. 2009).

Bobwhite populations continue to decline across their range as landscapes become increasingly homogenized and interest in bobwhite conservation fades with an aging generation that witnessed the most recent decline firsthand. Despite the grim outlook, modern conservation efforts are progressively more focused on wildlife conservation on private lands, and strategic landscape-level habitat planning for bobwhites through the National Bobwhite Conservation Initiative will aid in effective delivery of bobwhite conservation (Palmer et al. 2011). Although traditional agricultural practices produced bobwhite populations that are unlikely to be realized again in the Midwest (Leopold 1933, Dailey 2002), bobwhites continue to be a by-product of agricultural production across the Midwest, albeit a diminishing one (Peterson et al. 2002, Veech 2006). Because conversion to historical production practices is not a feasible means to restore viable bobwhite populations (Peterjohn 2003), contemporary management should focus on opportunity areas within current agricultural landscapes, such as forest edges or field margins, to provide suitable winter cover and improve population growth rates.

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Appendix A: Candidate model set for body mass analysis

Table A.1. Candidate model set of factors affecting body mass of northern bobwhites captured on 4 study sites in southwestern Ohio during the non-breeding season (October-March 2009-2011).

Model[a]	*k*	AIC	ΔAIC	w_i
SNOW + Year + SNOW * Year	4	3434.05	0.000	1.000
SNOW + Year	3	3493.60	59.546	0.000
Year	2	3494.26	60.207	0.000
Study Day	2	3528.98	94.928	0.000
SNOW + Technique + SNOW * Technique	4	3530.05	95.993	0.000
Technique	2	3530.37	96.318	0.000
SNOW + Technique	3	3532.64	98.584	0.000
SNOW	2	3540.50	106.445	0.000
Null	1	3543.36	109.310	0.000

[a] SNOW= snow depth (cm) on day of capture; Technique = capture technique (mist nets or traps); Study Day = capture date within year (1-182)

Appendix B: Candidate model set for residency time analysis

Table B.1. Ranking of all candidate models in analysis of habitat and weather effects on residency time for northern bobwhites on 4 study sites in southwestern Ohio during the non-breeding season (October- March 2009-2011).

Model [a]	k^b	$AIC_C{}^b$	$\Delta AIC_C{}^b$	$w_i{}^b$
Edge + Temp + Snow	4	9414.67	0.000	0.361
Edge + Temp + Edge x Temp	4	9414.84	0.167	0.332
Edge + Temp	3	9415.71	1.037	0.215
Day + ESH + ESH x Day	4	9418.29	3.615	0.059
ESW + Temp + Snow	4	9421.12	6.446	0.014
ESW + Temp	3	9422.75	8.073	0.006
Snow + Temp	3	9423.33	8.653	0.005
Temp	2	9424.72	10.043	0.002
ESW + Temp + ESW x Temp	4	9424.81	10.132	0.002
Snow + Temp + Snow x Temp	4	9425.61	10.938	0.002
ESH + RCR + ESH x RCR	4	9447.22	32.545	0.000
Day + Year + Day x Year	4	9449.02	34.343	0.000
Day + ESW + ESW x Day	4	9451.01	36.338	0.000
Day + Year	3	9454.68	40.008	0.000
Day	2	9455.85	41.173	0.000
SnowDay + FreezeDay	3	9468.03	53.353	0.000
Edge + Snow + Edge x Snow	4	9478.61	63.932	0.000
FreezeDay	2	9482.48	67.803	0.000
RCR + ESH	3	9484.65	69.972	0.000
ESW + RCR + ESH	4	9486.98	72.308	0.000
Edge + Snow	3	9487.24	72.566	0.000
RCR	2	9488.16	73.483	0.000
ESW + RCR	3	9490.08	75.410	0.000
SnowDay	2	9495.31	80.637	0.000

Continued

Table B.1 Continued

Model [a]	k^b	AIC_C^b	ΔAIC_C^b	w_i^b
Snow	2	9498.77	84.100	0.000
ESW + Snow	3	9498.80	84.125	0.000
ESW + Snow + ESW x Snow	4	9499.83	85.154	0.000
ESW + ESH + FOR	4	9501.11	86.432	0.000
ESH	2	9507.96	93.286	0.000
ESW + ESH	3	9509.04	94.362	0.000
Duration	2	9516.01	101.331	0.000
Edge	2	9531.46	116.790	0.000
Diversity	2	9533.94	119.262	0.000
Year	2	9543.00	128.324	0.000
FOR	2	9545.29	130.614	0.000
Null	1	9545.64	130.970	0.000
FOR + ESW	3	9546.71	132.032	0.000
ESW	2	9547.03	132.352	0.000

[a] Edge = woody edge density (m/ ha); Temp = average daily temperature (C); Snow = average snow depth (cm); ESH= % early successional herbaceous vegetation; ESW= % early successional woody vegetation; FOR = % forest; Diversity= Shannon diversity index of cover types; SnowDay= days with > 5 cm snow; FreezeDay = days < 0 C; DAY = linear trend for day within year

[b] *k*= number of parameters; AIC_c= AIC corrected for small sample sizes; ΔAIC_c= Difference between AIC_c for best model and model *i*; w_i=Akaike weight

Appendix C: Candidate model set for habitat use and survival analysis

Table C.1. Ranking of all candidate models in analysis of habitat effects on survival of northern bobwhites on 4 study sites in southwestern Ohio during the non-breeding season (October- March 2009-2011).

Scale[a]	Model[b,c]	*k*	$QAIC_c$	$\Delta QAIC_c$	w_i
HR	Time + ESW Edge	4	1039.39	0.000	0.428
HR	Time + ESW Edge + ESW Edge ^2	5	1040.77	1.380	0.214
HR	Time + FOR Edge + ESW Edge	5	1040.92	1.528	0.199
LA	Time + %ESH + %PHA	5	1044.87	5.480	0.028
LA	Time + %RCR	4	1046.99	7.600	0.010
--	Time	3	1047.33	7.945	0.008
HR	Time + FOR Edge	4	1047.44	8.055	0.008
HR	Time + %ESH	4	1047.79	8.400	0.006
Site	Time + Site	6	1047.86	8.468	0.006
LA	Time + %ESH	4	1048.09	8.703	0.006
HR	Time + %FOR	4	1048.22	8.831	0.005
MI	Time + %ESH	4	1048.29	8.897	0.005
MI	Time + %ESW	4	1048.33	8.937	0.005
MI	Time + %ESH + %ESW	5	1048.35	8.959	0.005
MI	Time + %RCR	4	1048.63	9.237	0.004
LA	Time + FOR Edge	4	1048.66	9.268	0.004
LA	Time + %RCR + %RCR^2	5	1048.66	9.273	0.004
HR	Time + SHDI	4	1048.78	9.396	0.004
HR	Time + ESH Edge	4	1048.80	9.407	0.004
HR	Time + %ESW	4	1049.01	9.625	0.003
LA	Time + ESH Patch + FOR Patch + RCR Patch	6	1049.09	9.697	0.003
LA	Time + SHDI	4	1049.11	9.722	0.003
LA	Time + ESH Edge	4	1049.15	9.757	0.003
HR	Time + %RCR	4	1049.21	9.820	0.003

Continued

Table C.1 Continued

Scale[a]	Model[b,c]	k	$QAIC_c$	$\Delta QAIC_c$	w_i
HR	Time + %ESH + %ESW	5	1049.22	9.836	0.003
LA	Time + %ESH + %ESH^2	5	1049.23	9.838	0.003
LA	Time + ESW Edge	4	1049.26	9.875	0.003
LA	Time + %FOR	4	1049.28	9.894	0.003
MI	Time + %FOR	4	1049.32	9.935	0.003
HR	Time + FOR Edge + FOR Edge ^2	5	1049.35	9.958	0.003
HR	Time + %ESH + %ESH^2	5	1049.79	10.397	0.002
HR	Time + %ESW + %FOR	5	1049.79	10.404	0.002
MI	Time + %RCR + %ESH	5	1050.05	10.663	0.002
LA	Time + FOR Edge + FOR Edge ^2	5	1050.43	11.043	0.002
LA	Time + %ESH + %FOR + %RCR	6	1050.48	11.089	0.002
LA	Time + ESW Edge + ESW Edge^2	5	1050.77	11.384	0.001
LA	Time + ESH # Patch + FOR # Patch + RCR # Patch	6	1051.16	11.769	0.001

[a] HR= home range scale model; LA= landscape scale model; MI = microhabitat scale model; ES = early successional

[b] ESW = early successional woody; ESH = early successional herbaceous; FOR = forest; RCR = row crop; EDGE = edge density

[c] Time = baseline temporal model (Null)

Appendix D: Study site habitat compositions

Table D.1. Habitat composition (%) of 4 study sites used to investigate non-breeding season habitat use of northern bobwhites in southwestern Ohio during October- March 2009-2011.

Habitat[a]	Fee	Peach	Thurner	Wildcat	Total
CRP Cool-season	8.36	16.49	3.01	14.54	9.73
CRP Warm-season	1.26	0.39	0.47	1.60	1.06
CRP Woody	0.00	0.07	0.00	0.26	0.08
Ditch	1.94	2.54	2.37	1.73	2.05
Fencerow	1.14	0.64	2.05	1.43	1.36
Forest	8.35	28.61	16.05	10.41	13.10
Grass Waterway	1.95	0.25	0.16	0.12	0.87
Hay	1.18	2.88	2.96	11.49	4.45
Non habitat	4.07	4.05	7.37	3.97	4.79
Old field- herbaceous	0.19	1.99	7.56	3.47	2.92
Old field- woody	0.29	1.54	2.14	0.80	0.99
Pasture	1.13	1.10	2.52	12.22	4.29
Row Crop	70.13	39.45	53.33	37.97	54.31

[a] CRP = Conservation Reserve Program

Appendix E: Home range and core use area habitat compositions

Table E.1. Habitat composition (%) of northern bobwhite home range and core use areas from 4 study site in southwestern Ohio during November- March 2009-2011

	Core Use Area (50% Isopleth)					Home Range (95% Isopleth)				
	Fee	Peach	Thurner	Wildcat	Total	Fee	Peach	Thurner	Wildcat	Total
CRP Cool season	19.55	13.75	0.01	12.38	12.09	19.46	11.88	1.38	16.21	14.04
CRP Warm season	14.94	0.00	0.00	7.66	7.72	9.03	0.00	0.00	4.96	4.82
CRP Woody	0.00	0.64	0.00	2.89	1.42	0.00	0.53	0.00	1.58	0.79
Ditch	7.48	16.01	4.53	4.36	5.96	8.03	8.51	3.12	2.99	4.72
Fencerow	4.95	8.13	2.64	5.85	5.15	2.89	3.41	2.37	3.74	3.23
Forest	9.29	8.80	31.85	11.78	14.68	8.86	7.41	17.79	9.70	10.85
Grass Waterway	1.00	2.07	0.00	0.15	0.47	1.01	1.12	0.03	0.10	0.40
Hay	1.09	6.98	1.63	9.91	5.79	1.73	8.13	5.08	10.83	7.12
Non habitat	3.78	1.23	3.97	3.93	3.73	2.65	1.87	6.88	3.89	3.99
Old field- herbaceous	0.12	1.71	16.62	4.92	5.61	0.14	1.05	16.70	3.45	4.89
Old field- woody	5.13	0.00	14.70	3.31	5.73	2.78	2.90	9.34	1.75	3.53
Pasture	0.00	0.00	3.35	6.12	3.56	0.43	0.32	5.03	6.06	3.98
Row Crop	32.65	40.68	20.70	26.75	28.08	42.99	52.87	32.28	34.74	37.64

[a] CRP = Conservation Reserve Program

Appendix F: Covey telemetry location habitat composition

Table F.1. Habitat composition (%) of telemetry locations (*n* = 4,485) of radiomarked northern bobwhite coveys (*n* = 48) on 4 study sites in southwestern Ohio during October – March 2009-2011.

Habitat[a]	Fee	Peach	Thurner	Wildcat	Total
Beans	0.78	1.15	0.51	0.63	0.68
Corn	11.15	7.32	0.62	2.58	4.83
CPP Warm season	2.22	4.76	0.00	3.46	2.56
CRP Cool season	20.62	6.84	0.15	10.06	10.86
CRP Woody	4.78	0.91	0.00	6.60	4.52
Ditch	18.24	43.83	10.35	16.62	17.58
Fencerow	17.03	15.28	15.55	28.34	22.06
Forest edge	16.60	12.14	25.31	11.07	15.30
Forest interior	3.68	0.81	14.39	3.48	5.41
Non habitat	0.30	0.00	0.29	0.54	0.39
Old Field - herbaceous	3.93	0.00	20.83	5.04	7.39
Old Field - woody	0.13	0.91	11.01	4.42	4.27
Pasture/ Hay	0.00	2.95	0.60	6.32	3.33
Waterway	0.55	3.10	0.37	0.83	0.81

[a] CRP = Conservation Reserve Program