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TEMPORAL AND SPATIAL ASSESSMENT OF USABLE SPACE AND COVER TYPE INTERSPERSION FOR NORTHERN BOBWHITES ON PRIVATE FARMLANDS IN SOUTHWESTERN OHIO

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ABSTRACT

Contemporary landscape change driven by socio-economic forces and advances in agricultural technology do not favor northern bobwhites (*Colinus virginianus*) in the Midwestern United States. The challenge of bobwhite conservation is to provide sufficient quantities of habitat with optimal configurations in proportions that satisfy needs throughout the year on private-owned working lands. We radio-tracked 58 coveys and 98 individual birds throughout the year in 2009-10 and 2010-11 on privately owned farmland in southwestern Ohio. We investigated temporal changes in usable space from use-availability data. Estimated proportions of usable space based on analyses of habitat selection across four study sites were 0.06-0.12 during the non-breeding season compared to 0.10-10.30 during the breeding season. We also modeled probabilities that radio-marked coveys or individual birds used points within individual cover types as a function of distance to other cover types. Locations of radio-marked coveys and individual birds within focal cover types were closer to other cover types compared to random points during breeding (mean = 44 m) and non-breeding (mean = 58 m) seasons. Probability of use within focal cover types declined with distance to other cover types, typically falling below 50% when distances exceeded 9-242 m. Locations of radio-marked coveys were concentrated near edges within used cover types, while locations of individual birds were more dispersed during the breeding season. Estimated proportions of usable space based on distances between locations of radio-marked bobwhites and nearest cover types were higher (0.30-0.53) than estimates based on habitat selection ratios, and were similar between non-breeding and breeding seasons. Potentially usable sites were not fully occupied in either season, but there was no relationship between crude covey densities and proportions of usable space estimated from habitat selection analyses during the breeding and non-breeding seasons across study sites and years ($r^2 < 0.166$, $P > 0.316$). With distance to cover type estimates of usable space (years combined), two study sites with the highest proportions of usable space (0.43-0.53) also had the largest crude covey densities (0.0065-0.153 coveys/ha) compared to the other two sites with lower proportions of usable space (0.30-0.32) and smaller covey densities ($0.004 - 0.006$ coveys/ha). Habitat enhancement should focus on providing protective cover near food for coveys during the non-breeding season and protective cover near nesting and brood-rearing habitat during the breeding season. Conserving Midwestern bobwhite populations requires innovative practices that can be implemented on private lands as economic incentives change for farm operators. Improving protective cover along habitat edges can increase usable space by improving cover type juxtaposition (e.g. food near cover) while minimizing impact on farming practices.

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Key words: *Colinus virginianus*, habitat use, interspersion, northern bobwhite, Ohio, private lands, quail, radio-telemetry, usable space

In contrast to migratory bird populations where conservation is delivered within discrete ecoregions to address limiting factors during separate stages of the annual life cycle (i.e. wintering, breeding, and migration), conservation planning for resident game bird populations such as northern bobwhite (*Colinus virginianus*; hereafter bobwhite) must efficiently allocate scarce resources to meet focal species' needs throughout their annual life cycle within the same landscape. Managers of resident bird populations must provide sufficient amounts of habitats in optimal proportions that satisfy needs during

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breeding and non-breeding seasons. Bobwhites are exceptionally challenging in this regard as they are a prototypical edge species with small seasonal home ranges and thrive in fine-grained landscapes (Roseberry and Sudkamp 1998).

Landscape change driven mostly by socio-economic forces, advances in agricultural technology, and urbanization do not favor bobwhites (Brennan 1991, Williams et al. 2004). Diversity and interspersion of cover types that satisfy food, cover, and other life requisites has declined and populations are increasingly isolated as the Midwestern landscape becomes more simplified and coarse-grained. Some habitats are over-supplied (e.g. croplands) while others are under-supplied (e.g. nesting and protective cover types) which limits the capacity of a focal area to support bobwhite populations. Although capable of relatively long-distance dispersal during fall and spring "shuffles" (Liberati 2012, Smith 2015), bobwhites are vulnerable to predation when they move long distances between food and protective cover during winter, resulting in unsustainably low over-winter survival (Janke and Gates 2012, Gates et al. 2012).

Given the challenge of managing habitat for bobwhites throughout the year and the potential sensitivities of population growth to vital rates during limiting stages of the annual life cycle, (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012), conservation planning can be informed by quantifying the capacity of an area to support bobwhites with knowledge of use, availability, and proximity of cover types. Guthery (1997) proposed the concept of usable space for northern bobwhite habitat assessment and management, shifting the focus of management and conservation away from individual landscape elements (i.e. food plots or discrete cover patches) and toward an emphasis on the composite suitability of a focal area. Addition of a time dimension allows a dynamic representation of how much of a focal area is usable for bobwhites at a given time within the constraints of "physical, behavioral, and physiological adaptations" of bobwhites (Guthery 1997: 294). Guthery et al. (2005) provided a method for temporal quantification of usable space from habitat use-availability data, providing the opportunity to identify periods of the annual life cycle when habitat might be most limiting.

Guthery's (1997) conception of usable space applies habitat selection coefficients from habitat use-availability data to areas of cover types within a focal area. Some cover types may be used in proportions less than available because they are overabundant on the landscape relative to what a species needs. Alternatively some cover types may have low use due to suboptimal interspersion and juxtaposition or because they lack suitable vegetation structure and composition (Wiley 2012). Usable space considers the quality of an entire area rather than quality of cover types within an area (Guthery 1997). Usable space estimates better represent use of space than home range estimators by reducing the influence of areas with minimal or no use (Hiller et al. 2009). Dividing abundance by usable space provides estimates of ecological density that are generally more informative than crude density (Roseberry and Klimstra 1984, Guthery 1997).

The usable space concept considers seasonal variation in resource requirements and availability (Guthery 1997). For instance, a row crop field may not provide food or cover during nesting, but can be important during brood rearing and winter (Janke and Gates 2012, Liberati and Gates 2017, *in review*). Temporal variation in usable space could affect seasonal demographic parameters (e.g. reproduction and survival) that determine population growth rates (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012). Combined with demographic data and estimates of ecological density, seasonal quantifications of usable space can identify periods when habitat is limiting and thereby inform efforts to improve the quality of a given area.

The Guthery et al. (2005) method of estimating usable space does not explicitly consider spatial distribution of cover types as a potential constraint on habitat use. Use of particular cover types is influenced by distance to surrounding cover types (Leopold 1933, Schroeder 1985). Fragmented habitats may have patches that are too isolated to be usable (Thomas and Taylor 2006). Spatial variation in use of cover types should be considered along with relative use of different cover types when applying the usable space concept. Together, these two approaches provide spatially and temporally explicit representations of suitability of a focal area for bobwhites, and prepare managers with information they need to make decisions about habitat management and restoration. We applied Guthery's (1997) concept of usable space to understand how availability and configuration of cover types affected capacities of four study sites with different habitat composition and configuration of land cover to support bobwhite populations throughout the year. Our objectives were to; 1) estimate usable space from habitat use-availability data 2) determine effects of cover type proximity on usable space during breeding and non-breeding seasons; and 3) compare usable space between breeding and non-breeding seasons. We illustrate an approach to target habitat conservation designed to address landscape- and regional-level limiting factors on private lands in the Midwestern United States.

STUDY AREA

Our study was conducted on four private land sites centered at 39° 04′59″, 83° 39′10″ in Highland and Brown Counties in southwestern Ohio (Figure 1) in the glaciated till plains physiographic region of Ohio (Ohio Division of Geologic Survey 1998). The Fee area was the most intensively-farmed study site, with relatively high proportions of row crop and low proportions of forest, early successional (ES) herbaceous, ES woody, and pasture/hay (Table 1). In contrast, the Wildcat and Peach Orchard study sites contained the largest proportions of ES herbaceous and woody cover types. Wildcat differed from Peach Orchard with a lower proportion of forest and more pasture/hay. The Thurner site had intermediate proportions of row crop, forest, and early successional

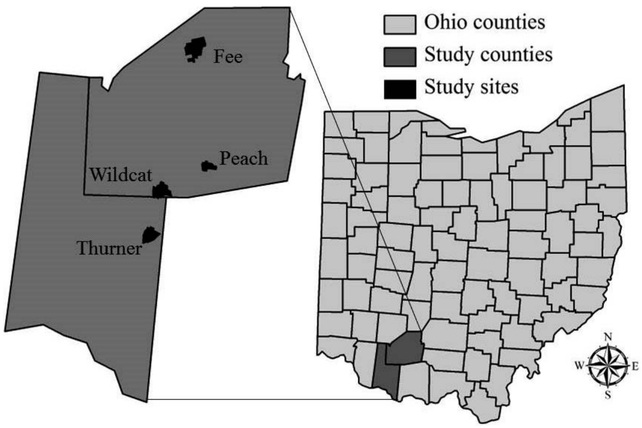

Fig. 1. Locations of four private land study sites where use of microhabitat and space by northern bobwhites was investigated in southwestern Ohio during 2009-2011.

cover types, but had the highest proportion of the ES woody cover type among all four study sites. Changes in cover type composition between years were largely due to adjustments of study area boundaries. The long-term (30 year) mean temperature during October-March was 10.5^0 C. The long-term mean annual snow accumulation was 67.5 cm and accumulation during 2009-10 and 2010-11 was 101.6 cm and 67.3 cm, respectively (National Climate Data Center 2011).

METHODS

Cover Mapping

We manually digitized ground-truthed cover maps of each study site in ArcGIS (version 9.3, ESRI Redlands, CA, USA) over high spatial resolution (0.305 m, acquisition date 2007) ortho-photographs (Ohio Statewide Imagery Program 2008) as described in Janke and Gates (2013). Contiguous cover types within and adjacent to study site boundaries were classified into six cover types; row crop, forest, ES herbaceous, ES woody, pasture/hay, and non-habitat. Early successional herbaceous included CRP or old-fields, fencerows, ditches, and odd areas dominated by grasses and forbs. Early successional woody comprised fencerows, ditches, old-fields, or portions of CRP fields where shrubs dominated. Pasture/hay included fields actively grazed or hayed during the study. Conservation Reserve Program fields that were mowed to low heights (e.g. mid-contract management) were included in pasture/hay since they were structurally more similar to that cover type. Areas >50 m width and dominated by mature trees were classified as forest, while areas <50 m width and dominated by a dense shrubby understory were classified as ES woody. The row crop cover type included corn (*Zea maize*), soybean (*Glycine max*), and winter wheat (*Triticum aestivum*) fields and mowed grass-ways within crop fields. Non-habitat included residential and commercial properties, roads and associated ditches, and water. Site boundaries varied among years depending on access granted by landowners and included only areas that were thoroughly searched to find coveys during the non-breeding season.

Capture and Radio-marking

We used covey call surveys and systematic searches with pointing dogs to locate coveys on each study site before 1 December in 2009 and 2010. Snow tracking or periodic dog searches continued within areas not occupied by radio-marked coveys during 1 December – 28 February 2009-11. We captured bobwhites with baited funnel traps (Stoddard 1931) and targeted mist netting (Wiley et al. 2012). Capture efforts continued throughout the year to maintain ≥1 radio-marked bird per covey during winter and to deploy radio-transmitters on additional bobwhites during the breeding season. Captured bobwhites were leg-banded and most were radio-marked with pendant-style mortality-sensing radio-transmitters (6.6 g; Advanced Telemetry Systems, Isanti, MN, USA) if they weighed ≥ 165 g. Bobwhites were released at capture sites immediately after marking. We obtained daily locations of radio-marked birds over 6-7 days each week during the non-breeding season (Oct-Mar) using homing from short distances (White and Garrott 1990). Birds that remained alive after covey break-up were tracked as individuals throughout the breeding season (Apr-Sep). We tracked 98 previously and newly radio-marked bobwhites after covey break-up and through the end of the breeding season (Apr-Sep). We used a global positioning system to mark covey locations and recorded the cover type where birds were found. Trapping,

Table 1. Cover types available to northern bobwhites on four study sites in southwestern Ohio, 2009-2011.

		Percent of Cover Type					
Study Site	Year	Row Crop	Forest	ES[a] Herbaceous	ES[a] Woody	Pasture/Hay	Other
Fee	2009-10	76.1	6.6	6.9	2.9	3.3	4.2
	2010-11	72.1	8.3	9.1	3.1	3.3	4.1
Peach	2009-10	41.5	30.9	19.5	3.7	0.0	4.4
	2010-11	39.7	28.6	21.0	4.7	2.0	4.1
Thurner	2009-10	52.3	16.2	10.1	6.2	8.0	7.2
	2010-11	53.5	16.1	9.9	6.5	6.6	7.4
Wildcat	2009-10	40.6	9.6	22.4	4.2	19.3	3.9
	2010-11	38.5	10.4	19.6	4.2	23.3	4.0

[a] ES = early successional

handling, and marking protocols were reviewed and approved by the Animal Care and Use Committee at The Ohio State University (protocol number 2007A0228).

Temporal Analysis of Usable Space

We used Guthery et al.'s (2005) method to estimate the quantity of usable space based on monthly use-availability data. We determined proportional use (p_i) and proportional availability (a_i) on each study site by cover type (i). Letting $u_i =$ the unknown proportion of usable space within cover type i and $A_i =$ the area (ha) of cover type i, we estimated usable space (U) according to Guthery et al.'s (2005) definition

$$U = \sum_{i=1}^{w} u_i A_i,$$

where $w =$ the number of cover types available ($i = 1, 2, \ldots, w$).

With the assumption that coveys or individuals distribute themselves randomly throughout all usable space, we expected that;

$$p_i = u_i A_i / U,$$

which implied that;

$$U_i = u_i A_i / p_i.$$

Since U and u_i are both unknown, we used the selection ratio (p_i/a_i; (Manly and McDonald 1993) to estimate u_i within each cover type. We first assumed that the cover type (m), with the highest monthly selection ratio was fully usable ($u_m = 1$). Interestingly under this assumption, total usable space across all habitats could simply be calculated with the following formula;

$$U_m = A_m / p_m.$$

However, to determine individual contributions of cover types to total usable space, the u_i for cover types other than m ($u_{i'}$) must be relativized to the selection ratio of the most preferred cover type (u_m) by dividing the selection ratio of cover type i by the selection ratio of cover type m as follows;

$$u_{i'} = u_i / u_{m.}$$

Given that A_i was measured without error and the assumption that $u_m = 1$ was without error, Guthery et al. (2005) concluded that variance can be estimated as

$$\mathrm{var}(U) = (A_m)^2 * (1 - p_m) / (np_m)^3$$

We determined U within cover type i (U_i) as the product of u_i and A_i. Monthly estimates of usable space provided a temporal analysis of usable space.

Habitat selection ratios were derived from compositional analyses reported from Janke and Gates (2013) and Liberati and Gates (2017, *in review*). We estimated usable space by years and study sites and by month with years pooled across study sites. We calculated ecological densities of coveys on each site using site-specific area estimates of usable space during the non-breeding season.

Distance to Cover Types

We used telemetry locations from radio-marked coveys (non-breeding season) or individual birds (breeding season) to estimate distances from points that were used by bobwhites within cover types (hereafter "focal cover type", excluding non-habitat) to each of four cover types nearest to the focal cover type (hereafter "nearest other cover type"). Radio-locations were pooled across years within the four study sites during non-breeding and breeding seasons. The same numbers of random points were selected as the numbers of radio-locations recorded in each cover type within sites and seasons. These points were used as pseudo-absence points in logistic regression analyses. Coordinates of radio-locations and random points were overlaid on cover maps in ArcGIS. Euclidean distances (m) were calculated between each radio-location or random point in the focal cover type and all nearest other cover types. Some of the distances to nearest cover type were not distances to focal cover type edges, as distances were sometimes measured to nearest other cover types that did not contact focal cover types.

We used logistic regression in Program R version 3.2.2 (R Development Core Team 2015) to estimate probability of use of random points within focal cover types as a function of distance to the nearest other cover types. We started with models for each focal cover type that included the main effects of distances to other nearest cover types and all combinations of 2-way interactions that included the main effects. We used stepwise selection with Akaike's information criterion (AIC) to select a single model for each cover type during breeding and non-breeding seasons. We presented standardized parameter estimates for ease of interpretation but we plotted probabilities of use of points within focal cover types as a function of unstandardized distances to other cover types. Distances from radio-location points to other cover types were allowed to vary over ranges that we observed with distance to other cover types held at their means.

Spatial Analysis of Usable Space

We overlaid a 50 m x 50 m grid of points on cover maps of each study site and applied the predict function in program R to estimate probability of use of grid points within each focal cover type based on logistic regression parameters from the best-fitting models identified by stepwise selection. We interpolated a continuous probability surface of predicted use by bobwhites from probability values of the 50 m grid using the kriging function with cell size = 15 m in the Spatial Analyst extension of ArcGIS 10.0. The 15 m resolution of the kriging response surface corresponded with accuracy (12.9 m) of our radio-locations (Janke 2011). The response surface provided spatial representations of usable space based on proximity of adjacent cover types for each study site during breeding and non-breeding seasons.

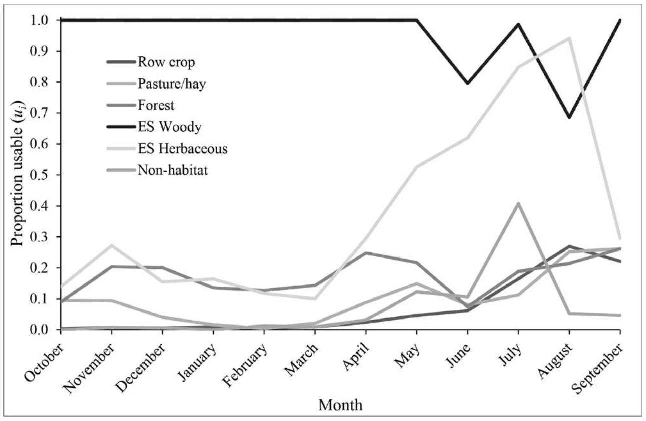

Fig. 2. Mean monthly estimates of proportional usable space within six cover types (u_i) based on radio-locations ($n = 3{,}664$ in 2009-10; $n = 4{,}636$ in 2010-11) of northern bobwhites in southwestern Ohio during 2009-2011 (years and study sites combined).

RESULTS

Temporal Analysis of Usable Space

We used radio-locations from 26 coveys ($n = 1{,}858$) and 51 individual birds ($n = 1{,}836$) to estimate usable space during breeding and non-breeding seasons in 2009-10. Equivalent numbers of radio-locations were recorded from 32 coveys ($n = 2{,}532$) and 47 individual birds ($n = 2{,}104$) and during non-breeding and breeding seasons in 2010-11.

The ES woody cover type had the highest selection ratios (p_i/a_i) of all cover types, ranging from 1.0 to 9.3 during the breeding season and from 8.5 to 16.6 during the non-breeding season (Appendices 1-4). Early successional herbaceous had the second highest selection ratios, ranging from 0.4 to 4.2 during the breeding season and from 0.8 to 3.1 during the non-breeding season. Selection ratios for forest ranged from 1.0 to 2.4 during April and May in 2010, in all months except for August during the breeding season in 2011, and all months except October 2009-10 during the non-breeding season. Selection ratios of row crop and pasture/hay were <1.0 in both seasons except during August 2010 and June 2011. Early successional woody was considered fully usable except during June-August 2010 when ES herbaceous had the highest selection ratio (Appendices 1-4).

Averaging proportional usability (hereafter u_i) across years, ES woody dominated all other cover types throughout the non-breeding season (Figure 2). However, u_i of ES herbaceous rose from 0.10 in March to 0.94 in August before falling to 0.3 in September. Similarly, u_i of row crop and pasture/hay increased from ≤ 0.02 in March to 0.22–0.27 in August and September. The usability proportion for forest varied monthly between 0.08 and 0.26 with no apparent seasonal pattern. Interestingly, u_i of non-habitat peaked at 0.41 in July when radio-marked bobwhites were sometimes found in road right-of-ways, raising the selection ratio of non-habitat to near 1.0 (Tables 2–3).

The ES woody cover type had the highest proportional use and was also the least abundant cover type on our study sites (Table 1). Conversely, row crop was the most abundant cover type but received low use relative to its availability. Consequently, small proportions (0.18 during 2009-10 and 0.13 during 2010-11) of our study sites were usable with estimates of usable space averaged across all months and study sites. Estimated proportions of usable space varied among study sites with months combined (Table 2). Thurner had the highest proportion of usable space (0.22), followed by Peach (0.15), Wildcat (0.13), and Fee (0.10).

Mean monthly proportions of usable space ranged from 0.06 - 0.12 during the non-breeding (Oct-Mar) season, to 0.11 to 0.36 during the breeding season (Apr-Sep) with study sites combined (Figure 3). The increase in proportion of usable space between non-breeding and breeding seasons corresponded with a large increase in proportional use of the ES herbaceous cover type, and smaller increases in proportional usability of row crop and pasture/hay during the breeding season (Figure 2). Proportions of usable space increased between non-breeding and breeding seasons on all four study sites. Seasonal variation in proportions of usable space was relatively consistent among study sites between years, although the increase in usable space between non-breeding and breeding seasons occurred much earlier during 2009-10 than in 2010-11 (Figure 3).

Crude covey densities were 1.4 -2.0 times higher on Wildcat compared to the other three study sites, although the Wildcat site ranked third in proportion of usable space

Table 2. Estimates of usable space and densities of northern bobwhite coveys by study site, year, and season in southwestern Ohio during 2009-2011.

			Usable Space (ha)			Covey Density/ha	
Study Site	Year	Total Area (ha)	Non-breeding	Breeding	No. Coveys	Total Area	Usable Space
Fee	2009-10	1106.7	72.7	168.3	7	0.0063	0.0963
	2010-11	1284.3	102.1	145.8	6	0.0047	0.0588
Peach	2009-10	310.2	17.1	92.5	2	0.0065	0.1170
	2010-11	397.7	36.4	55.4	1	0.0025	0.0275
Thurner	2009-10	593.7	126.7	176.7	3	0.0050	0.0237
	2010-11	738.8	120.7	154.3	6	0.0081	0.0497
Wildcat	2009-10	675.9	52.2	166.1	11	0.0163	0.2107
	2010-11	838.3	65.6	111.6	12	0.0143	0.1829

Table 3. Differences (use – random) of median distances (m) between northern bobwhite radiolocations and random points between focal and nearest other cover types during breeding (Apr-Sep) and non-breeding (Oct-Mar) seasons, 2009-2011 (years combined) in southwestern Ohio.

		Nearest Other Cover Type					
Focal Cover Type	Season	ES Herbaceous	ES Woody	Forest	Row Crop	Pasture/Hay	Row Mean
ES Herbaceous	Breeding		-4	76	-29	-61	-5
ES Woody	Breeding	-46		102	-3	-100	-12
Forest	Breeding	-120	-41		-14	-98	-68
Row Crop	Breeding	-180	-47	38		-155	-86
Pasture/Hay	Breeding	-87	-17	-50	-43		-49
Column Mean	Breeding	-108	-27	42	-22	-104	-44
ES Herbaceous	Non-Breeding		-46	0	-72	-77	-49
ES Woody	Non-Breeding	-29		32	-5	-96	-25
Forest	Non-Breeding	-104	-58		-23	-108	-73
Row Crop	Non-Breeding	-158	-92	-29		-115	-99
Pasture/Hay	Non-Breeding	-48	-44	-38	-49		-45
Column Mean	Non-Breeding	-85	-60	-9	-37	-99	-58

(Table 2). Consequently, ecological density (no. coveys/ha usable space) was highest on Wildcat, followed by Fee, Peach Orchard, and Thurner. There was no relationship between numbers of coveys and areas of usable space during the breeding ($r^2 = 0.166$, $P = 0.316$) and non-breeding seasons ($r^2 = 0.008$, $P = 0.837$) when covey densities were regressed on usable space estimates for each year and study site.

Distance to Cover Types

Frequency distributions of distances from radiolocations and random points to nearest other cover types were naturally right-skewed since negative distances were not possible. Therefore, we examined median distances to nearest cover types for used and random points. Median distances from radiolocations recorded in focal cover types were 25 m closer to other cover types than random points for 13 of 20 differences during the breeding season and 16 of 20 differences during the non-breeding season (Table 3).

We summarized differences (used - random) in median distances between used and random points for all pairs of cover types (Table 3). The resulting matrix was not symmetric so averaging differences across rows versus across columns produced different marginal means. The row marginal means summarized differences in distances between used and random points, averaged across nearest other cover types for each focal cover type. The column marginal means summarized differences in distances between used and random points averaged across focal cover types for each nearest other cover type.

Differences in distances between used and random points were more strongly negative when averaged across nearest other cover types within the forest, row crop, and pasture/hay focal cover types than for ES herbaceous and ES Woody focal cover types during the breeding and non-breeding seasons (row marginal means, Table 3). Differences in distances between used and random points were most strongly negative when averaged across focal cover types for the ES herbaceous, ES woody, and pasture/hay nearest other cover types during both the breeding and non-breeding seasons (column marginal means, Table 3).

Relative distances of used versus random points within the ES herbaceous and ES woody focal cover types varied among nearest other cover types during the breeding season (Table 3). Radio-marked bobwhites were closest to the pasture/hay cover types and were more distant from the forest cover type compared to random points when they occupied ES herbaceous and ES woody cover types. Bobwhites also were closest to ES herbaceous or pasture/hay within focal forest, row crop, and pasture/hay focal cover types during the breeding season.

Relative distances of used versus random points within focal cover types were consistently negative across all nearest other cover types except forest during the non-breeding season (Table 3). Radio-marked bobwhites were closest to ES woody, row crop, and pasture/hay cover types when they occupied the ES herbaceous cover type, and were closest to the ES herbaceous and pasture/hay cover types within the ES woody focal cover type during the non-breeding season. Bobwhites were closest to ES herbaceous, ES woody, or pasture/hay cover types when

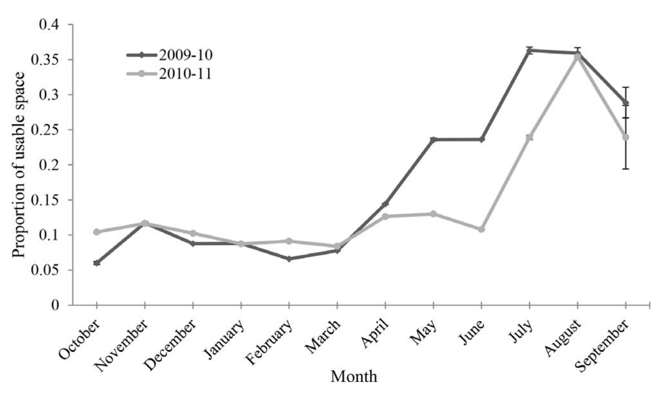

Fig. 3. Monthly trends in mean proportions of usable space by year for northern bobwhites in southwestern Ohio during 2009-11 (study sites combined). Error bars represent 95% confidence intervals.

Table 4. Mean predicted probability of use by northern bobwhites of 50 × 50 m grid points based on stepwise-selected logistic regression models of distance from focal to other nearest cover types. Grid points were distributed throughout four study sites in southwestern Ohio to generate predicted probability of use surfaces for each study site during non-breeding and breading seasons during 2009-2011.

			Breeding		Non-breeding		
Site	Cover Type	n[a]	Mean	SD	Mean	SD	P[b]
Fee	ES herbaceous	473	0.50	0.15	0.45	0.19	<0.0001
	ES Woody	162	0.41	0.23	0.39	0.19	0.1737
	Forest	417	0.29	0.25	0.33	0.27	<0.0001
	Pasture/hay	3710	0.27	0.26	0.25	0.25	0.2418
	Row Crop	175	0.27	0.22	0.29	0.23	<0.0001
	Total Area	4937	0.30	0.23	0.31	0.23	<0.0001
Peach	ES herbaceous	337	0.39	0.09	0.33	0.20	<0.0001
	ES Woody	70	0.28	0.18	0.35	0.17	<0.0001
	Forest	454	0.21	0.24	0.19	0.23	<0.0001
	Pasture/hay	28	0.66	0.11	0.59	0.14	0.0004
	Row Crop	647	0.34	0.25	0.36	0.24	0.0175
	Total Area	1536	0.32	0.23	0.30	0.24	0.0039
Thurner	ES herbaceous	296	0.46	0.08	0.46	0.23	0.7222
	ES Woody	202	0.39	0.18	0.46	0.14	<0.0001
	Forest	472	0.38	0.27	0.40	0.28	0.0001
	Pasture/hay	191	0.46	0.22	0.33	0.24	<0.0001
	Row Crop	1565	0.46	0.20	0.45	0.20	0.0362
	Total Area	2726	0.44	0.21	0.43	0.22	0.0417
Wildcat	ES herbaceous	663	0.49	0.10	0.40	0.22	<0.0001
	ES Woody	137	0.54	0.17	0.56	0.12	0.0226
	Forest	350	0.52	0.22	0.50	0.25	0.0002
	Pasture/hay	762	0.41	0.23	0.33	0.26	<0.0001
	Row Crop	1318	0.63	0.15	0.53	0.22	<0.0001
	Total Area	3230	0.53	0.20	0.45	0.24	<0.0001

[a] Number of grid points.
[b] Paired t-test.

they occupied forest, row crop, and pasture/hay cover types during the non-breeding season.

We evaluated 10 models that predicted probability of use of points within focal cover types as a function of distance to other cover types. We excluded non-habitat from analyses because this cover type received <1.0% use by radio-marked individuals or coveys during 16 of 24 months over 2 years and use never exceeded 8% in any month/year (Table 4). Stepwise selection retained all main effects of distance to cover types on use of points within ES woody, ES herbaceous, row crop, pasture/hay, and forest cover types (Appendices 5-6). Three to 5 of 10 possible 2-way interactions were retained after stepwise selection. Logistic regression coefficients on the log odds-ratio scale were negative for 16 of 20 main effects during the breeding season and 17 of 20 main effects during the non-breeding season. Interaction terms were significant ($P < 0.05$) for 15 of 18 retained interactions during the breeding season and 16 of 19 retained interactions during the non-breeding season (Appendices 5-6).

When graphed on the probability scale with all but one main effect held at their means, probabilities of use for 5 focal cover types declined with distance in 16 of 20 instances during the breeding season, and for 17 of 20 instances during the non-breeding season (Figures 4–8). Predicted probability of use of ES herbaceous cover was <0.50 and did not change with distance to ES woody during the breeding season and was >0.50 within 55 m of ES woody during the non-breeding season (Figure 4). Predicted probability of use of ES herbaceous was >0.50 within 75-81 m of row crop in each season. The probabilities of use for ES woody was >0.50 within 71-102 m from ES herbaceous, 14-31 m from row crop, and 129-237 m from pasture/hay during breeding and non-breeding seasons (Figure 5). Predicted probabilities of use for ES herbaceous and ES woody increased or changed very little with distance to forest and pasture/hay. Predicted probability of use for forest was >0.5 within 62-81 m of ES herbaceous cover, within 9-33 m of row crop, and within 110-112 m of pasture/hay (Figure 6).

Probability of use for forest was <0.5 at all distances to the ES woody cover type. Predicted probability of use for row crop was >0.5 within 170-217 m of ES herbaceous cover, within 37-60 m of ES woody cover, and within 203-242 m of pasture/hay during breeding and non-breeding seasons (Figure 7). Probability of use for row crop either increased or was <0.50 over nearly the entire range of distances to forest cover. Predicted probability of use for pasture/hay was >0.5 within 80-129 m of ES herbaceous cover and within 30-55 m of row crop during breeding and non-breeding seasons (Figure 8). Probability of use for pasture hay was <0.5 except within 29 m of ES woody and within 34 m of forest cover during the non-breeding season. Predicted probability of use for pasture/hay was <0.50 at all distances to the ES woody and forest cover types during the breeding season.

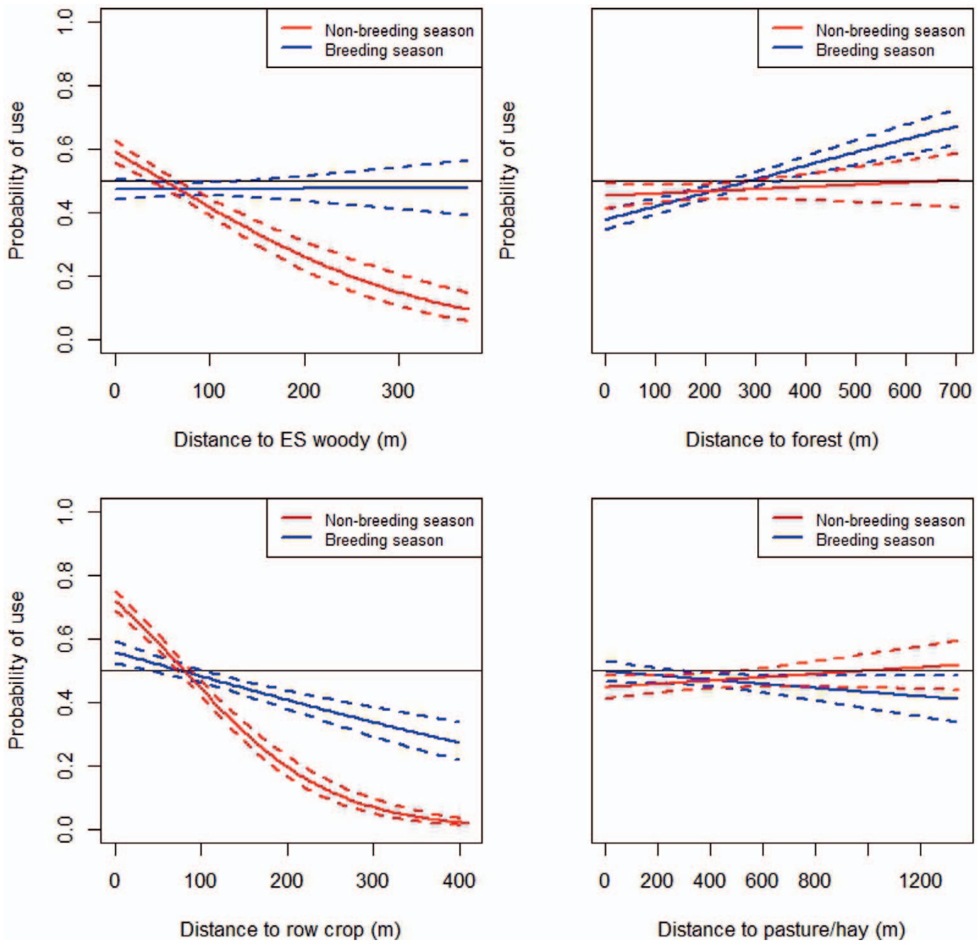

Fig. 4. Influence of distance to cover types on predicted probability of northern bobwhite use within the early successional herbaceous cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

Spatial Analysis of Usable Space

Mean probabilities of use predicted from distances to nearest cover types during the breeding and non-breeding seasons were lower on the Fee and Peach Orchard sites than on the Thurner and Wildcat sites when aggregated across cover types (Table 4). There were small differences in predicted probabilities of use between breeding and non-breeding seasons for all but the Wildcat site, where aggregate probability of use was higher during the breeding season compared to the non-breeding season.

With relatively large *n*-sizes, we readily detected statistically significant differences in predicted probability of use of cover types within sites between the breeding and non-breeding seasons (Table 4) but the largest difference was 0.10 and we did not consider differences <0.05 as biologically relevant. Applying these criteria, ES herbaceous had higher predicted probability of use during the breeding season compared to the non-breeding season on all sites except Thurner (Table 4). ES woody had higher probability of use during the nonbreeding season compared to the breeding season on the Peach Orchard and Thurner sites. Pasture/hay had higher probability of use during the breeding season compared to the nonbreeding season on all sites except Fee. Row crop had higher predicted probability of use during the breeding season than during the non-breeding season on the Wildcat site, while predicted probabilities of use for forest did not differ between seasons at any site.

Different patterns of variation in predicted probabilities of use among cover types were observed on our four study sites (Table 4). Predicted probability of use was highest for ES herbaceous and ES woody compared to forest, row crop, and pasture/hay on the Fee site, while probability of use was substantially higher than other cover types on the Peach Orchard site. Mean probabilities of use were more consistent among cover types on the Thurner and Wildcat sites compared to the Fee and Peach Orchard sites. Since the same distance to cover type relationships were applied to grid points on each site, differences in predicted probabilities of use were caused by spatial arrangements of cover types that varied among study sites.

The row-wise differences in distances for used versus random points from focal to nearest other cover types (Table 3) summarized the distributions of radiolocations overlain on cover types (Figures 9–12). Radio-locations were concentrated near habitat edges within high use

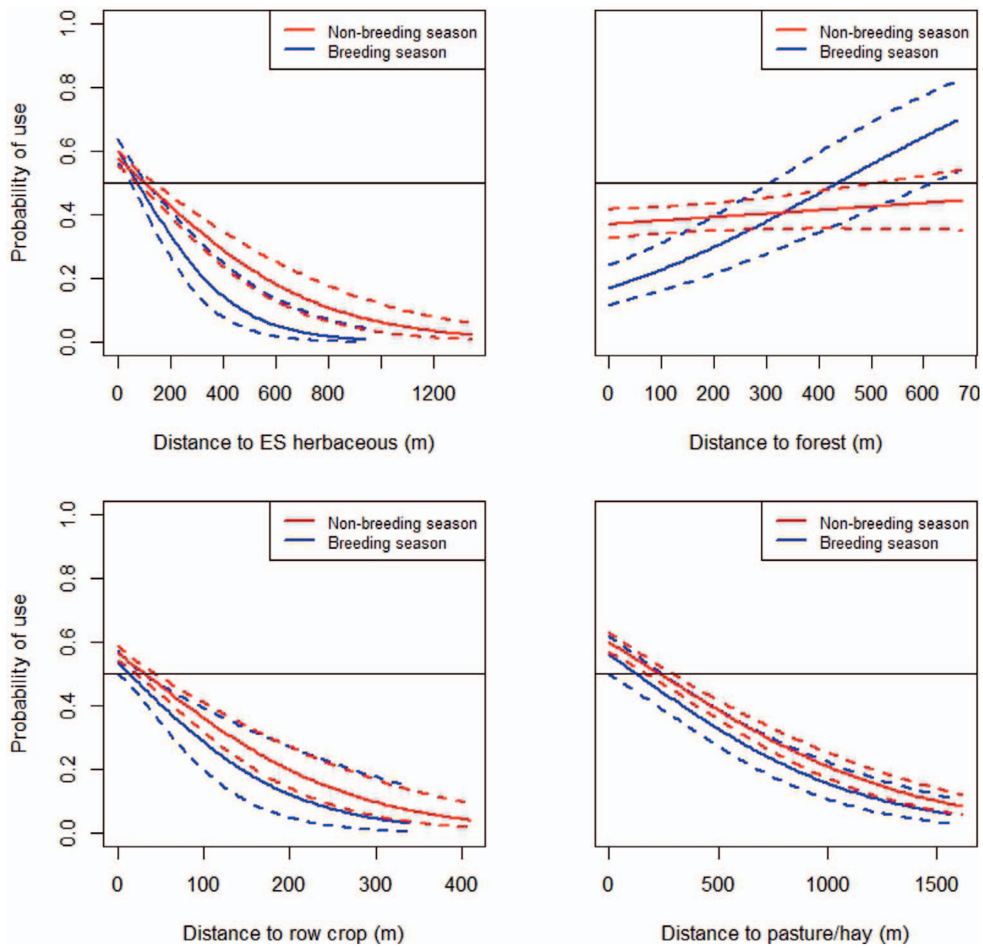

Fig. 5. Influence of distance to cover types on predicted probability of northern bobwhite use within the early successional woody cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

areas during the non-breeding season and were more widely dispersed within cover types during the breeding season. This was especially evident on the Fee and Wildcat sites (Figures 9 and 12).

Column-wise differences in distances for used versus random points (Table 3) corresponded to the probability of use surfaces shown in Figures 9–12. Early successional herbaceous, ES woody, and pasture/hay cover types were closer than forest and row crop cover types to locations of radio-marked bobwhites within focal cover types than predicted from a random distribution of points. Probability surfaces predicted from distances to cover types revealed areas with high probabilities of use where radio-marked coveys and individual birds were located, but also other areas with high predicted probability of use that were not known to be occupied during the breeding and non-breeding seasons The Fee and Peach Orchard sites stood out from the Thurner and Wildcat sites in having large contiguous areas with low probabilities of use. Spatial distributions of radiolocations and areas with high probabilities of use differed between breeding and non-breeding seasons on all study sites with the possible exception of Peach Orchard. Areas with high probabilities of use were more fully occupied by radio-marked birds during the breeding season compared to distributions of radio-marked coveys during the non-breeding season on the Fee and Thurner sites (Figures 9 and 11).

DISCUSSION

Swift and Hannon (2010) suggested a critical threshold of 10-30% usable habitat for birds and mammals, below which fragmentation begins to negatively impact populations in addition to net habitat loss. Two methods that we used to estimate usable space provided very different results, each with their own implications for conservation of bobwhites. Sensitive mostly to relative use and abundance of cover types, the habitat selection ratio method produced estimated proportions of usable space that were lower (0.06-0.30) than distance to cover type estimates (0.30-0.53) which were sensitive to size, interspersion, and juxtaposition of cover types; and to the mobility of bobwhites that used those cover types. The difference in estimates from these two methods may be arbitrary; we selected a naïve cutoff (0.5 probability of use) to estimate usable space with the distance-based method.

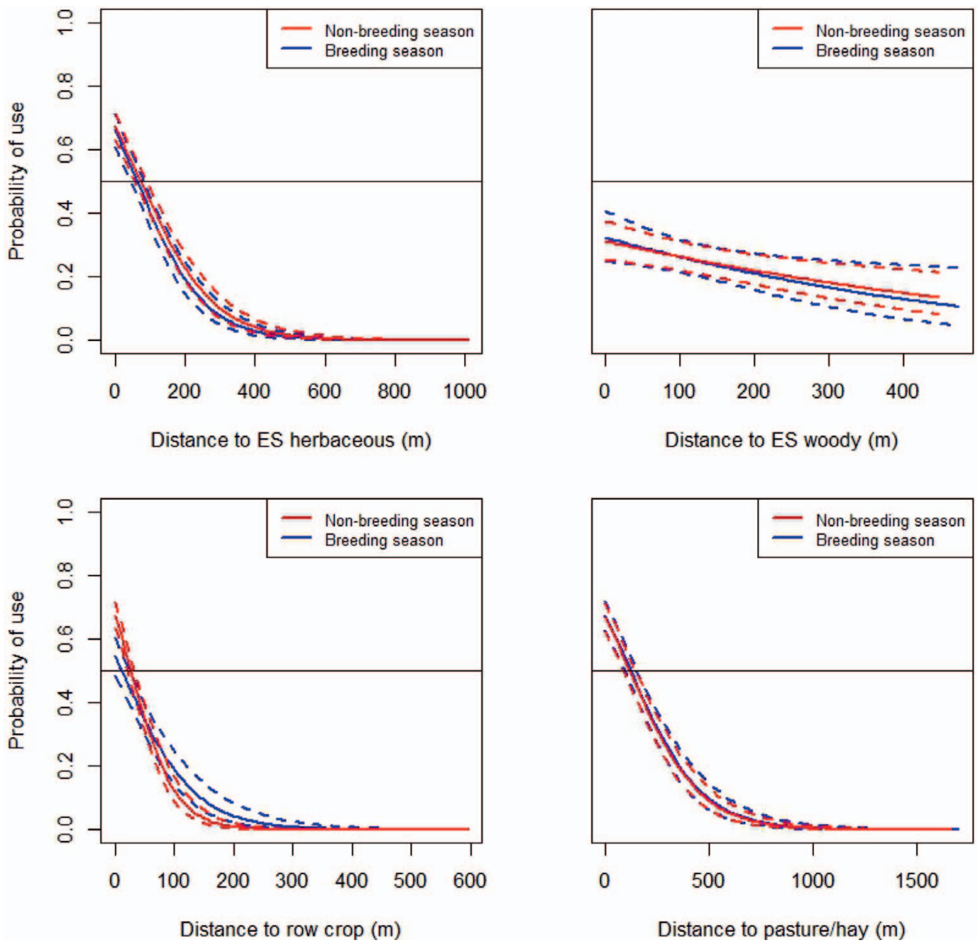

Fig. 6. Influence of distance to cover types on predicted probability of northern bobwhite use within the forest cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

Estimates of usable space based on cover type selection ratios provided insights into temporal changes, while distance to cover type analyses based on distance to cover type provided insights into spatial variation in usable space within and among cover types. Though methods of analysis and interpretation of results differ between these approaches to estimating usable space, both can inform bobwhite habitat management and restoration. The habitat selection method quantifies usable space at a coarse scale that is more suited to regional conservation planning (Brennan 1991, and Williams et al. 2006) if habitat selection coefficients are generalized from studies conducted within a region. The distance-based method could be applied at regional scales but is better suited to targeting delivery of habitat conservation at the farm or management area scale. Generalized regional (i.e. by Bird Conservation Region) distance to cover type functions would need to be developed from empirical relationships such as we derived for our study areas.

The cover type selection ratio method revealed large seasonal variation in usable space. Low estimated proportions of usable space (<0.15) during the non-breeding season were associated with low use relative to high availability of row crops on our study sites. Proportions of usable space (selection ratio method) approached 0.35 on our study areas as bobwhites made greater use of row crop late in the breeding season. Row crop contributed the largest proportions of total areas of our study sites and was highly selected during brood-rearing (Liberati and Gates 2017, *in review*). Actively growing and mature row crops provide overhead concealment and bare ground during summer and early fall, allowing free movement and foraging by broods and coveys until fields are harvested (Janke and Gates 2013, Liberati 2011). Row crop fields are sources of food for bobwhites after fields are harvested (Hanson and Miller 1961, Guthery 1997). Although row crop fields averaged >100 ha of usable space (selection ratio method) across the four sites, row crop was still far more abundant on the landscape than necessary to meet the needs of bobwhites, as revealed by selection ratios that were <0.126 during the non-breeding season and <0.918 during the non-breeding season.

Seasonal comparisons of usable space based on cover type selection ratios assume that 1 ha of usable space during the non-breeding season equals 1 ha of usable space during the breeding season. This is a tenuous assumption because space use by bobwhites may differ

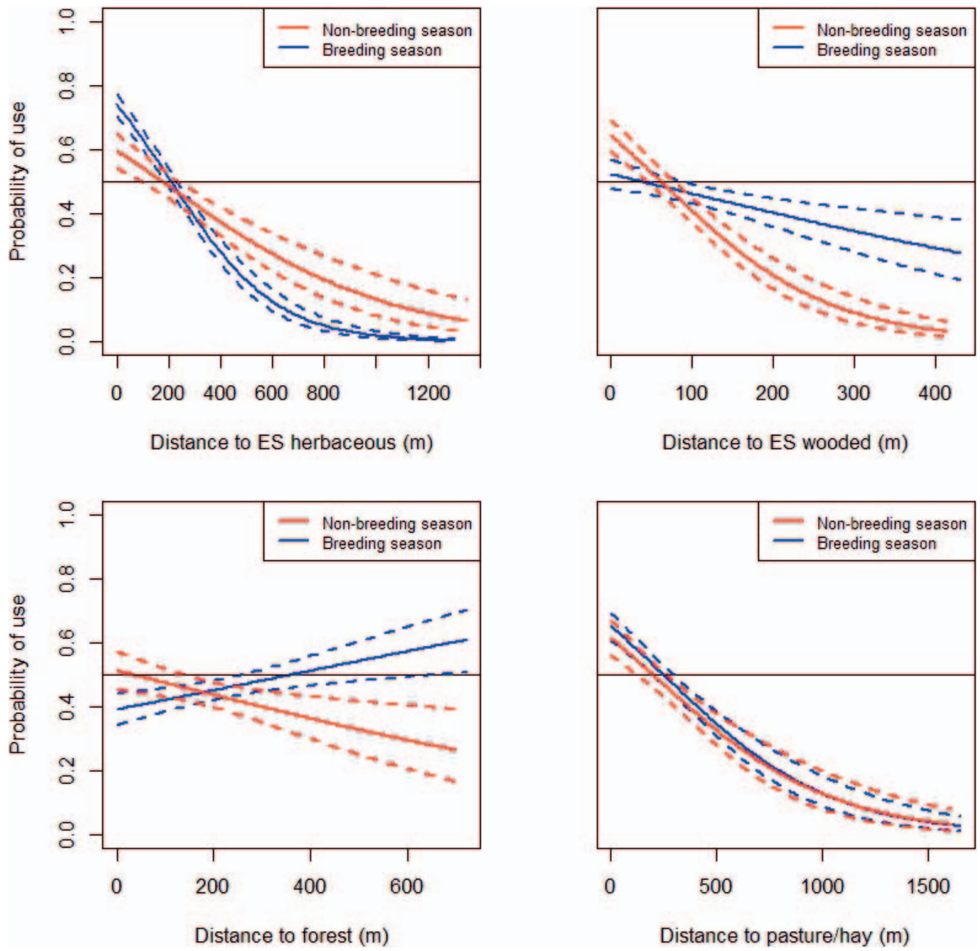

Fig. 7. Influence of distance to cover types on predicted probability of northern bobwhite use within the row crop cover type early in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

between breeding and non-breeding seasons. There was little or no overlap of covey home ranges during the non-breeding season in our study population (Janke et al. 2013). Home ranges of individual radio-marked birds overlapped during the breeding season (Liberati, unpublished data) when social units were single birds, mated pairs, or broods. Seasonal home range sizes also were larger for individual birds during the breeding season (mean = 125 ha; Liberati 2011) compared to coveys during the non-breeding season (mean = 26 ha; Janke and Gates 2013).

Our distance-based estimates of proportional usable space revealed overall differences between breeding and non-breeding seasons and only marginal differences (0.03-0.09) between seasons within cover types. Differences were more evident when we compared usable space among study sites. The Fee and Peach Orchard sites had the lowest crude densities of coveys (0.004-0.006 coveys/ha), and large contiguous areas of low use when probability of use was mapped as a response surface over cover type maps during the non-breeding season (mean probability = 0.30-0.31). The Thurner site had a somewhat higher mean crude density of coveys (0.007 coveys/ha) with a larger distance-based estimate of proportional usable space (0.43) during the non-breeding season. Crude densities of coveys were >2 times higher on the Wildcat site where mean probability of use was 0.45 during the non-breeding season.

Stoddard (1931: 374) stressed the importance of cover type diversity within a landscape and recommended a balance of open woodland, thickets, weedy and grassy fields, and cultivated ground to provide "the essentials in each [covey] range". Distances between cover types are known to limit resource availability (Schroeder 1985, Guthery 1999), and dispersal (Williams et al. 2004). Cover types that Hanson and Miller (1961) deemed critical to supporting bobwhites (cultivated crop fields, herbaceous fields, and early successional shrubs and / forbs) were all represented in our distance to cover type models that predicted probability of use within cover types.

Cover types with the lowest mean selection ratios (e.g. forest, row crop, and pasture-hay) were also the cover types where radio-marked bobwhites were located closer to ES herbaceous and ES woody cover types than expected from random distributions of use points. We conclude that these cover types were not more fully utilized because field sizes on our study area were larger

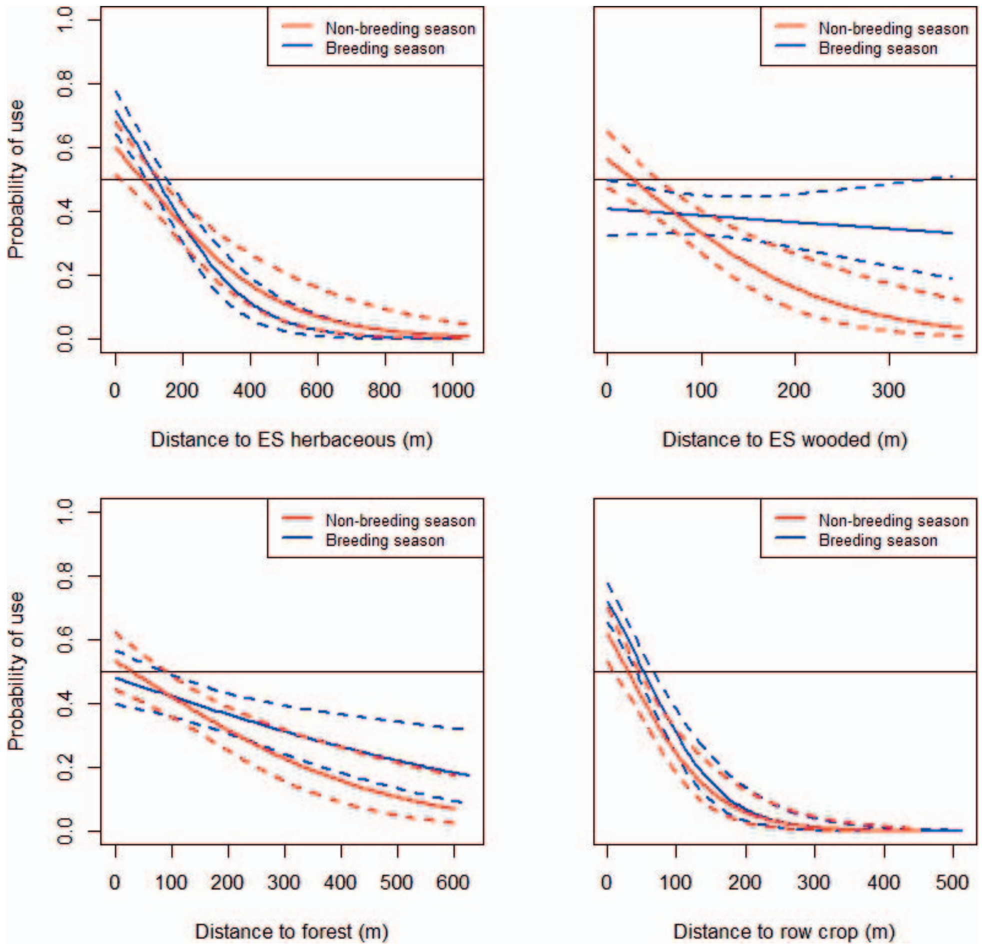

Fig. 8. Influence of distance to cover types on predicted probability of northern bobwhite use within the pasture/hay cover type in southwestern Ohio (years and study sites combined). Dashed horizontal curves represent 95% confidence intervals. The horizontal line represents the 0.50 threshold of predicted probability of use.

than necessary to supply food and cover requirements, or these habitats did not provide sufficient security when bobwhites moved farther into relatively open or homogeneous cover types, particularly during the non-breeding season. We found that bobwhites did not move far into cover types that lacked protective cover (forest, row crop and pasture/hay) during the non-breeding season and early stages of the breeding season. Used points averaged 73-135 m from nearest other cover types compared to random points that were located 118-222 m farther from nearest other cover types during breeding and non-breeding seasons. Affinity of bobwhites for habitat edges at least partially explains the low selection ratios we observed for forest, row crop, and pasture hay cover types that contributed to low overall estimates of usable space (selection ratio method), particularly during the non-breeding season.

Our results support Hanson and Miller's (1961) recommendation that establishing patches of ES woody cover 100-200 m apart in areas near ES herbaceous and row crop cover can improve usability. Proximity to ES woody cover strongly influenced probability of use within ES herbaceous and row crop cover types during the non-breeding season. Janke and Gates (2013) showed that selection of ES woody cover was highest during the non-breeding season but accounted for only 4% of total area of our study sites. The importance of ES woody cover is well established, particularly during the non-breeding season (Roseberry and Klimstra 1984, Schroeder 1985, Williams et al. 2000). Selection for ES woody and row crop cover types within the home range core indicated that bobwhites established home ranges where protective cover (e.g. woody edges) is close to food resources (e.g. row crops) during the non-breeding season (Janke and Gates (2013). Furthermore, row crop fields were used mostly within 10-53 m of ES woody and within 100-135 m of ES herbaceous cover types during breeding and non-breeding seasons.

With low selection ratios, forest and pasture/hay cover types contributed little or no usable space compared to other cover types. Usability was near zero for pasture/hay during most of the non-breeding season and increased only slightly during the breeding season. Pastures on our study sites were typically intensively grazed or mowed and rarely provided protective cover. Forest cover maintained a relatively low level of usability throughout each year with little or no seasonal variation, although bobwhites used interior areas of lightly grazed woodlots

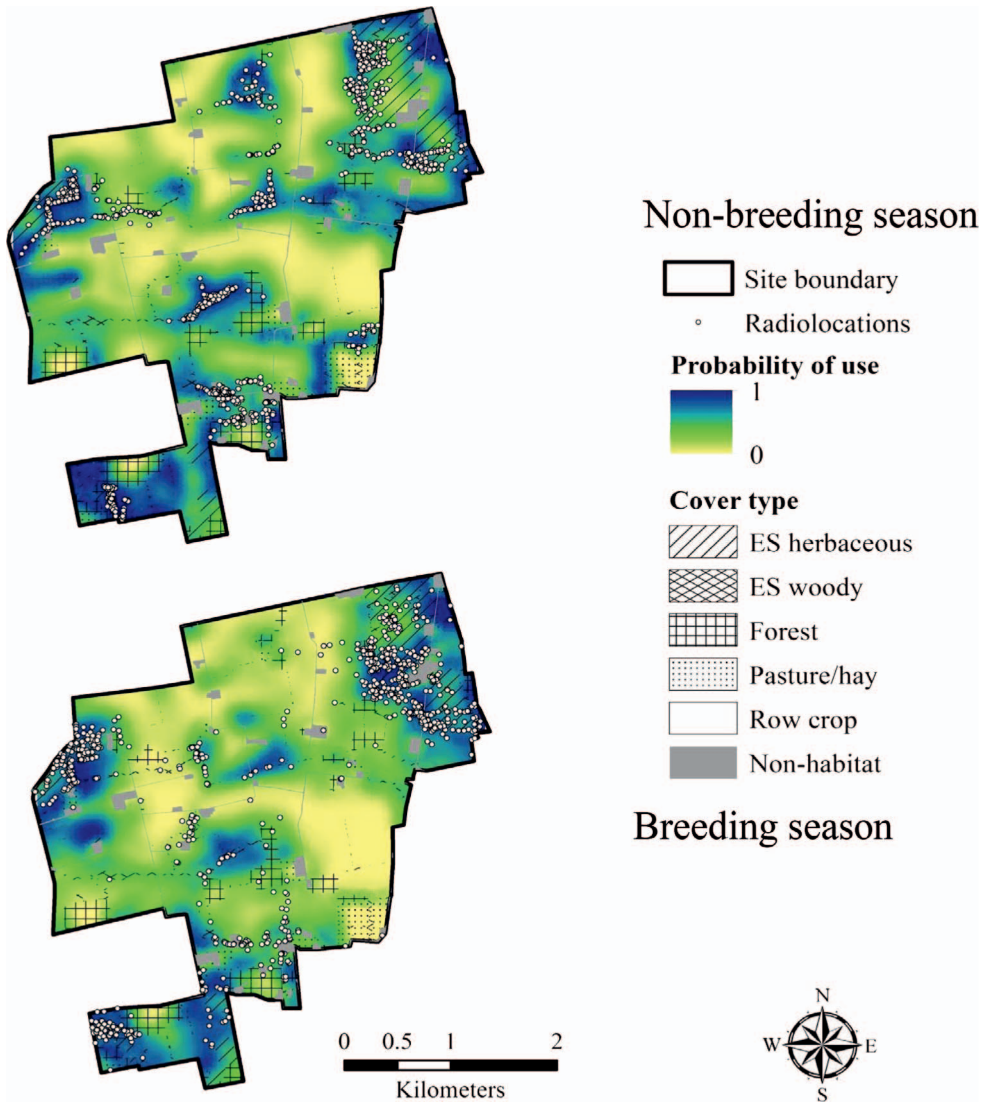

Fig. 9. Cover map and probability surface predicting use by northern bobwhites within the Fee study site in southwestern Ohio during 2009-2011 (years combined). Predicted use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding seasons.

during the non-breeding season. Otherwise, individual birds or coveys used only very narrow forest edges near early successional herbaceous (50-66 m) and row crop (28-40 m) cover types during breeding and non-breeding seasons.

Our findings explain why others (Roseberry and Sudkamp 1998, Veech 2006, Bowling et al. 2014) found that bobwhite populations fare better in landscapes with more grassland, cropland, and woody edge than landscapes dominated by forest, pasture, or urban land cover. Schroeder (1985) suggested that bobwhite densities are maximized when food, cover, and nesting habitat occur in proper amounts and with proper spacing. Guthery (1999) suggested that there is no ideal configuration of different cover types (i.e. dispersion and quantity) and called this apparent plasticity "slack". Slack arises because bobwhites respond to general structural characteristics of vegetation and cover types that serve interchangeable purposes (Errington and Hamerstrom 1936). If bobwhites are attracted to ES woody cover for concealment and protection, it is reasonable to suggest that other cover types, such as ES herbaceous or forest cover, could serve as surrogates if vegetation structure is suitable for bobwhites (Guthery 1999).

Although slack exists in the ideal amount of various cover types within a management area, thresholds likely exist where too much or too little of any cover type reduces usability of an area (Guthery 1999). Cover patch size is known to affect bobwhite habitat suitability (Schroeder 1985). However, patch size was not included as a predictor variable in models that we used to develop probability of use maps for our study sites. We digitized all cover type patches and some may have been too small to benefit bobwhites.

Distance to ES herbaceous cover influenced year-round use of all cover types, though at greater distances than ES woody cover. As expected, comparing seasonal effects of distance to ES herbaceous cover suggested that

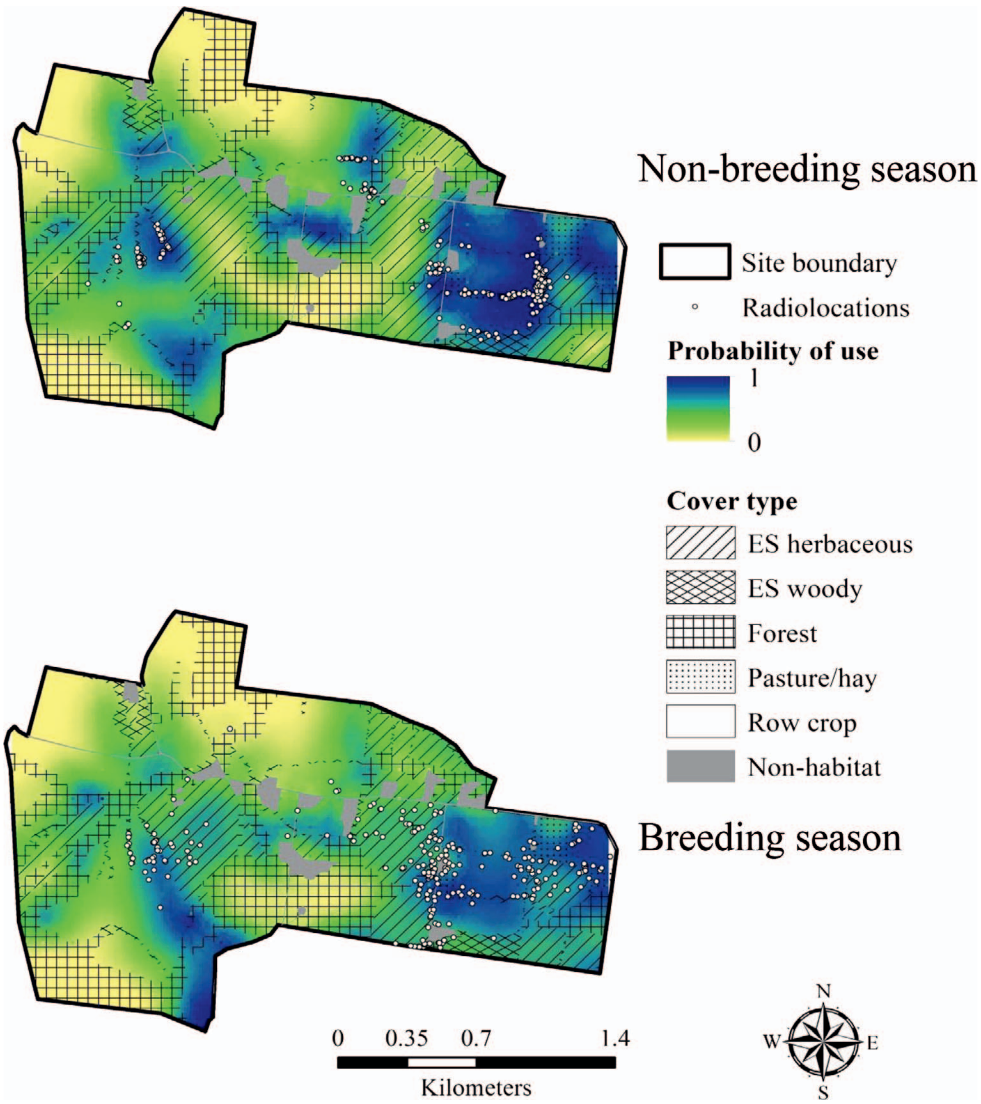

Fig. 10. Cover map and probability surface predicting use by northern bobwhite within the Peach Orchard study site in southwestern Ohio during 2009-2011 (years combined). Probability of use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding seasons.

this cover type was more important during the breeding season compared to the non-breeding season. Early successional herbaceous fields provided cover, forage, and nesting habitat on our study sites during breeding (Liberati and Gates 2017, *in review*), and were the second most highly-selected cover type during non-breeding (Janke and Gates 2013).

We expected to observe a positive relationship between covey densities and usable space across study sites during the non-breeding season. The wildcat study site had the highest crude and ecological densities of coveys and the third lowest proportion of usable space (0.078) based on the habitat selection method. Crude and ecological covey densities were lower on the Fee, Peach, and Thurner sites where the proportions of usable space (habitat selection method) ranged from 0.073 to 0.188. The Wildcat site averaged higher probabilities of use (distance-based method) followed in similar rank order as crude or ecological densities by the Thurner, Peach Orchard, and Fee sites. The cover type selection-based estimate of usable space could only be used to compare study sites and did not represent fine-scale variation within sites like the distance-based method which provided spatially explicit and finer-scale estimates of usable space on a continuous 0 to 1 scale.

Absence or low density of a species does not necessarily mean that habitat conditions are unsuitable (Wiens 1989). Population density and demography also determine occupancy (Wiens et al. 1987, Haila et al. 1996). Demographic sensitivity analyses of empirically-determined vital rates revealed that reproductive rates were insufficient to offset mortality during the non-breeding season (Gates et al.2012). As a result, we expected to find that some usable space was unoccupied when radio-locations of individual birds and coveys were overlaid on use probability maps. Consistent with higher ecological densities of coveys, usable areas were more fully occupied by radio-marked birds during the non-

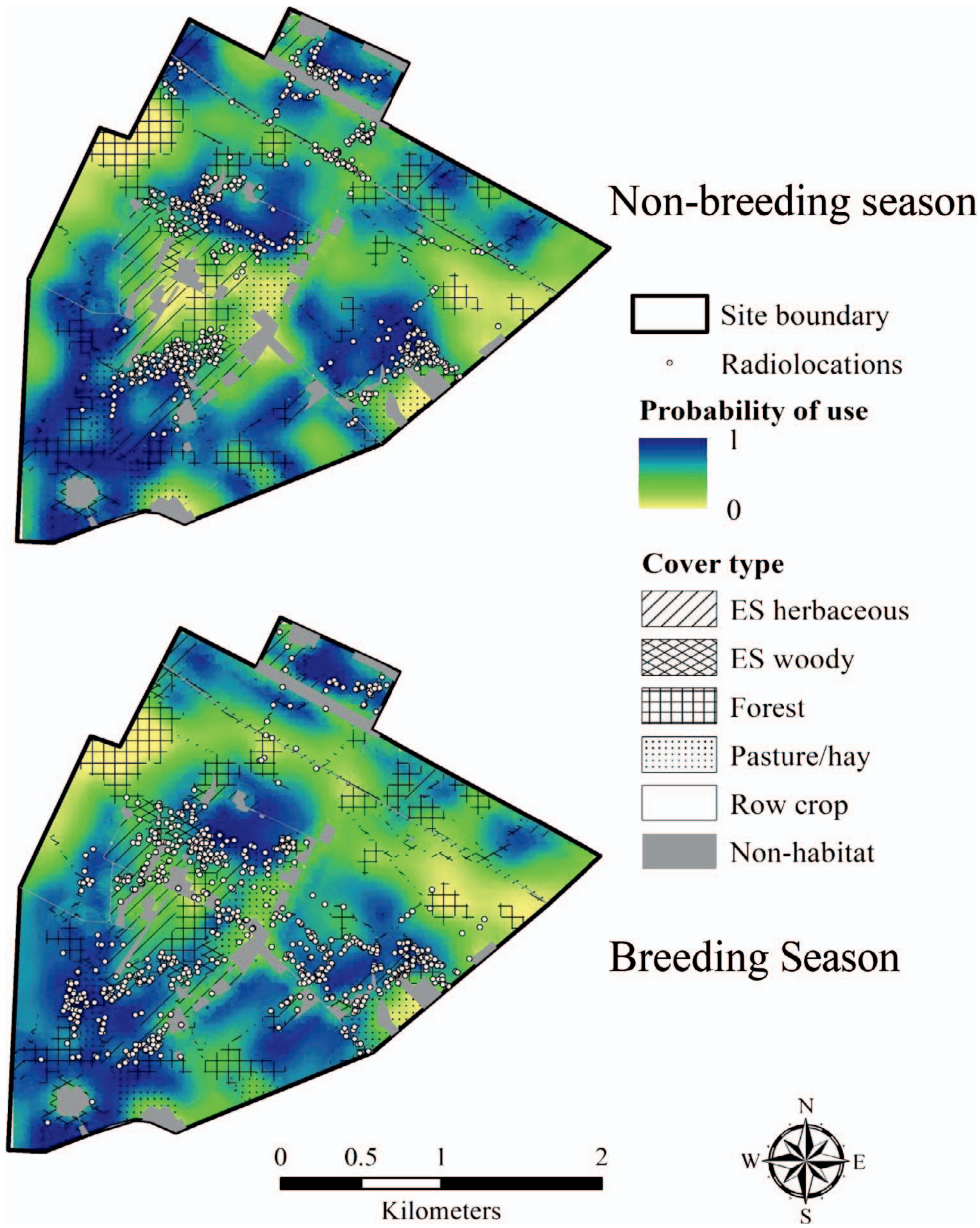

Fig. 11. Cover map and probability surface predicting use by northern bobwhite within the Thurner study site in southwestern Ohio during 2009-2011 (years combined). Probability of use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding seasons.

breeding season on the Wildcat site, while usable areas of Thurner, Fee, and Peach were only partially occupied by radio-marked birds when we overlaid radio-locations on predicted probability of use maps. Underutilization of usable space could also be explained by differences in vegetation structure and composition at the microhabitat scale. Wiley (2012) showed that use of cover types was affected by ground cover, overhead cover, and visual obstruction. Macro-habitat variables not included in our analyses of usable space (e.g. patch size and configuration) may have affected space use by bobwhites (Kopp et al. 1998).

Availability of suitable habitat is thought to be the most limiting environmental factor in northern areas of bobwhite range (Guthery 1997). Survival was negatively associated with depth and duration of snow cover during December-February in our study population (Janke and Gates 2012, Knapik 2015). Furthermore, individual survival during periods of prolonged snow cover increased with ES woody edge density within 95 m of areas used by radio-marked bobwhites (Janke et al. 2015). We found that bobwhites used points within focal cover types that were 44-92 m closer to the ES woody cover type than expected from random use during the non-breeding season. We contend that growth of our study population is limited by availability of protective cover (e.g. ES woody) near food sources (e.g. row crop), exposing bobwhites to high levels of predation during

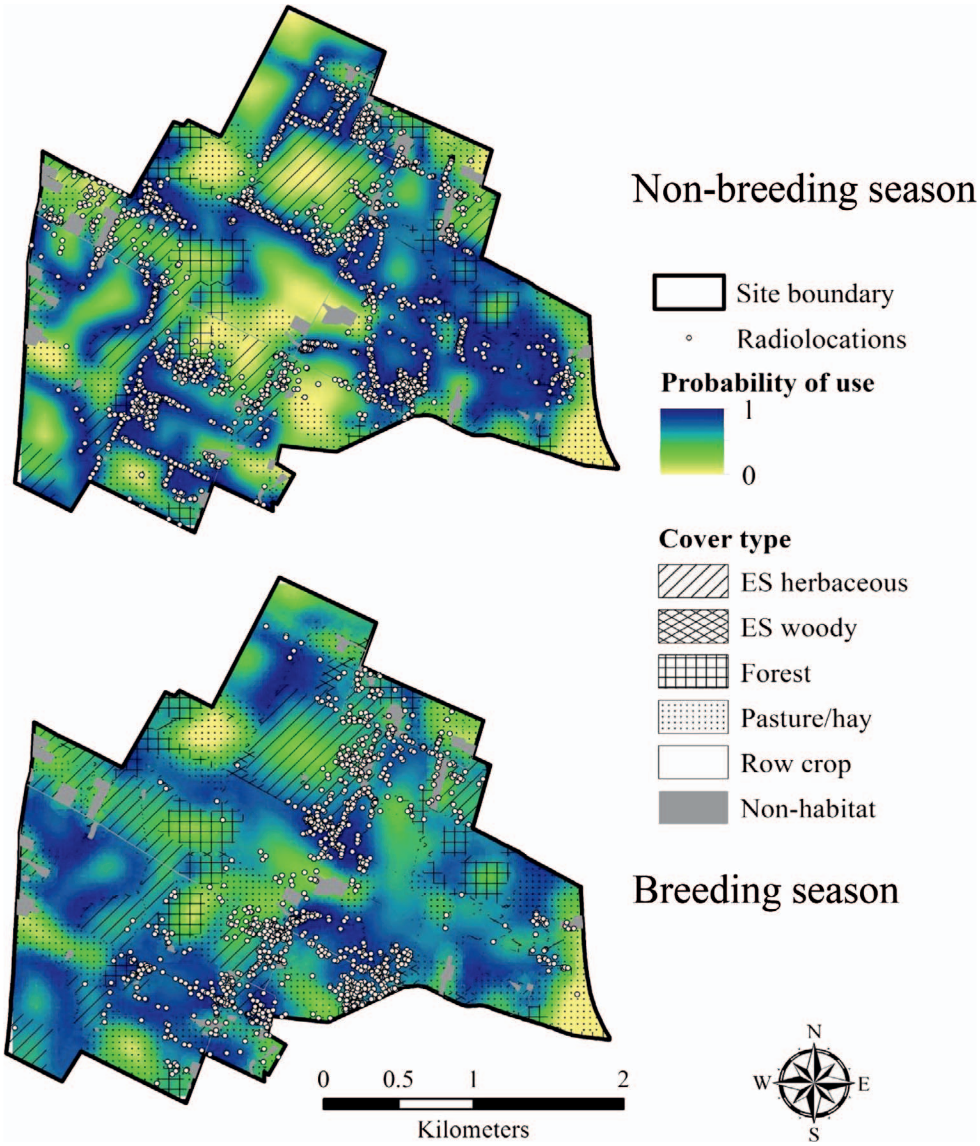

Fig. 12. Cover map and probability surface predicting use by northern bobwhite within the Wildcat study site in southwestern Ohio during 2009-2011 (years combined). Probability of use was based on distances between radio-locations of coveys and individuals and nearby cover types, pooled across sites, during the non-breeding and breeding season.

winters with prolonged snow cover that covers food resources. Roseberry and Sudkamp (1998) emphasized the importance of woody edge as a habitat component that sustained bobwhite populations in Illinois. Evans et al. (2013) found only small increases in bobwhite covey densities associated with establishment of herbaceous field borders in the Eastern Tallgrass Prairie region that included our study areas. All of this points to woody cover and not herbaceous cover as the most limiting habitat factor in southwestern Ohio.

Habitat conservation for grassland- or early succession-dependent wildlife has focused on converting crop fields to perennial herbaceous cover. This strategy follows recommendations that range-wide recovery of northern bobwhite populations should focus on increasing usable space at the regional level by restoring native grasses and forbs with the assumption that populations are limited by reproduction (Burger et al. 2006). This may be true in southern areas of bobwhite range but we have argued that bobwhite populations on our study areas (and possibly in other northern areas of bobwhite range) are most limited by protective cover near food sources during the non-breeding season (Gates et al. 2012). This is not to say that sustaining reproduction by providing adequate nesting and brood-rearing habitat is not essential to conserving bobwhite populations throughout their range.

Small proportional changes in primary land use can leverage disproportionate increases in grassland and edge-dependent birds during winter (Evans et al. 2013). The strong association of bobwhites with habitat edges such as we and many others before us have demonstrated suggests that buffer strips of early successional woody vegetation or native grasses and forbs can be added to agricultural landscapes to sustain bobwhite populations. Establishing buffers has produced positive but mixed results that vary regionally Evans et al. 2013) with, amount of forest land (Riddle et al. 2008), predator reduction (Palmer et al. 2005) and regional abundance of bobwhites (Bowling et al. 2014).

MANAGEMENT IMPLICATIONS

Conservation challenges are intensified in working landscapes where production-focused land uses create inhospitable conditions for bobwhites. Conserving early successional woody and herbaceous cover types are essential to sustaining bobwhite populations in Midwestern agricultural landscapes. This is challenging because habitat acquisition, protection, and maintenance are costly, especially when agricultural commodity prices rise. Removing land from agricultural production also limits earning potential of private-owned working lands, thereby diminishing incentives for landowners to conserve wildlife habitat. Private lands managers must work within the constraints of technological, policy, and economic forces that are beyond their control, and seek ways to integrate bobwhite conservation with production agriculture.

Though certainly beneficial, converting large contiguous tracts of cropland to perennial cover may not be the most efficient way to improve habitat for bobwhites on agricultural working lands where opportunities are limited or cost-prohibitive. We found that use of preferred cover types by bobwhites was influenced by distance to other cover types. A more practical alternative might be to create and sustain early successional cover along wooded edges (including woodlots) near cover types that provide critical food and cover (e.g. ES herbaceous and row crop) throughout the annual life cycle. Adding small tracts or buffer strips of ES woody and herbaceous cover near habitats that are less selected for by bobwhites (e.g. row crop and pasture/hay) could leverage increased usable space while minimizing impact on production agriculture. Most radio-marked bobwhites were located in focal cover types within 50-250 m of other cover types so conserving small (0.25-6.25 ha) areas of ES herbaceous and woody cover in areas that are difficult to farm should increase usable space if they are strategically placed relative to other cover types that provide food and protective cover during breeding and non-breeding seasons.

Locations of radio-marked bobwhites were more strongly associated with edges during the non-breeding season than during the breeding season. Our study sites were characterized by "hard edges" of maturing woodlots adjacent to open cropland. More attention should be given to enhancing protective cover along woodlot edges that adjoin row cropland to improve non-breeding habitat. Adding buffers of ES herbaceous habitat near woody edges could provide nesting and brood-rearing habitat near protective cover. Reduction of tree basal area to promote growth of early successional vegetation (i.e. "edge feathering") was implemented during 2012 and 2013 to improve protective cover on the Fee and Peach Orchard sites (Brooks 2015, Knapik 2015). With distance to cover type functions similar to what we used, a digital habitat coverage and GIS, managers can identify gaps where focal habitat restoration and management are best applied to leverage increases in usable space while minimizing impact on the capacity of working lands to produce agricultural or forest products.

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Appendix 1. Cover type selection and usable space for 51 individual northern bobwhites on four study sites (combined) in southwestern Ohio during the breeding season in 2010.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i/a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
April	Row Crop	99	0.162	0.579	0.280	0.040	62.8	1555.5
	Pasture Hay	36	0.059	0.080	0.740	0.107	22.8	213.8
	Forest	102	0.167	0.123	1.360	0.196	64.7	329.8
	ES Woody	172	0.282	0.041	6.934	1.000	109.1	109.1
	ES Herb	193	0.316	0.130	2.434	0.351	122.4	348.6
	Non Habitat	9	0.015	0.048	0.305	0.044	5.7	129.7
May	Row Crop	73	0.157	0.579	0.271	0.064	99.5	1555.5
	Pasture Hay	31	0.067	0.080	0.838	0.198	42.3	213.8
	Forest	62	0.133	0.123	1.086	0.256	84.5	329.8
	ES Woody	80	0.172	0.041	4.238	1.000	109.1	109.1
	ES Herb	200	0.430	0.130	3.314	0.782	272.6	348.6
	Non Habitat	19	0.041	0.048	0.846	0.200	25.9	129.7
June	Row Crop	104	0.271	0.579	0.468	0.110	171.8	1555.5
	Pasture Hay	6	0.016	0.080	0.196	0.046	9.9	213.8
	Forest	11	0.029	0.123	0.233	0.055	18.2	329.8
	ES Woody	39	0.102	0.041	2.502	0.591	64.4	109.1
	ES Herb	211	0.549	0.130	4.234	1.000	348.6	348.6
	Non Habitat	13	0.034	0.048	0.701	0.166	21.5	129.7
July	Row Crop	76	0.394	0.579	0.680	0.247	384.0	1555.5
	Pasture Hay	5	0.026	0.080	0.326	0.118	25.3	213.8
	Forest	7	0.036	0.123	0.295	0.107	35.4	329.8
	ES Woody	21	0.109	0.041	2.680	0.973	106.1	109.1
	ES Herb	69	0.358	0.130	2.755	1.000	348.6	348.6
	Non Habitat	15	0.078	0.048	1.610	0.584	75.8	129.7
August	Row Crop	52	0.437	0.579	0.755	0.271	421.6	1555.5
	Pasture Hay	11	0.092	0.080	1.162	0.417	89.2	213.8
	Forest	7	0.059	0.123	0.479	0.172	56.8	329.8
	ES Woody	5	0.042	0.041	1.035	0.372	40.5	109.1
	ES Herb	43	0.361	0.130	2.784	1.000	348.6	348.6
	Non Habitat	1	0.008	0.048	0.174	0.063	8.1	129.7
September	Row Crop	34	0.531	0.579	0.918	0.265	412.0	1555.5
	Pasture Hay	5	0.078	0.080	0.982	0.283	60.6	213.8
	Forest	12	0.188	0.123	1.527	0.441	145.4	329.8
	ES Woody	9	0.141	0.041	3.464	1.000	109.1	109.1
	ES Herb	3	0.047	0.130	0.361	0.104	36.4	348.6
	Non Habitat	1	0.016	0.048	0.324	0.093	12.1	129.7

Appendix 2. Cover type selection and usable space for 47 individual northern bobwhites on four study sites (combined) in southwestern Ohio during the breeding season in 2011.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i/a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
April	Row Crop	21	0.030	0.553	0.055	0.007	12.4	1802.1
	Pasture Hay	35	0.050	0.090	0.557	0.070	20.7	294.1
	Forest	217	0.312	0.131	2.381	0.301	128.3	426.8
	ES Woody	240	0.345	0.044	7.921	1.000	141.9	141.9
	ES Herb	178	0.256	0.134	1.902	0.240	105.2	438.1
	Non Habitat	5	0.007	0.048	0.150	0.019	3.0	156.1
May	Row Crop	66	0.122	0.553	0.221	0.029	51.7	1802.1
	Pasture Hay	38	0.070	0.090	0.778	0.101	29.8	294.1
	Forest	96	0.177	0.131	1.355	0.176	75.3	426.8
	ES Woody	181	0.335	0.044	7.685	1.000	141.9	141.9
	ES Herb	151	0.279	0.134	2.076	0.270	118.4	438.1
	Non Habitat	9	0.017	0.048	0.347	0.045	7.1	156.1
June	Row Crop	23	0.067	0.553	0.122	0.013	23.6	1802.1
	Pasture Hay	33	0.096	0.090	1.069	0.115	33.9	294.1
	Forest	39	0.114	0.131	0.871	0.094	40.1	426.8
	ES Woody	138	0.404	0.044	9.269	1.000	141.9	141.9
	ES Herb	102	0.298	0.134	2.219	0.239	104.9	438.1
	Non Habitat	7	0.020	0.048	0.427	0.046	7.2	156.1
July	Row Crop	62	0.191	0.553	0.346	0.083	149.1	1802.1
	Pasture Hay	13	0.040	0.090	0.445	0.106	31.3	294.1
	Forest	48	0.148	0.131	1.131	0.270	115.4	426.8
	ES Woody	59	0.182	0.044	4.183	1.000	141.9	141.9
	ES Herb	127	0.392	0.134	2.916	0.697	305.4	438.1
	Non Habitat	15	0.046	0.048	0.966	0.231	36.1	156.1
August	Row Crop	75	0.419	0.553	0.758	0.268	483.7	1802.1
	Pasture Hay	4	0.022	0.090	0.248	0.088	25.8	294.1
	Forest	17	0.095	0.131	0.725	0.257	109.6	426.8
	ES Woody	22	0.123	0.044	2.823	1.000	141.9	141.9
	ES Herb	60	0.335	0.134	2.494	0.883	386.9	438.1
	Non Habitat	1	0.006	0.048	0.117	0.041	6.4	156.1
September	Row Crop	9	0.409	0.553	0.740	0.177	319.2	1802.1
	Pasture Hay	2	0.091	0.090	1.007	0.241	70.9	294.1
	Forest	1	0.045	0.131	0.347	0.083	35.5	426.8
	ES Woody	4	0.182	0.044	4.177	1.000	141.9	141.9
	ES Herb	6	0.273	0.134	2.029	0.486	212.8	438.1
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	156.1

Appendix 3. Cover type selection and usable space for 26 northern bobwhites coveys on four study sites (combined) in southwestern Ohio during the non-breeding season in 2009-2010.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i /a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
October	Row Crop	0	0.000	0.579	0.000	0.000	0.0	1555.5
	Pasture Hay	2	0.050	0.080	0.628	0.038	8.1	213.8
	Forest	3	0.075	0.123	0.611	0.037	12.1	329.8
	ES Woody	27	0.675	0.041	16.627	1.000	109.1	109.1
	ES Herb	8	0.200	0.130	1.541	0.093	32.3	348.6
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	129.7
November	Row Crop	12	0.051	0.579	0.087	0.010	16.0	1555.5
	Pasture Hay	13	0.055	0.080	0.689	0.081	17.3	213.8
	Forest	35	0.148	0.123	1.203	0.141	46.5	329.8
	ES Woody	82	0.346	0.041	8.523	1.000	109.1	109.1
	ES Herb	95	0.401	0.130	3.089	0.362	126.3	348.6
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	129.7
December	Row Crop	12	0.035	0.579	0.060	0.005	8.2	1555.5
	Pasture Hay	18	0.052	0.080	0.658	0.058	12.3	213.8
	Forest	59	0.172	0.123	1.397	0.123	40.5	329.8
	ES Woody	159	0.462	0.041	11.386	1.000	109.1	109.1
	ES Herb	95	0.276	0.130	2.128	0.187	65.2	348.6
	Non Habitat	1	0.003	0.048	0.060	0.005	0.7	129.7
January	Row Crop	40	0.074	0.579	0.128	0.011	17.6	1555.5
	Pasture Hay	9	0.017	0.080	0.210	0.019	4.0	213.8
	Forest	82	0.152	0.123	1.241	0.109	36.1	329.8
	ES Woody	248	0.461	0.041	11.355	1.000	109.1	109.1
	ES Herb	159	0.296	0.130	2.277	0.201	69.9	348.6
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	129.7
February	Row Crop	21	0.053	0.579	0.091	0.006	9.3	1555.5
	Pasture Hay	2	0.005	0.080	0.063	0.004	0.9	213.8
	Forest	63	0.158	0.123	1.283	0.085	27.9	329.8
	ES Woody	246	0.615	0.041	15.149	1.000	109.1	109.1
	ES Herb	66	0.165	0.130	1.271	0.084	29.3	348.6
	Non Habitat	2	0.005	0.048	0.104	0.007	0.9	129.7
March	Row Crop	29	0.097	0.579	0.168	0.013	20.3	1555.5
	Pasture Hay	9	0.030	0.080	0.378	0.029	6.3	213.8
	Forest	73	0.244	0.123	1.989	0.155	51.0	329.8
	ES woody	156	0.522	0.041	12.852	1.000	109.1	109.1
	ES Herb	31	0.104	0.130	0.799	0.062	21.7	348.6
	Non Habitat	1	0.003	0.048	0.069	0.005	0.7	129.7

Appendix 4. Cover type selection and usable space for 32 northern bobwhites coveys on four study sites (combined) in southwestern Ohio during the non-breeding season in 2010-2011.

Month	Cover type	No. radio-locations	Prop. use (p_i)	Prop. available (a_i)	Selection ratio (p_i /a_i)	Prop. Usable (u_i)	Usable space (U_i in ha)	Total area (A_i in ha)
October	Row Crop	7	0.033	0.553	0.059	0.006	11.2	1802.1
	Pasture Hay	28	0.131	0.090	1.457	0.152	44.6	294.1
	Forest	38	0.178	0.131	1.362	0.142	60.6	426.8
	ES Woody	89	0.418	0.044	9.598	1.000	141.9	141.9
	ES Herb	51	0.239	0.134	1.781	0.186	81.3	438.1
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	156.1
November	Row Crop	9	0.028	0.553	0.050	0.006	10.6	1802.1
	Pasture Hay	27	0.083	0.090	0.924	0.108	31.7	294.1
	Forest	97	0.299	0.131	2.286	0.266	113.7	426.8
	ES Woody	121	0.373	0.044	8.579	1.000	141.9	141.9
	ES Herb	68	0.210	0.134	1.561	0.182	79.7	438.1
	Non Habitat	2	0.006	0.048	0.129	0.015	2.3	156.1
December	Row Crop	12	0.034	0.553	0.061	0.006	11.4	1802.1
	Pasture Hay	7	0.020	0.090	0.220	0.023	6.6	294.1
	Forest	126	0.357	0.131	2.725	0.279	119.2	426.8
	ES Woody	150	0.425	0.044	9.761	1.000	141.9	141.9
	ES Herb	57	0.161	0.134	1.201	0.123	53.9	438.1
	Non Habitat	1	0.003	0.048	0.059	0.006	0.9	156.1
January	Row Crop	29	0.053	0.553	0.096	0.008	15.1	1802.1
	Pasture Hay	7	0.013	0.090	0.141	0.012	3.6	294.1
	Forest	132	0.240	0.131	1.836	0.161	68.6	426.8
	ES Woody	273	0.497	0.044	11.423	1.000	141.9	141.9
	ES Herb	108	0.197	0.134	1.463	0.128	56.1	438.1
	Non Habitat	0	0.000	0.048	0.000	0.000	0.0	156.1
February	Row Crop	22	0.043	0.553	0.077	0.007	12.6	1802.1
	Pasture Hay	2	0.004	0.090	0.043	0.004	1.1	294.1
	Forest	126	0.244	0.131	1.861	0.170	72.4	426.8
	ES Woody	247	0.478	0.044	10.975	1.000	141.9	141.9
	ES Herb	115	0.222	0.134	1.655	0.151	66.1	438.1
	Non Habitat	5	0.010	0.048	0.202	0.018	2.9	156.1
March	Row Crop	19	0.033	0.553	0.060	0.005	9.0	1802.1
	Pasture Hay	7	0.012	0.090	0.135	0.011	3.3	294.1
	Forest	119	0.207	0.131	1.577	0.132	56.5	426.8
	ES Woody	299	0.519	0.044	11.924	1.000	141.9	141.9
	ES Herb	128	0.222	0.134	1.653	0.139	60.7	438.1
	Non Habitat	4	0.007	0.048	0.145	0.012	1.9	156.1

Appendix 5. Standardized logistic regression coefficients (β) with standard errors (SE) of models selected by stepwise selection to predict probability of use of 5 cover types as a function of distance to other cover types for northern bobwhites during the breeding season in southwestern Ohio. Years and study sites were combined for analyses.

Cover Type	Covariate	B	SE(β)	P
ES Herbaceous	Intercept	-0.1029	0.0412	0.0125
	ESW	0.0034	0.0491	0.9440
	F	0.2731	0.0400	<0.0001
	RC	-0.2518	0.0433	<0.0001
	PH	-0.0758	0.0444	0.0876
	ESW*PH	0.3084	0.0418	<0.0001
	F*RC	-0.2263	0.0438	<0.0001
	F*PH	0.1140	0.0434	0.0086
ES Wooded	Intercept	-0.3394	0.1161	0.0035
	ESH	-0.9916	0.1703	<0.0001
	F	0.6669	0.0695	<0.0001
	RC	-0.7381	0.1826	<0.0001
	PH	-0.5782	0.0733	<0.0001
	ESH*RC	-0.8833	0.2709	0.0011
	ESH*PH	-0.2543	0.1006	0.0114
	F*RC	-0.2089	0.0769	0.0066
	F*PH	0.2752	0.0789	0.0005
	RC*PH	0.1411	0.0771	0.0671
Forest	Intercept	-1.0450	0.1366	<0.0001
	ESH	-1.8211	0.1665	<0.0001
	ESW	-0.2333	0.0957	0.0148
	RC	-1.2949	0.1608	<0.0001
	PH	-1.9038	0.1854	<0.0001
	ESH*ESW	0.1660	0.1073	0.1217
	ESH*RC	-0.7011	0.1540	<0.0001
	ESH*PH	-1.4646	0.1932	<0.0001
	ESW*PH	0.5535	0.1294	<0.0001
	RC*PH	-1.3344	0.1979	<0.0001
Row Crop	Intercept	-0.1549	0.0621	0.0126
	ESH	-1.1520	0.0816	<0.0001
	ESW	-0.2197	0.0636	0.0006
	F	0.1934	0.0627	0.0020
	PH	-0.6681	0.0719	<0.0001
	ESH*PH	-0.4344	0.0991	<0.0001
	ESH*F	0.1155	0.0723	0.1100
	ESW*F	-0.5399	0.0765	<0.0001
Pasture/Hay	Intercept	-0.4558	0.1331	0.0006
	ESH	-1.3371	0.1931	<0.0001
	ESW	-0.0683	0.1027	0.5058
	F	-0.3283	0.1096	0.0027
	RC	-1.3747	0.1865	<0.0001
	ESH*RC	-0.9253	0.2429	0.0001
	ESW*RC	0.1852	0.0883	0.0361
	F*RC	-0.2533	0.1517	0.0949

[a] Cover type to which models were applied
[b] RC = row crop; PH = pasture/hay; F = forest; ESW = early successional woody; ESH = early successional herbaceous

Appendix 6. Standardized logistic regression coefficients (β) standard errors (SE) of models selected by stepwise selection to predict probability of use of 5 cover types as a function of distance to other cover types for northern bobwhites during the non-breeding season in southwestern Ohio. Years and study sites were combined for analyses.

Cover Type	Covariate	B	SE(β)	P
ES Herbaceous	Intercept	-0.1373	0.0490	0.0051
	ESW	-0.5248	0.0616	<0.0001
	F	0.0411	0.0481	0.3934
	RC	-0.9449	0.0614	<0.0001
	PH	0.0619	0.0461	0.1798
	ESW*PH	0.1640	0.0472	0.0005
	F*PH	0.1455	0.0546	0.0077
	RC*PH	0.1133	0.0568	0.0460
ES Wooded	Intercept	-0.1020	0.0521	0.0501
	ESH	-0.5785	0.0733	<0.0001
	F	0.1246	0.0407	0.0022
	RC	-0.5864	0.0788	<0.0001
	PH	-0.5001	0.0431	<0.0001
	ESH*F	-0.2710	0.0492	<0.0001
	ESH*RC	-0.2642	0.1212	0.0293
	ESH*PH	-0.1257	0.0548	0.0219
	F*PH	0.1277	0.0455	0.0050
Forest	Intercept	-1.0560	0.1203	<0.0001
	ESH	-1.8874	0.1537	<0.0001
	ESW	-0.2108	0.0669	0.0016
	RC	-1.9753	0.1624	<0.0001
	PH	-1.7884	0.1420	<0.0001
	ESH*RC	-1.4054	0.1779	<0.0001
	ESH*PH	-0.9724	0.1303	<0.0001
	RC*PH	-1.1198	0.1642	<0.0001
Row Crop	Intercept	-0.2385	0.0792	0.0026
	ESH	-0.5956	0.0912	<0.0001
	ESW	-0.8432	0.0885	<0.0001
	F	-0.2249	0.0798	0.0048
	PH	-0.6358	0.0922	<0.0001
	ESH*ESW	0.2415	0.0921	0.0088
	ESH*PH	-0.7202	0.1242	<0.0001
	ESW*F	-0.3475	0.0971	0.0003
	ESW*PH	0.1289	0.0884	0.1449
	F*PH	0.2008	0.0861	0.0197
Pasture/Hay	Intercept	-0.5694	0.1407	0.0001
	ESH	-0.8671	0.1689	<0.0001
	ESW	-0.8150	0.1845	<0.0001
	F	-1.1518	0.1887	<0.0001
	RC	-0.6104	0.1415	<0.0001
	ESH*ESW	-0.7557	0.2279	0.0009
	ESH*RC	-0.3883	0.2431	0.1102
	ESW*F	-1.1152	0.1886	<0.0001
	RC*F	0.3547	0.1955	0.0696

[a] Cover type to which models were applied
[b] RC = row crop; PH = pasture/hay; F = forest; ESW = early successional woody; ESH = early successional herbaceous