



RESEARCH ARTICLE

Habitat influences Northern Bobwhite survival at fine spatiotemporal scales

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ABSTRACT

Habitat quality influences individual survival at widely varying spatial and temporal scales. Understanding interactions between habitat and survival among individuals in declining populations that occupy highly modified landscapes can inform conservation strategies aimed at improving survival and population growth. We used radiotelemetry to monitor space use and daily survival of wintering Northern Bobwhites (*Colinus virginianus*) at the northern end of their range to test for fine spatial- and temporal-scale relationships between individual survival and habitat composition around radio-locations in agricultural landscapes in Ohio, USA. Habitat composition within daily and seasonal movement ranges of individuals ($n = 189$) during periods without snow cover did not explain variation in daily survival rates. However, mortality increased substantially in the presence of snow cover, and availability of woody cover and row crops within 95 m of an individual radio-location were positively associated with daily survival during those periods. A similar relationship between row crop availability and survival was supported at a larger scale that reflected composition of seasonal ranges (300-m buffer) but was less influential than fine-scale influences of woody cover and row crops. Our results suggest that previously documented selection for woody cover in our agricultural study areas was an adaptive behavior to improve individual survival during periods of snow cover. Positive associations between survival and row crop cover at daily and seasonal range scales suggest that agricultural landscapes confer improved survival probabilities when underlying constraints on occupancy related to woody cover are met. Collectively, our results suggest that targeted conservation practices focused on provision of suitable woody cover in agricultural landscapes in the northern end of the Northern Bobwhite's range has potential to improve winter survival and perhaps abate long-term population declines in the region.

Keywords: agricultural landscape, *Colinus virginianus*, generalized linear mixed models, habitat, Northern Bobwhite, radiotelemetry, survival, winter weather

El hábitat influencia la supervivencia de *Colinus virginianus* a escalas espaciotemporales finas

RESUMEN

La calidad del hábitat influencia la supervivencia de los individuos a escalas espaciales y temporales muy diversas. Entender las interacciones entre el hábitat y la supervivencia de individuos de poblaciones en disminución que ocupan paisajes muy modificados puede aportar a las estrategias de conservación que buscan aumentar la supervivencia y el crecimiento poblacional. Empleamos radio telemetría para monitorear el uso del espacio y la supervivencia diaria de individuos invernantes de *Colinus virginianus* en el extremo norte de su rango, y evaluamos las relaciones espaciales y temporales a escala fina entre la supervivencia individual y la composición del hábitat alrededor de las localizaciones de radio en paisajes agrícolas en Ohio. La composición del hábitat dentro de los rangos de movimiento diarios y estacionales de los individuos ($n = 189$) durante periodos sin cobertura de nieve no explicaron la variación en las tasas de supervivencia diaria. Sin embargo, las tasas de mortalidad aumentaron enormemente con la presencia de cobertura de nieve, y la disponibilidad de cobertura boscosa y de cultivos en surco dentro de los 95 m desde la radiolocalización de un individuo estuvieron positivamente asociadas con la supervivencia diaria durante estos periodos. Una relación similar entre la disponibilidad de cultivos en surco y la supervivencia fue apoyada a una escala más grande que reflejó la composición de los cambios estacionales (300 m de amortiguamiento), pero fue menos influyente que los efectos a escala fina de la cobertura boscosa y los cultivos en surco. Nuestros resultados sugieren que la selección de cobertura boscosa documentada previamente en nuestras áreas de estudio agrícolas fue un comportamiento adaptativo para mejorar la supervivencia individual durante los periodos de cobertura de nieve. Las asociaciones positivas entre la supervivencia y la cobertura de cultivos en surco en rangos de escala diaria y estacional sugirieron que los paisajes agrícolas brindan mejores probabilidades de supervivencia cuando se cumplen las restricciones subyacentes relacionadas a la cobertura boscosa. De modo colectivo, nuestros resultados sugieren que las prácticas de

conservación enfocadas a la provisión de cobertura boscosa adecuada en los paisajes agrícolas en el extremo norte del rango de *C. virginianus* tienen potencial para mejorar la supervivencia invernal y tal vez disminuir las declinaciones poblacionales de largo plazo en la región.

Palabras clave: clima de invierno, *Colinus virginianus*, hábitat, modelos lineales mixtos generalizados, radio telemetría, supervivencia

INTRODUCTION

Environmental conditions encountered during the non-breeding period can affect individual fitness indirectly through physiological impacts on subsequent reproduction (i.e. carryover effects; Harrison et al. 2011) or directly via mortality (McNamara and Houston 1986). Many behavioral and physiological traits (e.g., Hilton et al. 1999, Swanson 2010, Carr and Lima 2014) have evolved to improve survival and thermoregulation of wintering birds to facilitate efficient foraging and metabolism during periods of cold or food limitation (Lima 1986, 1990). Habitat selection is an important and measurable behavior used to improve nonbreeding-season survival and, therefore, fitness among wintering birds.

Habitat selection should improve fitness through intrinsic (e.g., ability to escape predation) and extrinsic (e.g., predator abundance and resource availability) mechanisms (Block and Brennan 1993). Extensive research on avian nesting ecology and habitat selection revealed a high degree of flexibility in nest-site selection and behavioral responses to predation or resource availability during the breeding season (e.g., Rodewald and Yahner 2001, Thomson et al. 2006, Marzluff et al. 2007). However, links between fitness (i.e. survival) and habitat selection among wintering birds are more equivocal. Some experimental work with wintering birds has shown evidence for relationships between predator densities and survival (Redpath and Thirgood 1999, Thirgood et al. 2002) or fine-scale plasticity in foraging behavior in response to predation (Grubb and Greenwald 1982, Watson et al. 2007). However, knowledge of fine-scale relationships between individual daily survival and habitat selection in wintering resident birds is limited.

Northern Bobwhites (*Colinus virginianus*) are ground-dwelling resident birds with a wide geographic distribution in eastern North America (Brennan 1999). Northern Bobwhites are characteristically poor dispersers (Lehmann 1946, Murphy and Baskett 1952, Smith et al. 1982) that exhibit strong seasonal selection for habitats (e.g., Williams et al. 2000, Lohr et al. 2011, Janke and Gates 2013) and have low annual survival driven by diverse predator assemblages (Burger et al. 1994, Rollins and Carroll 2001, Cox et al. 2004, Terhune et al. 2007). Life-history theory predicts that low survival in *r*-selected species should have less influence on population growth rates than breeding productivity (Sæther and Bakke 2000, Stahl and

Oli 2006), which has been supported with empirical research from Northern Bobwhite populations at southern latitudes (DeMaso et al. 2011). However, Northern Bobwhite populations along the northern tier of their geographic distribution in the Midwest and Mid-Atlantic states have characteristically low and variable winter survival (e.g., Roseberry and Klimstra 1984, Burger et al. 1994, Lohr et al. 2011, Janke and Gates 2012) that more strongly influences population growth rates than breeding-season vital rates (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012, Williams et al. 2012). Therefore, winter survival is an important population vital rate and a potentially strong determinant of individual fitness among Northern Bobwhites in northern populations. Thus, natural selection should favor habitat selection behavior that confers the greatest survival advantages throughout the nonbreeding period.

Previous studies of Northern Bobwhites have determined that low winter survival can be exacerbated by severe winter weather (Robel and Kemp 1997, Janke and Gates 2012) and that selection for certain habitat elements (e.g., woody cover) could mediate these effects, especially in landscapes with deficient winter cover (Williams et al. 2000, Hughes et al. 2005, Seckinger et al. 2008). We asked whether habitat selection affected daily survival of radio-tagged Northern Bobwhites in a declining population in Ohio, USA (Spinola and Gates 2008). Previous work in this population found that Northern Bobwhites selected fine-grained habitat elements associated with woody cover, row crop fields, and herbaceous cover in our agricultural study areas at home-range and daily-use location scales. We postulated that the variability in home-range habitat composition and landscape characteristics throughout our study area would lead to measurable variation in survival associated with habitat around individual radio-locations. We also predicted that such influences may be dependent on the presence of snow because of the previously documented potential for high mortality and behavioral shifts common among Northern Bobwhites in the presence of snow (Roseberry 1964, Janke and Gates 2012).

METHODS

Study Area

We worked on 4 privately owned study sites in Highland and Brown counties in southwestern Ohio. Sites occurred near the southern periphery of the glacial extent in Ohio

and therefore had relatively weathered silt-loam soils and rolling topography (4.5–9.7% slopes). Site area ranged from 400 to 1,200 ha and occurred in landscapes distributed across a gradient from highly agricultural (39–72% of land area within 10 km of sites was cropland and pasture) to forested (20–50% forested within 10 km). Habitat composition within study sites spanned a similar gradient, with forest cover ranging from 8% to 29% and agricultural cover ranging from 41% to 75%. Grasslands were present on all sites, with 9–20% grassland cover. Row crop fields were generally planted with corn (35%) or soybeans (61%), and most (91%) had undisturbed residual crop cover (i.e. no-till) throughout winter. Upland woodlots were primarily composed of oaks (*Quercus* spp.) and hickories (*Carya* spp.) and typically had closed canopies with little understory vegetation. Riparian and bottomland woodlots also had closed canopies and were composed of black walnut (*Juglans nigra*), elms (*Ulmus* spp.), and green ash (*Fraxinus pennsylvanica*). Grass fields were either enrolled in the Conservation Reserve Program or were fallow fields of herbaceous vegetation. Most grass fields (90%) were cool-season grasses, primarily fescue (*Festuca* spp.) or cool-season bunch grasses such as timothy (*Phleum pratense*) or orchardgrass (*Dactylis glomerata*). Some grass fields were planted with warm-season grasses, primarily Indiangrass (*Sorghastrum nutans*). Fencerows and drainage ditches contributed a small percentage (3%) of the area on each site and were composed of blackberry (*Rubus allegheniensis*), black raspberry (*R. occidentalis*), and multiflora rose (*Rosa multiflora*).

Long-term (30-yr) mean temperature from a weather station near the study sites was 10.5°C during October–March, and mean annual snowfall for the same period was 67.5 cm (National Climate Data Center 2011). Our study was conducted during 2 severe winters with relatively high snowfall (101.6 cm in 2009–2010 and 67.3 cm in 2010–2011) and low temperatures (mean 8.5°C in both winters). There were 51 days with ≥ 2.5 cm of snow during December 1, 2009, to February 28, 2010, and 62 days with ≥ 2.5 cm of snow during December 1, 2010, to February 28, 2011.

Field Methods

We captured Northern Bobwhites using baited funnel traps (Stoddard 1931) and targeted mist netting (Wiley et al. 2012) during October–March, 2009–2011. We attached an aluminum leg band to each individual and recorded its age, sex, and covey affiliation. A subset of individuals in each covey weighing > 165 g were fitted with a 6.6-g ($\leq 4\%$ body mass) mortality-sensing necklace-style radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). We released all birds at capture sites within 30 min.

We monitored survival and habitat use of all radio-tagged individuals during winter (December–February) by recording locations once per day, at least 6 days per week. We located radio-tagged individuals by homing or triangulation from short distances (≤ 20 m; White and Garrott 1990) and recorded locations on a global positioning system (Garmin GPS Map 76; Garmin International, Olathe, Kansas, USA). We opportunistically recorded locations at different times (i.e. mornings or afternoons) on consecutive days to capture a range of diurnal activity patterns. We immediately located transmitters after detecting mortality signals and attempted to confirm that mortalities were not investigator induced (e.g., capture myopathy or transmitter entanglement) on the basis of field signs at recovery sites (Einarsen 1956) and the condition of transmitters. We excluded the first 7 days after capture from each individual encounter history to minimize potential for capture- or transmitter-related biases in survival (Guthery and Lusk 2004, Holt et al. 2009a).

Data Analysis

Many studies have related survival to season-specific metrics of habitat use by radio-tagged individuals (e.g., Thirgood et al. 2002, Moynahan et al. 2006, Seckinger et al. 2008). However, fixed or pooled estimates of habitat use over long periods (e.g., seasons) may obscure factors that influence survival at finer spatial and temporal scales. Logistic regression offers analytical flexibility that can accommodate temporally changing metrics of habitat use or availability and produce informative estimates of daily survival rates of marked individuals in relation to time-dependent covariates (Dinsmore et al. 2002, Arnold et al. 2012). We used generalized linear mixed-effects models to estimate the probability that an individual alive on day i would survive to day $i + 1$ as a function of habitat around radio-locations. Excluding observations when fates were not recorded on subsequent days (e.g., $i + 2$) would have been problematic if our objective had been to estimate seasonal survival rates or if our monitoring frequency was more sporadic. However, we were only interested in understanding the relationship between habitat around daily locations and daily survival probabilities; therefore, the analysis was appropriate because there was no bias on days when a fate was not recorded and because extrapolation to a seasonal survival estimate was not desired.

We divided the analysis into days with snow (≥ 2.5 cm of snow recorded on 1 of the 2 days in the interval) and days without snow to test the influence of habitat on daily survival during periods with and without snow cover. We included individual covey affiliation as a random effect to control for potential dependency among individuals in the same covey (Schmutz et al. 1995, Williams et al. 2003). Covey affiliation was defined as the covey an individual was

associated with on each day and rarely changed during the study (cf. Janke et al. 2013).

We reviewed literature for habitat-related factors that influence survival of Northern Bobwhites and other birds during winter to identify important covariates to test in our analysis. We identified 4 covariates that we hypothesized would influence daily survival rates: woody-edge density, row crop area, early-successional herbaceous cover area, and woodlot area. We predicted that higher woody-edge density would positively influence survival because Northern Bobwhites use woody cover extensively throughout winter (Williams et al. 2000, Janke and Gates 2013) and because woody-edge habitat increases interspersed and provides protective cover near food resources (Guthery and Bingham 1992). The 3 other covariates represented areas of the 3 most abundant cover types on our study areas (woodlots, early-successional herbaceous fields, and row crop fields) and allowed us to evaluate whether dominant habitat types available to individuals on daily and seasonal time scales were associated with variability in daily survival (e.g., Williams et al. 2000, Hughes et al. 2005).

We manually digitized land cover on each site in ArcGIS version 9.3 (ESRI, Redlands, California, USA) over high-spatial-resolution (0.305-m) orthophotographs. We collapsed the digitized site coverage into 6 general categories: early-successional herbaceous, early-successional woody, woodlot, pasture and hay fields, row crop fields, and nonhabitat. Early-successional herbaceous included all fields enrolled in the CRP and idle fields that were dominated by herbaceous vegetation. Early-successional woody was primarily fencerows and ditches with early-successional woody vegetation (i.e. shrubs) in the understory. This category also included patches of woody cover in grass fields that were ≥ 500 m². The woodlot category included all riparian and upland woodlots that were >50 m wide. Pasture and hay included grass fields that were mowed or grazed during the preceding growing season. We classified all residential and commercial properties, roads, and water as nonhabitat. We converted all woody landscape elements (early-successional woody and woodlot) in the habitat coverage to line features to measure woody-edge density, expressed in meters of woody edge per hectare.

We derived habitat covariates from the land-cover data within 95-m-radius and 300-m-radius circular buffers around each radio-location. The 2 scales were intended to represent habitat immediately accessible to an individual on a daily basis (95 m) and larger-scale habitat availability characteristic of seasonal ranges (300 m). The median minimum daily movement rate during winter in our study was 95 m (Janke et al. 2013). Therefore, we considered the 95-m-radius buffer (2.8 ha) to represent habitat immediately accessible to an individual during the

1-day exposure period of the analysis. The 300-m buffer (28.3 ha) represented habitat around the individual at a scale similar to the nonbreeding-season home range of coveys on our study areas (mean home range = 26.1 ha; Janke and Gates 2013). We compared coefficients of variation of covariate values between spatial scales to confirm that the 300-m-scale habitat covariates were less dynamic than those measured at the 95-m scale. A *t*-test confirmed that covariate values at the 95-m scale had a larger coefficient of variation ($CV \pm SE = 1.08 \pm 0.06$) than those at the 300-m scale (0.54 ± 0.03 ; paired *t*-test, $t = 8.5$, $P < 0.001$). Mean correlation among habitat variables measured at the 95-m and 300-m scales was 0.71 (range: 0.59–0.84). Habitat variables measured within scales were not highly correlated (*r* range: 0.04–0.60).

Our objective was to evaluate relationships between survival and habitat covariates on the basis of main effects of individual covariates (i.e. variable selection, *sensu* Burnham and Anderson 2002:167). Therefore, we tested all possible combinations of additive covariates at each spatial scale and interpreted support for individual covariates on the basis of relative importance values and effect sizes of parameter estimates. Relative importance values were calculated as the sum of Akaike's Information Criterion (AIC) weights calculated for each model ($n = 8$ models per covariate per scale; Burnham and Anderson 2002). We also reported weights of null models for comparison and discussion. We interpreted results from the 95-m and 300-m spatial scales individually (scale-specific) and collectively in the same analysis (overall) to understand scale-specific importance and overall relative importance of variables. Relative ranking of scale-specific terms in the overall analysis revealed the most important covariates for survival in our analyses, whereas scale-specific terms revealed relative effects within each scale. We standardized covariate values (*z*-transformation) to facilitate direct comparisons of effect sizes (Schielzeth 2010). We used model averaging to calculate weighted-average coefficients for individual covariates from all models in which the covariate was included (Burnham and Anderson 2002). We calculated standard error of the standardized coefficients following Burnham and Anderson (2004) and interpreted effect sizes with 85% confidence intervals (Arnold 2010). The same analytical procedures were applied to observations from snow days and non-snow days in 2 independent analyses.

RESULTS

We included daily observations from 189 individuals in the analysis. There were 2,670 daily observations and 12 mortalities (0.4%) on days without snow; there were 3,697 daily observations and 80 mortalities (2.2%) on days with snow. Cumulative weights in the analysis on days without

TABLE 1. Model-averaged parameter estimates and cumulative Akiake's Information Criterion (AIC) weights (w_i) from generalized linear mixed models examining daily survival rates of radio-tagged Northern Bobwhites on days with >2.5 cm snow (snow days) and without snow (non-snow days) in relation to standardized habitat covariates measured within 300 m and 95 m of radio-locations in southwestern Ohio, USA, during December–February, 2009–2011.

Scale	Parameter ^a	Cumulative w_i ^b		β	SE	85% CI
		Scale	Overall			
Non-snow days						
–	Null model	–	0.164	–	–	–
300 m	Woody edge	0.413	0.169	–0.117	0.34	(–0.607, 0.374)
	ES herbaceous	0.346	0.142	–0.165	0.32	(–0.626, 0.297)
	Woodlot	0.403	0.165	–0.135	0.33	(–0.616, 0.347)
	Row crop	0.355	0.145	0.106	0.36	(–0.415, 0.627)
95 m	Woody edge	0.333	0.142	0.028	0.33	(–0.441, 0.498)
	ES herbaceous	0.424	0.181	0.184	0.41	(–0.407, 0.776)
	Woodlot	0.362	0.154	0.101	0.37	(–0.438, 0.641)
	Row crop	0.486	0.207	0.264	0.41	(–0.329, 0.857)
Snow days						
–	Null model	–	0.006	–	–	–
300 m	Woody edge	0.480	0.053	0.163	0.13	(–0.025, 0.35)
	ES herbaceous	0.446	0.049	–0.157	0.15	(–0.375, 0.062)
	Woodlot	0.316	0.035	–0.053	0.14	(–0.254, 0.149)
	Row crop	0.709	0.079	0.268	0.14	(0.063, 0.474)
95 m	Woody edge	0.823	0.726	0.302	0.14	(0.103, 0.501)
	ES herbaceous	0.335	0.296	–0.082	0.17	(–0.322, 0.158)
	Woodlot	0.336	0.297	–0.091	0.14	(–0.29, 0.109)
	Row crop	0.812	0.717	0.300	0.14	(0.103, 0.497)

^a ES = Early-successional.

^b Cumulative AIC sum of weights across all models with the covariate included ($n = 8$). Scale = weights from models evaluated against all covariates measured at each spatial scale (i.e. 95 m or 300 m). Overall = weights from models evaluated with covariates measured from both scales (i.e. 95 and 300 m) in the same analysis.

snow cover were similar across all covariates and had little separation from the null model (Table 1 and Appendix Table 2). Model-averaged parameter estimates for covariate effects on days without snow were similarly weak and all contained zero, which suggests that habitat covariates at both spatial scales failed to explain variation in survival on days without snow. By contrast, there was wide separation among cumulative weights of models within scales and overall in the analysis from days with snow cover (Table 1 and Appendix Table 3), which suggests that habitat composition around radio-locations explained additional variation in survival in the presence of snow.

Woody-edge density and row crop area at the 95-m scale had high cumulative weights within the scale-specific models, and their confidence intervals excluded zero (Table 1). Beta coefficients of the model-averaged covariates indicated that above-average woody-edge density and row crop area (Figure 1) were associated with higher daily survival rates. Row crop area within the 300-m buffer was the most important covariate measured at that scale (Table 1) and was positively associated with daily survival (Figure 2 and Table 1). The overall cumulative weights from the snow-day analysis revealed that covariates were more influential at the 95-m scale (w_i

range: 0.296–0.726) than at the 300-m scale (w_i range: 0.035–0.079; Table 1).

DISCUSSION

Winter survival is characteristically low among Northern Bobwhites (Burger et al. 1994, Hughes et al. 2005, Terhune et al. 2007) and can be highly depressed in populations exposed to severe winter weather (Robel and Kemp 1997). Our results indicate that daily variation in habitat composition measured at fine spatial scales around individuals during periods of high mortality influenced daily survival outcomes. Evidence for spatial variation in survival based on relatively fine-scale habitat composition near an individual suggests that mortality risk was spatially heterogeneous across our study area. Previously reported strong selection for woody cover during our study (Janke and Gates 2013) was apparently insufficient to offset high observed mortality, which suggests that Northern Bobwhites in our study area were not distributed in a way that stabilized mortality risk, likely because of constraints on mobility or habitat availability imposed by highly modified agricultural landscapes (Hughes et al. 2005, Lohr et al. 2011).

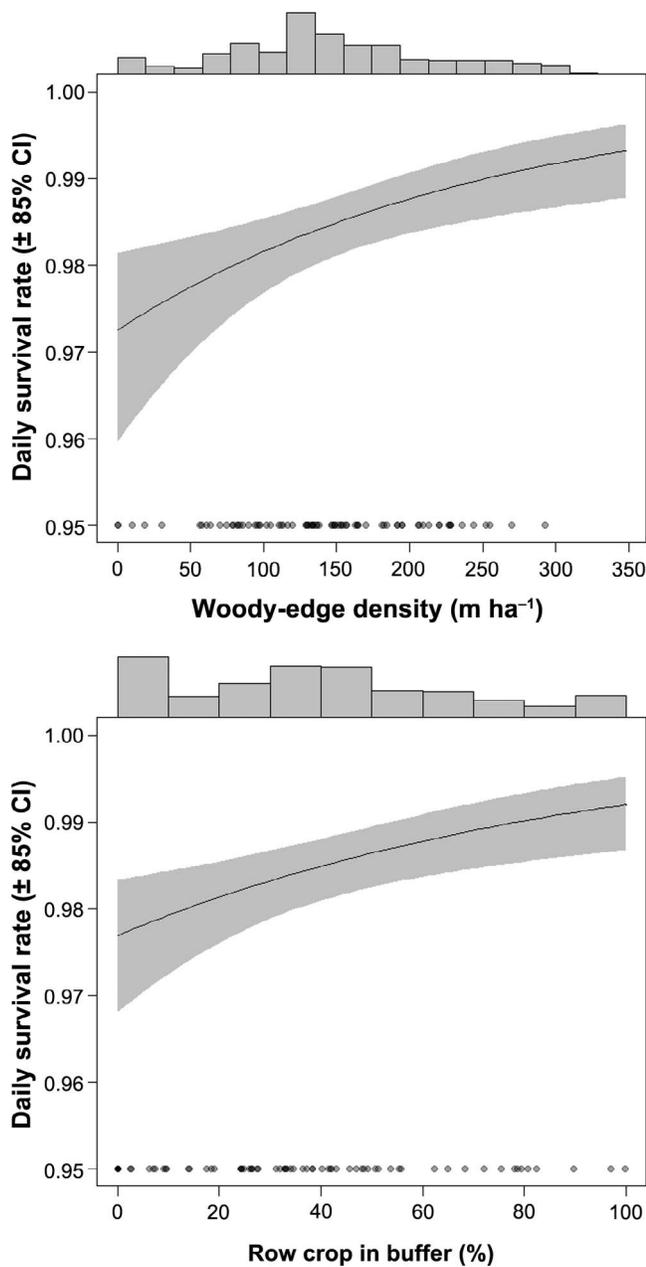


FIGURE 1. Relationship between daily survival and woody-edge density or row crop area (%) within a 95-m-radius buffer of locations of radio-tagged Northern Bobwhites on days with snow cover in southwestern Ohio, USA, during December–March, 2009–2011 (\pm 85% confidence intervals [CI]). Predictions are based on model-averaged regression coefficients across all models that included covariate effects. The histograms at the top of the figures show frequency of observations across the range of covariate values recorded ($n = 3,697$ observations). Points along the bottom represent mortalities during the interval and are shaded to identify overlapping points.

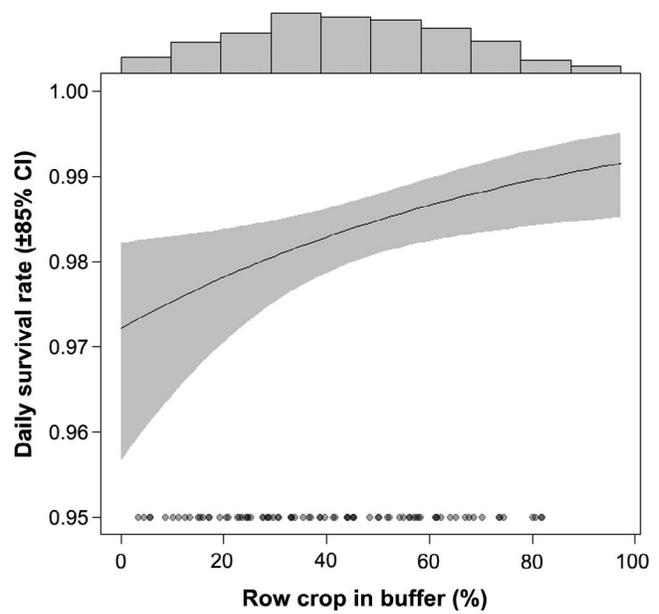


FIGURE 2. Relationship between daily survival rates and row-crop area (%) within a 300-m-radius buffer of locations of radio-tagged Northern Bobwhites on days with snow cover in southwestern Ohio, USA, during December–March, 2009–2011 (\pm 85% confidence intervals [CI]). Predictions are based on model-averaged regression coefficients across all models that included row crop area. The histogram at the top of the figure shows frequency of observations across the range of row crop areas recorded ($n = 3,697$ observations). Points along the bottom represent mortalities during the interval and are shaded to identify overlapping points.

Survival did not vary with habitat composition during periods without snow, which is consistent with previous research on Northern Bobwhite winter survival in an agricultural landscape in the southern portion of their range (Holt et al. 2009b). This homogeneity in mortality risk associated with habitat composition around use locations is also consistent with predictions of a “binary quality model” (Taylor et al. 1999:682), whereby a point in time and space is either fully suitable or unsuitable for Northern Bobwhites (Guthery 1997). In this context, Northern Bobwhites would distribute in an ideal free manner (*sensu* Fretwell and Lucas 1970), ensuring constant fitness probabilities among all habitat patches. However, our results illustrate that introduction of environmental stochasticity associated with winter weather resulted in heterogeneity in mortality risks among habitat patches. Therefore, although survival in the absence of snow may not be strongly linked to variation in habitat composition, habitat selection leading up to and during snow events has the potential to strongly influence individual survival and, ultimately, population growth (Gates et al. 2012).

Woody-edge density at the 95-m scale was the most influential covariate in the analysis, based on overall



FIGURE 3. Northern Bobwhite prints in the snow in the foreground of this image indicate foraging locations in a soybean field in relation to the nearest early-successional escape cover (background) associated with a drainage ditch in our study area in southwestern Ohio, USA.

weights and standardized regression coefficients. This result provides evidence that woody cover was the primary habitat factor affecting survival. The absence of such an influence at the 300-m scale suggests that the relationship between survival and woody edge was manifest at a scale that reflected fine-scale accessibility of protective habitat. Considerable theoretical and observational research on foraging birds during winter has defined the role of availability of woody escape cover at fine spatial scales (Grubb and Greenwald 1982, Lima 1990, Watts 1991). However, direct links between survival and access to escape cover have generally been inferred only from foraging behavior of birds or predators (e.g., Grubb and Greenwald 1982, Roth et al. 2006). Our results provide empirical evidence for a link between individual survival and access to woody escape cover during periods of high mortality. Our results also demonstrate the adaptive significance of previously documented selection for woody cover by Northern Bobwhites during the nonbreeding season (Williams et al. 2000, Janke and Gates 2013), which

has direct implications for conservation of these habitats in agricultural landscapes, especially in the northern tier of the Northern Bobwhite range.

Greater abundance of row crops was associated with higher survival at the 95-m and 300-m scales. The positive relationship between row crops and survival rising asymptotically to 100% cropland reveals a limitation of our analyses and study design because the result superficially implies that landscapes with only row crops would be maximally beneficial to Northern Bobwhites. However, our study design only allowed us to test whether landscapes that already met habitat suitability constraints (i.e. they were used) were associated with variation in individual survival. Therefore, we can conclude from our analysis that increasing row crop cover is associated with improved individual survival within landscapes that meet minimum use requirements. In most cases, Northern Bobwhites' use of row crop fields is related to availability of woody escape cover along field edges (Guthery and Bingham 1992, Guthery 1999, Janke and Gates 2013). Therefore, our results underscore the importance of woody cover in row-cropped agricultural landscapes, which collectively provide favorable habitat for wintering Northern Bobwhites.

The similar response to row crop availability at both scales was likely related to 2 factors. First, agricultural fields provide important resources and access to food at local scales and should confer benefits in trade-offs between foraging and predation risk during winter (Roseberry 1964, Robel and Kemp 1997). Abundant agricultural food sources are likely most important when snow cover increases the physiological demands of foraging and reduces the accessibility of food (Figure 3; Errington and Hamerstrom 1936, Roseberry 1964). Increased area of available food sources during these periods should reduce foraging movements and increase survival by reducing exposure to predation (Roseberry 1964).

Abundance of row crops at large spatial scales could influence the spatial distribution of predators and thereby modify exposure to predation among different habitat patches (Thomson et al. 2006). Field observations during our study implicated avian predators—primarily Sharpshinned Hawks (*Accipiter striatus*) or Cooper's Hawks (*A. cooperii*)—and red foxes (*Vulpes vulpes*) as the primary Northern Bobwhite predators on our sites (Janke and Gates 2012). Northern Bobwhites in our study area were unlikely to occur in high enough densities to influence the spatial distribution of these predators (Roseberry and Klimstra 1984). Rather, predators likely responded to landscape composition (Gehring and Swihart 2003, Wilson et al. 2010) and abundance or accessibility of primary prey (i.e. small mammals and passerines; Preston 1990). Previous research on mammalian and avian predators in agricultural landscapes has shown that they are generally more abundant in landscapes with more herbaceous cover than in landscapes dominated by row crops (Kuehl and

Clark 2002, Gehring and Swihart 2003, Roth et al. 2008, Wilson et al. 2010). Because generalist predators characteristic of our study area depend on a diversity of prey species (Andersson and Erlinge 1977), opportunistic predation on Northern Bobwhites may have been lower in areas dominated by row crops where alternative prey—and, therefore, predators—were less abundant (Redpath and Thirgood 1999). Further research is needed to understand trade-offs among the 3 primary habitats of Northern Bobwhites in agricultural landscapes—woody cover, grasslands, and row crops—and identify minimum annual cover constraints needed to improve winter survival and maintain reproductive capacity.

Demographic analyses on northern populations of Northern Bobwhites have revealed a high degree of sensitivity of population growth in response to variation in winter survival (Folk et al. 2007, Gates et al. 2012, Williams et al. 2012), which is highly influenced by environmental stochasticity associated with winter weather (Robel and Kemp 1997). Accordingly, availability of early-successional winter habitat is necessary to ensure population stability in populations exposed to severe winter weather. However, long-term declines in availability of early-successional vegetation in agricultural landscapes are pervasive throughout the Northern Bobwhite's range in the Midwest and Mid-Atlantic regions (Warner 1994, Demers et al. 1995, Trani et al. 2001) and coincide with population declines in the species (Link et al. 2008, Spinola and Gates 2008). Our results provide a mechanism to link the co-occurrence of Northern Bobwhite and early-successional vegetation declines in agricultural landscapes. Accordingly, management and conservation strategies in these landscapes have potential to improve population stability through targeted efforts to increase accessibility and abundance of woody cover. Such a program could be implemented in working agricultural landscapes, with mutual benefits to agricultural users (Barbour et al. 2007), Northern Bobwhites, and other birds that depend on early-successional vegetation during winter or migration (Best 1983, Best et al. 1998, McClure et al. 2012).

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APPENDIX

TABLE 2. Model selection results for logistic regression on daily survival of Northern Bobwhites monitored over days without snow on the ground in southwestern Ohio, USA, during December–February, 2009–2011.

Scale ^a	Model ^b	k^a	AIC ^a	All models		Scale-specific	
				Δ AIC ^a	w_i^a	Δ AIC ^a	w_i^a
–	Base	0	157.09	0.000	0.164	–	–
95	Base + Row crop	1	158.74	1.648	0.072	0.000	0.169
300	Base + Woodlot	1	158.86	1.768	0.068	0.000	0.165
300	Base + Woody edge	1	158.89	1.803	0.067	0.036	0.163
95	Base + ES herbaceous	1	159.01	1.918	0.063	0.270	0.148
300	Base + ES herbaceous	1	159.35	2.263	0.053	0.496	0.129
300	Base + Row crop	1	159.42	2.327	0.051	0.559	0.125
95	Base + Woodlot	1	159.63	2.535	0.046	0.887	0.109
95	Base + Woody edge	1	159.65	2.560	0.046	0.911	0.107
95	Base + ES herbaceous + Row crop	2	160.19	3.103	0.035	1.455	0.082
95	Base + Woodlot + Row crop	2	160.67	3.576	0.027	1.927	0.064
300	Base + Woody edge + Woodlot	2	160.71	3.619	0.027	1.851	0.066
95	Base + Woody edge + Row crop	2	160.74	3.647	0.027	1.999	0.062
300	Base + Woody edge + Row crop	2	160.76	3.669	0.026	1.901	0.064
95	Base + ES herbaceous + Woodlot	2	160.98	3.887	0.024	2.239	0.055
300	Base + ES herbaceous + Woodlot	2	161.13	4.044	0.022	2.276	0.053
300	Base + Woody edge + ES herbaceous	2	161.27	4.175	0.020	2.408	0.050
300	Base + ES herbaceous + Row crop	2	161.32	4.229	0.020	2.462	0.048
300	Base + Woodlot + Row crop	2	161.38	4.292	0.019	2.524	0.047
95	Base + Woody edge + Woodlot	2	161.61	4.519	0.017	2.870	0.040
95	Base + Woody edge + ES herbaceous	2	161.62	4.533	0.017	2.884	0.040
95	Base + ES herbaceous + Woodlot + Row crop	3	161.63	4.541	0.017	2.892	0.040
95	Base + Woody edge + ES herbaceous + Row crop	3	162.19	5.101	0.013	3.452	0.030
300	Base + Woody edge + Woodlot + Row crop	3	162.64	5.550	0.010	3.782	0.025
95	Base + Woody edge + Woodlot + Row crop	3	162.66	5.573	0.010	3.925	0.024
300	Base + Woody edge + ES Herbaceous + Woodlot	3	163.08	5.987	0.008	4.220	0.020
300	Base + ES herbaceous + Woodlot + Row crop	3	163.13	6.036	0.008	4.268	0.020
300	Base + Woody edge + ES herbaceous + Row crop	3	163.26	6.168	0.008	4.400	0.018
95	Base + Woody edge + ES herbaceous + Woodlot	3	163.55	6.464	0.006	4.816	0.015
95	Base + Woody edge + ES herbaceous + Woodlot + Row crop	4	163.61	6.524	0.006	4.876	0.015
300	Base + Woody edge + ES herbaceous + Woodlot + Row crop	4	165.05	7.956	0.003	6.189	0.007

^a Scale = buffer size in which the variable was measured around a radiolocation (m); k = number of parameters in model; AIC = Akaike's Information Criterion; Δ AIC = change in AIC from lowest model; w_i = Akaike weight.

^b Base = baseline null model with covey random effect; ES = early-successional.

TABLE 3. Model selection results for logistic regression on daily survival of Northern Bobwhites monitored over days with snow on the ground in southwestern Ohio, USA, during December–February, 2009–2011.

Scale ^a	Model ^b	<i>k</i> ^a	AIC ^a	All models		Scale-specific	
				Δ AIC ^a	<i>w_i</i> ^a	Δ AIC ^a	<i>w_i</i> ^a
95	Base + Woody edge + Row crop	3	706.61	0.000	0.309	0.000	0.349
95	Base + Woody edge + Woodlot + Row crop	4	708.53	1.918	0.118	1.918	0.134
95	Base + Woody edge + ES herbaceous + Row crop	4	708.60	1.990	0.114	1.990	0.129
95	Base + Row crop	2	709.85	3.240	0.061	3.240	0.069
95	Base + Woody edge + ES herbaceous + Woodlot + Row crop	5	710.43	3.817	0.046	3.817	0.052
95	Base + Woody edge + ES herbaceous + Woodlot	4	710.57	3.954	0.043	3.954	0.048
95	Base + Woody edge + ES herbaceous	3	710.79	4.175	0.038	4.175	0.043
95	Base + Woody edge	2	710.88	4.269	0.036	4.269	0.041
95	Base + Woodlot + Row crop	3	711.06	4.448	0.033	4.448	0.038
95	Base + ES herbaceous + Row crop	3	711.80	5.192	0.023	5.192	0.026
95	Base + Woody edge + Woodlot	3	711.88	5.267	0.022	5.267	0.025
300	Base + Row crop	2	712.05	5.442	0.020	0.000	0.183
300	Base + Woody edge + Row crop	3	712.11	5.496	0.020	0.055	0.178
95	Base + ES herbaceous + Woodlot	3	712.81	6.199	0.014	6.199	0.016
95	Base + ES herbaceous + Woodlot + Row crop	4	712.93	6.322	0.013	6.322	0.015
300	Base + ES herbaceous	2	713.57	6.957	0.010	1.515	0.086
300	Base + ES herbaceous + Row crop	3	713.76	7.148	0.009	1.706	0.078
300	Base + Woody edge + ES herbaceous + Row crop	4	713.80	7.190	0.008	1.748	0.076
95	Base + Woodlot	2	714.05	7.439	0.007	7.439	0.008
300	Base + Woodlot + Row crop	3	714.05	7.441	0.007	2.000	0.067
300	Base + Woody edge + Woodlot + Row crop	4	714.10	7.492	0.007	2.050	0.066
300	Base + Woody edge + ES herbaceous	3	714.45	7.838	0.006	2.396	0.055
–	Base	1	714.50	7.884	0.006	2.442	–
300	Base + ES herbaceous + Woodlot	3	714.54	7.931	0.006	2.489	0.053
95	Base + ES herbaceous	2	714.93	8.321	0.005	8.321	0.005
300	Base + Woody edge + ES herbaceous + Woodlot	4	715.22	8.610	0.004	3.169	0.038
300	Base + ES herbaceous + Woodlot + Row crop	4	715.62	9.008	0.003	3.567	0.031
300	Base + Woody edge + ES herbaceous + Woodlot + Row crop	5	715.71	9.101	0.003	3.659	0.029
300	Base + Woody edge	2	715.89	9.274	0.003	3.832	0.027
300	Base + Woodlot	2	716.30	9.687	0.002	4.245	0.022
300	Base + Woody edge + Woodlot	3	717.67	11.055	0.001	5.614	0.011

^a Scale = buffer size in which the variable was measured around a radiolocation (m); *k* = number of parameters in model; AIC = Akaike's Information Criterion; Δ AIC = change in AIC from lowest model; *w_i* = Akaike weight.

^b Base = baseline null model with covey random effect; ES = early-successional.