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BREEDING SEASON MOVEMENTS AND DISPERSAL OF NORTHERN BOBWHITES IN FRAGMENTED HABITATS OF VIRGINIA

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ABSTRACT

To better understand dispersal patterns of northern bobwhites (*Colinus virginianus*) in fragmented habitats, we measured breeding season movements of 198 radiomarked bobwhites in central and eastern Virginia during 1994–1996. Mean distance between arithmetic centers of winter (1 Feb–15 Apr) and early breeding season (16 Apr–30 Jun) activity areas was 1,194 $\pm$ 137 m. Distance between centers of winter and late breeding season (1 Jul–15 Sep) activity areas averaged 1,644 $\pm$ 209 m and was greater for juveniles than adults ($P = 0.04$). Maximum distances moved between winter and breeding season locations (early, late, and combined) was also greater for juveniles than adults ($P \leq 0.05$). Forty-nine of 198 (25%) bobwhites dispersed more than 2 km. A greater proportion of juveniles (28%) than adults (10%) dispersed >2 km. Juvenile males were more likely to disperse than any other sex/age group ($P = 0.02$). Adult males were least likely to disperse ($P < 0.01$). We suggest that breeding season movements of bobwhites may be greater in fragmented landscapes than in areas with large blocks of suitable habitat. We recommend that researchers utilize dispersal information to help define the spatial distribution of habitat patches necessary to perpetuate bobwhite populations at a regional level.

INTRODUCTION

Knowledge of dispersal and movement patterns is essential for understanding the population dynamics of wildlife species, particularly those associated with fragmented habitats. Unfortunately, empirical data needed to characterize dispersal patterns are usually lacking (Walters 2000). In fragmented landscapes, immigration from productive populations is necessary to ensure the persistence of declining populations. Martin et al. (2000) describes this process as "dispersal rescue," whereby populations that experience poor reproduction or high mortality can escape extinction by immigration of other individuals from within the metapopulation system. The metapopulation persists if the recolonization rate of individual patches exceeds their rate of extinction (McCullough 1996:2).

Metapopulation theory appears relevant to northern bobwhite populations, since bobwhites are one of the least mobile gallinaceous species (Leopold 1933:77) and frequently occupy fragmented landscapes. However, efforts to develop a spatially explicit metapopulation model have been hampered by a lack of information on northern bobwhite dispersal patterns

and colonization rates. While some studies suggest that bobwhites are sedentary (Stoddard 1931:182, Errington 1933, Smith et al. 1982), others show them to be capable of travelling significant distances (Duck 1943, Kabat and Thompson 1963, Lehmann 1984:119). Even in these studies, however, documented movements >1.6 km were uncommon.

Prior to widespread use of radiotelemetry, estimates of northern bobwhite dispersal distances were likely biased because they were based on relocations of banded birds. Bobwhites dispersing the farthest distances, particularly those leaving defined study areas, were least likely to be detected, resulting in conservative estimates (Koenig et al. 1996). Even recent telemetry studies frequently do not provide reliable dispersal information, because birds leaving the study area are often censored from analyses. Also, many telemetry studies have been on areas intensively managed for bobwhites, where inter-patch connectivity is high and dispersal distances are likely lower than in unmanaged landscapes (Urban 1972). In our study, we measured breeding season movements and dispersal of northern bobwhites in fragmented habitats of Virginia without study area boundary constraints.

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METHODS

Study Area

We conducted our study in fragmented agricultural landscapes of Amelia and James City counties, Virginia. Amelia County is located approximately 40 km southwest of Richmond in the Piedmont region of southcentral Virginia; James City County is located in the Coastal Plain region of southeastern Virginia, near Williamsburg. Both study areas were 10–15% cropland and 60–75% woodland. Common crops were corn, soybeans, wheat, and alfalfa. Pastureland was more abundant in Amelia County, consisting primarily of grazed or hayed fields of tall fescue (*Festuca arundinacea*). Woodland habitats in both counties were usually mixtures of mature hardwoods (*Quercus* spp., *Liriodendron tulipifera, Acer* spp.) and pine (*Pinus taeda, P. virginiana*). Cutovers of recently planted loblolly pine were distributed throughout both study areas. Although we never measured the level of habitat fragmentation on our study areas, northern bobwhites typically occupied small patches of suitable cover within a matrix of mostly unsuitable habitat types. For this reason, we considered the habitat on both study areas to be fragmented.

Field Procedures

We captured northern bobwhites from February through April during 1994 to 1996 in modified funnel entrance cage traps (Stoddard 1931: 442–445) baited with cracked corn. All captured bobwhites were aged, sexed, weighed, and leg-banded. Each bird was equipped with a necklace radio transmitter (Advanced Telemetry Systems Inc., Isanti, MN and American Wildlife Enterprises, Monticello, FL) that weighed about 6 g and contained a 12-hour mortality sensor. Bobwhites trapped in the morning were released within 4 hours at their capture site; birds trapped in the late afternoon were held overnight and released the next morning.

We monitored radiomarked bobwhites daily to determine survival. If radio contact was lost for more than 2 days, we used vehicles to systematically search the area within approximately 5 km of the bird's last known location. When vehicle searches failed, we used fixed-wing aircraft to search an area at least 20 km from the last known coordinates.

Beginning 1 May through 15 September, we attempted to locate each bird once/week by flushing or closely approaching them (<50 m). Prior to that time (1 Feb to 30 Apr), the precise location of each bird was determined only periodically, as time permitted. These locations were plotted on aerial photos or recorded using a global positioning system (GPS) unit. Locations collected with GPS units were differentially corrected to remove selective availability error and believed to be within 35 m of their true geographic position 95% of the time (Dussault et al. 2001). All locations were later entered into a computerized geographic information system using ArcView® software

(Environmental Systems Research Institute, Inc., Redlands, California).

Data Analysis

We analyzed northern bobwhite movement patterns by measuring the distance (m) between arithmetic centers of seasonal activity areas defined by clusters of locations within selected time intervals. We chose the arithmetic center (versus the center of a harmonic mean or kernel home range) because it was simple to calculate, could be estimated from fewer data points, and has been used by others to measure the distance between seasonal point clusters (Garrott et al. 1987). We also measured the maximum distance (m) between points within and among these clusters. The animal movement extension (Hooge and Eichenlaub 1997) designed for ArcView® was used to perform these calculations.

Seasons were defined as winter (1 Feb to 15 Apr), early breeding season (16 Apr to 30 Jun), and late breeding season (1 Jul to 15 Sep). Since coveys were beginning to break up in early April, bobwhites trapped between 1 April and 15 April were excluded from analysis unless they were trapped with 2 or more other birds. Birds that died prior to 1 May were also excluded. Breeding seasons were separated into early and late periods coinciding with peak hatch periods known to occur in Virginia during June and July (Fies, unpublished data). Mortality locations were excluded from analysis, since predators may have transported carcasses from their original kill sites.

Most studies suggest that movements within a bobwhite's winter range rarely exceed 1 km (Lehmann 1946, Murphy and Basket 1952, Lewis 1954, Agee 1957). We classified a bird as a disperser if the maximum straight-line distance between any single winter and breeding season location was greater than 2 km, twice the maximum winter home range diameter (Townsend et al. 2001). Bobwhites that never moved more than 2 km from any winter location were classified as non-dispersers.

We tested for differences among mean seasonal movement distances using analysis of variance (PROC GLM; SAS Institute 1989) with sex and age as the main effects. We used Chi-square procedures to test for overall differences between proportions of bobwhites that dispersed by sex and age class. A Z-test was used to compare proportions of bobwhites that dispersed by combined sex and age classes.

RESULTS

We placed radio transmitters on 424 northern bobwhites captured on 30 farms during 1994–1996. Of these, 198 bobwhites provided data that could be included in the analyses (captured before 15 Apr and survived past 1 May). During the study period, the area in which we monitored bobwhites was approximately 520 km² in Amelia County and 300 km² in James City County.

Table 1. Mean distance (m) between arithmetic centers of seasonal activity areas of radiomarked northern bobwhites monitored in Amelia and James City counties, Virginia, 1994–1996.

Sex	Age	Winter[a]–Early Breeding Season[b]			Winter–Late Breeding Season[c]			Winter–Combined Breeding Season[d]			Early–Late Breeding Season		
		n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Female	Juvenile	71	1015	195	50	1898	402	42	1234	310	42	674	146
	Adult	13	794	238	8	744	335	8	729	287	8	582	218
	Pooled	84	981	169	58	1739	353	50	1153	265	50	659	127
Male	Juvenile	78	1645	267	51	1816	322	49	1747	337	49	449	66
	Adult	26	526	98	18	854	176	18	685	141	18	489	90
	Pooled	104	1365	207	69	1565	247	67	1462	255	67	460	54
Pooled	Juvenile	149	1345	169	101	1857	256	91	1510	231	91	553	77
	Adult	39	615	103	26	820	156	26	699	129	26	517	90
	Pooled	188	1194	137	127	1644	209	117	1330	185	117	545	63

[a] 1 Feb–15 Apr
[b] 16 Apr–30 Jun
[c] 1 Jul–15 Sep
[d] 16 Apr–15 Sep

Movement Distance

Distance between centers of seasonal activity areas.—Mean distance between the arithmetic centers of winter and early breeding season (WEB) activity areas was 1,194 ± 137 m (range 30–11,988 m) (Table 1). Mean WEB did not differ significantly ($F_{1,181} = 0.42$, $P = 0.515$) between males (1,365 ± 207 m) and females (981 ± 169 m). Mean WEB appeared to be higher for juveniles (1,345 ± 169 m) than adults (615 ± 103 m), but this difference was not significant ($F_{1,181} = 3.49$, $P = 0.063$) at the $P \leq 0.05$ level.

Bobwhites appeared to move farther from their winter activity areas as the breeding season progressed. Distance between the centers of winter and late breeding season (WLB) activity areas averaged 1,644 ± 209 m (range 39–13,532 m). Mean WLB did not differ by sex ($F_{1,120} = 0.34$, $P = 0.559$), but was significantly higher ($F_{1,120} = 4.29$, $P = 0.041$) for juvenile (1,857 ± 256 m) than adult (820 ± 156 m) bobwhites. Distance between centers of the early and late breeding season activity areas averaged 545 ± 63 m (range 7–4,247 m) and did not differ by sex ($F_{1,110} = 0.35$, $P = 0.556$) or age ($F_{1,110} = 0.21$, $P = 0.651$).

Of the birds with locations in both the early and late breeding seasons ($n = 117$), the mean distance between the centers of winter and combined breeding season activity areas (WCB) was 1,330 ± 185 m (range 43–11,718 m). We found no difference in mean WCB between sexes ($F_{1,110} = 0.98$, $P = 0.324$). Mean WCB appeared to be greater for juvenile bobwhites (1,510 ± 231 m) than adults (699 ± 129 m). This difference approached statistical significance ($F_{1,110} = 3.33$, $P = 0.071$), but was not different at the $P \leq 0.05$ level.

Maximum movement distances.—The maximum distance that bobwhites moved between winter and early breeding seasons (MWEB) averaged 1,528 ± 141 m (range 39–12,054 m) (Table 2). Mean MWEB did not differ by sex ($F_{1,181} = 0.48$, $P = 0.488$), but was greater ($F_{1,181} = 3.85$, $P = 0.051$) for juvenile birds (1,684 ± 174 m) than adults (929 ± 109 m). Mean maximum distance between winter and late breeding season (MWLB) locations was 1,842 ± 210 m (range 72–13,540 m). Mean MWLB was similar ($F_{1,120} = 0.35$, F = 0.553) for males (1,753 ± 249 m) and females (1,948 ± 353 m), but was greater ($F_{1,120} = 4.95$, $P = 0.028$) for juveniles (2,070 ± 256 m) than adults (958 ± 155 m). The maximum distance

Table 2. Mean maximum distance (m) between seasonal locations of radiomarked northern bobwhites monitored in Amelia and James City counties, Virginia, 1994–1996.

Sex	Age	Winter[a]–Early Breeding Season[b]			Winter–Late Breeding Season[c]			Winter–Combined Breeding Season[d]			Early–Late Breeding Season		
		n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Female	Juvenile	71	1393	216	50	2116	402	42	1844	353	42	1286	218
	Adult	13	1055	220	8	900	326	8	1025	310	8	983	257
	Pooled	84	1341	186	58	1948	353	50	1713	303	50	1238	187
Male	Juvenile	78	1949	266	51	2025	323	49	2218	339	49	1091	128
	Adult	26	865	123	18	984	177	18	1164	167	18	1004	141
	Pooled	104	1678	206	69	1753	249	67	1935	257	67	1068	100
Pooled	Juvenile	149	1684	174	101	2070	256	91	2046	244	91	1181	121
	Adult	39	928	109	26	958	155	26	1121	147	26	998	123
	Pooled	188	1528	141	127	1842	210	117	1840	196	117	1141	98

[a] 1 Feb–15 Apr
[b] 16 Apr–30 Jun
[c] 1 Jul–15 Sep
[d] 16 Apr–15 Sep

Table 3. Mean maximum distance (m) between locations within breeding seasons for radiomarked northern bobwhites monitored in Amelia and James City counties, Virginia, 1994–1996.

Sex	Age	Early Breeding Season[a]			Late Breeding Season[b]			Combined Breeding Season[c]		
		n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Female	Juvenile	61	924	137	41	674	151	42	1321	216
	Adult	11	621	171	7	323	72	8	1000	266
	Pooled	72	878	120	48	623	131	50	1269	187
Male	Juvenile	65	797	89	44	552	66	49	1146	129
	Adult	24	778	119	13	461	62	18	1047	144
	Pooled	89	792	72	57	531	53	67	1119	101
Pooled	Juvenile	126	859	81	85	611	80	91	1226	121
	Adult	35	729	97	20	413	49	26	1032	126
	Pooled	161	830	67	105	573	66	117	1183	98

[a] 16 Apr–30 Jun
[b] 1 Jul–15 Sep
[c] 16 Apr–15 Sep

between winter and combined breeding season locations (MWCB) averaged 1,840 ± 196 m (range 43–11,718 m). Mean MWCB of male (1,935 ± 257 m) and female (1,713 ± 303 m) bobwhites did not differ ($F_{1,110} = 1.16$, $P = 0.283$), but was greater ($F_{1,110} = 4.78$, $P = 0.031$) for juveniles (2,046 ± 244 m) than adults (1,121 ± 147 m).

Maximum movement distances were generally greater between than within breeding seasons. The maximum distance between early and late breeding season locations (MEBLB) averaged 1,141 ± 98 m (range 81–6,584 m) and did not differ by sex ($F_{1,110} = 0.03$, $P = 0.860$) or age ($F_{1,110} = 1.69$, $P = 0.196$). In contrast, the maximum distance between locations within the early breeding season (MEB) was 830 ± 67 m (range 58–5,155 m) (Table 3). Mean MEB also did not differ by sex ($F_{1,154} = 0.19$, $P = 0.662$) or age ($F_{1,154} = 1.78$, $P = 0.184$). Mean maximum distance between late breeding season (MLB) locations was 573.0 ± 66 m (range 19–6,092 m). We observed no significant difference in mean MLB distance between males and females ($F_{1,98} = 0.08$, $P = 0.782$), or juveniles and adults ($F_{1,98} = 1.87$, $P = 0.175$). Maximum distance between locations during the combined breeding season averaged 1,183 ± 98 m (range 81–6,583 m),

and also did not differ by sex ($F_{1,110} = 0.08$, $P = 0.776$) or age ($F_{1,110} = 1.93$, $P = 0.167$).

Dispersal

Forty-nine of 198 (24.7%) bobwhites were classified as dispersers (maximum distance between winter and breeding season locations greater than 2 km) (Table 4). We observed no difference ($\chi^2 = 0.64$, 1 df, $P = 0.800$) in the proportion of dispersing male (25.5%) and female (23.9%) bobwhites. However, juvenile birds were almost 3 times more likely to disperse than adult birds ($\chi^2 = 5.48$, 1 df, $P = 0.019$). Forty-five of 159 (28.3%) juvenile bobwhites dispersed, compared to only 4 of 39 (10.3%) adults.

The proportion of bobwhites dispersing varied by combination of sex and age ($\chi^2 = 8.72$, 3 df, $P = 0.033$). More juvenile males dispersed (32.5%) than any other sex/age group ($Z = 2.08$, $P = 0.019$). In contrast, only 1 of 26 (3.9%) adult male bobwhites dispersed. Adult males were significantly less likely to disperse than other sex/age group ($Z = 2.65$, $P = 0.004$). There was no difference in the proportion of juvenile and adult females that dispersed ($Z = 0.076$, $P = 0.470$).

DISCUSSION

Spring dispersal is likely an innate behavioral characteristic that enables bobwhites to expand and replenish their range by colonizing newly created or depleted habitats (Howard 1960). Immigration of individuals from productive populations into areas with declining populations is vital for metapopulation stability, particularly in fragmented landscapes. The relative sensitivity of some avian species, including bobwhites, to habitat fragmentation is very likely dependent upon their propensity to disperse (Walters 1998). Innate dispersal also promotes gene flow between populations and reduces inbreeding.

Unfortunately, accurate estimates of bobwhite dispersal distance are lacking in the current literature. As Lehmann (1946) acknowledged, most early bobwhite movement studies were measures of the "travels of

Table 4. Proportion of radiomarked northern bobwhites with a maximum distance between winter (1 Feb–15 Apr) and breeding season (16 Apr–15 Sep) locations <2 km (non-dispersers) or ≥2 km (dispersers) in Amelia and James City counties, Virginia, 1994–1996.

Sex	Age	n	Maximum Distance Moved			
			<2 km		≥2 km	
			%	SE	%	SE
Female	Juvenile	79	76.0	4.8	24.0	4.8
	Adult	13	76.9	12.2	23.1	12.2
	Pooled	92	76.1	4.5	23.9	4.5
Male	Juvenile	80	67.5	5.3	32.5	5.3
	Adult	26	96.1	3.9	3.9	3.9
	Pooled	106	74.5	4.3	25.5	4.3
Pooled	Juvenile	159	71.7	3.6	28.3	3.6
	Adult	39	89.7	4.9	10.3	4.9
	Pooled	198	75.3	3.1	24.7	3.1

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We propose that northern bobwhite populations in the fragmented agricultural landscapes of Virginia fit many of the criteria of traditional metapopulation structure. Although not measured, we observed local extinction and subsequent recolonization of isolated patches in the areas we studied. While bobwhites are known to be capable of dispersing long distances, their probability of successfully locating a suitable habitat patch is almost certainly affected by the spatial distribution of these areas. Theoretically, bobwhites could have difficulty locating and subsequently colonizing a habitat patch if the distance between patches exceeds their normal dispersal distance (Weins 1996:59). If bobwhites are to persist in fragmented landscapes, managers must define the spatial characteristics of large areas and maintain suitable habitats within a yet-to-be-defined critical dispersal distance. Spatially explicit population models that incorporate measures of population performance (survival and reproductive success) and measures of dispersal distance and colonization rates are needed to further define these optimal landscape-level habitat characteristics.

Although site-specific management will remain an important component of future bobwhite recovery efforts, it seems clear that managers will need to address the problem of declining populations from a regional or landscape perspective. The viability of local bobwhite populations is affected not only by their own reproduction and survival characteristics, but also by interactions with neighboring populations. Public wildlife agencies with limited resources may need to prioritize their future site-level management efforts in areas where the overall landscape matrix is most suitable for bobwhites. Roseberry and Sudkamp (1998) and Schairer et al. (1999) have suggested using Landsat imagery and geographic information systems to identify these priority areas. Modern managers will need to incorporate traditional habitat management prescriptions with these emerging technologies (Roseberry 1993). Additional information regarding bobwhite dispersal behavior will be useful in improving our ability to make ''real world'' management decisions within a theoretical metapopulation context.

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