BREEDING SEASON MOVEMENTS AND DISPERAL 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 ± 137 m. Distance between centers of winter and late breeding season (1 Jul–15 Sep) activity areas averaged 1,644 ± 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 ≤ 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.


Key words: breeding season, Colinus virginianus, dispersal, habitat fragmentation, metapopulations, movements, northern bobwhite, Virginia

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 re-colonization 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.
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.
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 \(1,194 \pm 137\) m (range 30–11,988 m) (Table 1). Mean WEB did not differ significantly \((F_{1,18} = 0.42, P = 0.515)\) between males \((1,365 \pm 207\) m) and females \((981 \pm 169\) m). Mean WEB appeared to be higher for juveniles \((1,345 \pm 169\) m) than adults \((615 \pm 103\) m), but this difference was not significant \((F_{1,18} = 3.49, P = 0.063)\) 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 \(1,644 \pm 209\) m (range 39–13,532 m). Mean WLB did not differ significantly \((F_{1,18} = 0.34, P = 0.559)\), but was significantly higher \((F_{1,18} = 4.29, P = 0.041)\) for juvenile \((1,857 \pm 256\) m) than adult \((820 \pm 156\) m) bobwhites. Distance between centers of the early and late breeding season activity areas averaged \(545 \pm 63\) 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 \(1,330 \pm 185\) 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 \((1,510 \pm 231\) m) than adults \((699 \pm 129\) 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 \(1,528 \pm 141\) m (range 39–12,054 m) (Table 2). Mean MWEB did not differ by sex \((F_{1,18} = 0.48, P = 0.488)\), but was greater \((F_{1,110} = 3.85, P = 0.051)\) for juvenile birds \((1,684 \pm 174\) m) than adults \((929 \pm 109\) m). Mean maximum distance between winter and late breeding season (MWLB) locations was \(1,842 \pm 210\) m (range 72–13,540 m). Mean MWLB was similar \((F_{1,120} = 0.35, F = 0.553)\) for males \((1,753 \pm 249\) m) and females \((1,948 \pm 353\) m), but was greater \((F_{1,120} = 4.95, P = 0.028)\) for juveniles \((2,070 \pm 256\) m) than adults \((958 \pm 155\) m). The maximum distance

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Table 2. Mean maximum distance (m) between seasonal locations of radiomarked northern bobwhites monitored in Amelia and James City counties, Virginia, 1994–1996.
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 ($F_{1,114} = 0.19, P = 0.662$) or age ($F_{1,114} = 1.78, P = 0.184$). 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 ($F_{1,119} = 0.08, P = 0.782$), 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 ($F_{1,110} = 1.93, P = 0.167$).

**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). Inmate 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
sedi
tary birds,” because the probability of detecting long distance movements was low. For example, Murphy and Baskett (1952) reported that 93% of Missouri bobwhites dispersed <1.2 km from their winter range during the spring. Several years later, Lewis (1954) found that 88% of banded quail dispersed <1.2 km on the same study area. In both of these studies, however, recovery of banded birds that moved long distances was mostly accidental. As a result, the proportion of birds moving long distances was likely underesti-

Although comparable data are lacking, northern bobwhites in our study dispersed greater distances than those reported by most other researchers. In Florida, the average distance between successive year captures of 710 bobwhites trapped during winter was only 228 m (Smith et al. 1982). Simpson (1976) reported similar annual movements for bobwhites in Georgia; 96% of banded birds were recaptured within 800 m of their previous year winter capture site. In both these studies, however, bobwhites were not trapped during the breeding season. Movements of banded birds that dispersed farther distances during the spring and summer, then moved back towards their original capture sites the following winter, would have been undetected. In a more comparable study conducted in North Carolina, mean distance between first capture site and first nest of radiomarked bobwhites was 340 m and 1,460 m on areas with and without field borders, respectively (Puckett et al. 1995). However, most bobwhites that dispersed off the study areas were censored from analyses, likely biasing overall dispersal distance esti-

Several researchers reported dispersal distances greater than those we observed. In Wisconsin, the av-

verage distance moved by bobwhites from winter through mid-July was 2.1 km (Kabat and Thompson 1963), compared to 1.8 km during a similar time period in our study. Rosene (1969:99–100) hypothesized that bobwhites moved shorter distances in the southern portion of their range, presumably because satisfactory nesting cover was closer to winter ranges. Recent research in Oklahoma (Townsend et al. 2001), however, does not support this theory. In their study, 42% of radiomarked bobwhites moved more than 2 km from their winter capture sites during the breeding season. Although the authors did not report the average distance from winter to spring for all bobwhites moni-
tored, we presume that this distance was greater than we observed, since only 25% of the birds in our study dispersed more than 2 km.

For most avian species, females are the predomi-
nant dispersers, choosing mates that have defended ter-
ritories with the best resources (Clark et al. 1997). Fe-

male-biased dispersal has been reported for some gal-

linaceous species, including ruffed grouse (Bonasa umbellus) (Small and Rusch 1989). In our study, we found no evidence that female bobwhites dispersed longer distances than males. We also observed no dif-

ference in the proportion of male and female bob-
whites dispersing more than 2 km. Contrary to the idea of female-biased dispersal, most researchers suggest that male bobwhites move longer distances than fe-

males (Hood 1955, Loveless 1958, Kabat and Thomp-

son 1963, Smith et al. 1982). Others report no differ-
ence in movements between sexes (Stoddard 1931: 176, Simpson 1976). Since bobwhites are polygamous (Curtis et al. 1993), generally non-territorial, and ex-
hit a highly flexible mating system (Burger et al. 1995), female-biased dispersal would likely offer little ecological advantage to this species.

Although data are lacking for bobwhites, juveniles of most avian species disperse greater distances than adults, possibly avoiding inbreeding (Howard 1960). This premise is consistent with our observation that juvenile bobwhites moved longer distances from their winter range and were more likely to disperse >2 km than adult birds. In particular, juvenile males were more likely to disperse than any other sex/age group. Smith et al. (1982) also reported that juveniles moved longer distances and were more likely to make exten-
sive movements than adult bobwhites. In Illinois, the home range of unmated males (presumably subadults) was almost twice as large as mates males during the late spring and summer months (Urban 1972). Others have also suggested that the birds most likely to dis-
perse unusually long distances are unmated males (Loveless 1958).

Our observation that adult males were less likely to disperse than other birds has not been previously reported in the literature. Most likely, adult males were able to find mates more successfully than juvenile males and did not find it necessary to disperse in search of a mate. Adult females may have been more likely to disperse than adult males as they searched for suitable nest sites, particularly after a failed incubation attempt. We observed several long distance move-

ments by hens following nest failure; this phenomenon has also been documented by others (Urban 1972).

The maximum distance moved by an individual bobwhite in our study was 13.5 km (a juvenile fe-

male). Only 4 other birds (3 juvenile males, 1 juvenile female) moved more than 10 km. Other researchers

have documented long distance movements of 6.4–8.0 km in Wisconsin (Kabat and Thompson 1963), 8.2 km in Indiana (Hoekstra and Kirkpatrick 1972), 11.3 km in Georgia (Stoddard 1931:176), and 15.3 km in Flor-
da (Loveless 1958). Unusually long distance move-

ments of 40 km (Townsend et al. 2001), 41.8 km (Dav-

ison, in Duck 1943), and 59.5 km (DeMaso et al. 1997) have been reported in Oklahoma, and 38.6 km (Jackson 1969:66), 104.6 km (Kiel 1976), and 164.1 km (Green 1966) in Texas. Such long distance move-

ments, however, are generally considered to be rare dispersal events.

Results of this and several other studies suggest that bobwhites may disperse greater distances in frag-

mented habitats. Loveless (1958) and Smith et al. (1982) reported little mobility on areas managed spe-

cifically for quail, while Kabat and Thompson (1963) noted larger movements in landscapes consisting of mostly marginal habitat. It seems likely that bobwhite dispersal distance increases as inter-patch connectivity decreases.
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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