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SPRING DISPERSAL OF NORTHERN BOBWHITES IN SOUTHWESTERN OHIO

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ABSTRACT

Northern bobwhites (*Colinus virginianus*) historically occurred throughout Ohio but their core range has contracted to 18 southwestern counties. The Ohio Division of Wildlife has used trapping and transplanting to reintroduce wild bobwhites to unoccupied habitats within the species' historic range. Bobwhite dispersal information is necessary to understand population dynamics and the species' capacity to recolonize unoccupied habitats. Bobwhites were captured and radiomarked on 4 private-land study sites in southwestern Ohio. Radio-marked bobwhites ($n = 66$) were tracked by homing or triangulation during spring 2010 and 2011 to ascertain dispersal distances between winter and breeding ranges. The spring dispersal period was defined by break-up of coveys and subsequent occupation of breeding season home ranges. The dispersal period, defined by non-affiliation with coveys, long directional daily movements, and observed breeding activity, varied among individuals and ranged from 2 April to 26 May. Dispersal distances were measured as the net Euclidean distance between locations recorded at the beginning and end of the dispersal period. Dispersers were defined as birds that moved $> 2\times$ the diameter of the mean home-range size (26.1 ha) observed during October-March 2010 and 2011. Movements of 1–2 home-range diameters were classified as home range shifts. Non-dispersing bobwhites traveled < 1 home-range diameter. Mean movement for all birds was 1.54 km. Twenty-eight (42.4%) radio-marked bobwhites were non-dispersers, 15 (22.7%) shifted home ranges, and 23 (34.8%) dispersed. Non-dispersers moved a mean of 0.31 km (range = 0.03–0.56 km), home range shifts averaged 0.78 km (range = 0.60–0.99 km), and dispersers traveled a mean distance of 3.6 km (range = 1.18–11.5 km). Dispersal distance was lowest for adult females and increased in order for adult males, juvenile females, and juvenile males. Dispersal distance decreased as the proportion of early successional wooded habitat within winter home ranges increased. Sex, age, and dispersal distance did not affect survival. Our results suggest Ohio bobwhites are capable of expanding their range into historically-populated areas.

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Key words: Northern bobwhite, *Colinus virginianus*, dispersal, early successional habitat, home range shift, Ohio

INTRODUCTION

Habitat loss has been the primary cause of declining northern bobwhite populations range-wide (Klimstra 1982, Brennan 1991, Guthery et al. 2000, Williams et al. 2004, Veech 2006). Bobwhite habitat in Ohio has been lost to increasing agricultural development and land-use changes that leave residual usable habitats in a fragmented matrix. Habitat losses are compounded by severe winters experienced by populations on the northern fringe of the bobwhite range. The bobwhite range in Ohio contracted concurrent with a state population decline of 76% between 1984 and 2004 (Spinola and Gates 2008). Formerly distributed state-wide, the current geographic core range is now confined to southwestern Ohio (Spinola and Gates 2008, Ohio Breeding Bird Atlas 2012). There is some evidence that bobwhites are patchily distributed even in the core of the species range in southwestern Ohio (Gates et al. 2012).

Avian dispersal provides important ecological and evolutionary benefits such as outbreeding and gene flow (Howard 1960, Greenwood and Harvey 1982, Walters

2000). The ability to colonize vacant habitats and establish new populations may be the most important aspect of this behavior for bobwhites. Dispersal rescue (Townsend et al. 2003) can supplement declining populations or re-establish bobwhite populations in historically-occupied areas (Martin et al. 2000). Dispersal has been viewed as costly for avian species (Bélíchon et al. 1996) because individuals are thought to have increased risk of mortality after moving into novel areas (Yoder et al. 2004). Dispersing individuals also risk missed breeding opportunities by moving into areas without conspecifics or by expending time and energy to search for mates and nest sites (Danchin and Cam 2002).

Bobwhites have traditionally been considered a sedentary species because of limited mobility. They are primarily terrestrial and their movements are mostly on foot rather than in flight (Kassinis and Guthery 1996, Guthery 2000). Bobwhites may be particularly susceptible to risks associated with dispersal behavior

The Ohio Division of Wildlife has trapped and transplanted wild bobwhites into historically-occupied areas that contain suitable habitat but lack habitat connectivity with extant populations. The ability of

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Table 1. Physical and land-cover characteristics of 4 study sites in southwestern Ohio on which northern bobwhites were captured and radiomarked prior to and during the breeding seasons of 2010 and 2011.

| | Fee | Peach | Wildcat | Thurner |
|---|---------|-------|---------|---------|
| Area (ha) | 1,284.4 | 397.7 | 838.3 | 738.8 |
| Mean slope (%) | 5.0 | 9.7 | 5.1 | 4.5 |
| Mean covey density (coveys/km ²) | 0.59 | 0.45 | 1.47 | 0.7 |
| Mean row crop field size (ha) | 12.6 | 7.6 | 7.6 | 10.0 |
| CRP (ha) | 123.6 | 75.2 | 137.4 | 25.7 |
| CRP composition (%) ^a | | | | |
| Cool season grasses | 86.9 | 98.0 | 88.8 | 86.5 |
| Warm season grasses | 13.1 | 2.0 | 11.2 | 13.5 |
| Landscape composition (%) ^b | | | | |
| Row crop | 61.6 | 17.6 | 34.9 | 31.8 |
| Developed | 6.4 | 4.1 | 5.2 | 6.3 |
| Forest | 20.7 | 50.0 | 32.0 | 28.1 |
| Grassland/Shrub | 0.6 | 6.8 | 5.7 | 6.2 |
| Pasture/Hay | 10.4 | 21.4 | 21.9 | 27.1 |
| Other | 0.3 | 0.1 | 0.2 | 0.6 |
| Site composition (%) ^c | | | | |
| ES Herbaceous ^d | 12.5 | 21.5 | 19.6 | 12.2 |
| ES Woody ^d | 3.4 | 7.2 | 3.2 | 4.9 |
| Forest | 8.1 | 27.8 | 10.0 | 14.6 |
| Non habitat | 4.0 | 4.7 | 3.9 | 9.3 |
| Pasture/Hay | 2.6 | 2.3 | 23.6 | 6.7 |
| Row crop | 69.5 | 36.4 | 39.8 | 52.3 |

^a Proportion of area of all CRP fields in respective categories.

^b Proportion NLCD habitat cover within 10-km buffer around the centroid of study site.

^c Proportion of the maximum extent of the site boundaries from 2 non-breeding seasons (Oct-Mar 2009–2011) in each habitat type.

^d ES = early successional.

bobwhites to travel and disperse in fragmented agricultural landscapes is unclear and previous studies are not necessarily applicable to Ohio. Opportunistic and anecdotal observations of marked birds provide conservative estimates of dispersal distances and do not effectively capture long-distance movements (Stoddard 1931, Lehmann 1946, Murphy and Baskett 1952, Lewis 1954, Smith et al. 1982). Dispersal studies that use radiotelemetry have been conducted either in areas managed exclusively for bobwhites (Liu et al. 2002; Terhune et al. 2006, 2010) or in ecosystems that differ from the agricultural landscape of Ohio (Liu et al. 2002, Townsend et al. 2003, Cook et al. 2006, Terhune et al. 2006). Application of dispersal information from landscapes dominated by rangelands (Townsend et al. 2003), pine (*Pinus* spp.) plantations (Cook et al. 2006; Terhune et al. 2006, 2010), or forested habitats (Fies et al. 2002, Liu et al. 2002) to fragmented Ohio landscapes dominated by row crops is tenuous at best. In addition, areas managed specifically for bobwhites may not require birds to travel as far to find suitable breeding habitat or mates and may not accurately reflect the cost of dispersal in less hospitable or unmanaged landscapes.

Dispersal is essential to recolonizing historically-occupied areas in Ohio that are now fragmented and isolated. Radiotelemetry was used to study spring dispersal of bobwhites on 4 private-land study sites in southwestern Ohio. Dispersal distances, survival during dispersal, and habitat influences on dispersal distances were evaluated during spring 2010 and 2011. Our objectives were to: (1) ascertain the proportion of dispersing individuals in the population; (2) compare spring dispersal distances among age-sex classes, study sites, and years; (3) examine the effect of dispersal distance on survival of dispersing birds; and (4) investigate the influence of winter home-range composition on spring dispersal distance.

STUDY AREA

This study was conducted on 4 study sites in southwestern Ohio in the current geographic core of the bobwhite range (Spinola and Gates 2008). Sites were in Highland and Brown counties (39° 04' 59" N, 83° 39' 10" W) within the Till Plains and Illinois Till Plains regions of Ohio (Ohio Division of Geologic Survey 1998) and the Eastern Tall Grass Prairie Bird Conservation Region of the National Bobwhite Conservation Initiative (NBTC 2011). The region was mostly rural (6% developed; Homer et al. 2004) and agriculture was the primary land use (39% row crops, 17% pasture/hay) with interspersed grassland (3%) and forest (33%). The gently undulating topography resulting from glaciation in these counties was not as favorable for modern, large-scale agricultural production and cropping; land-use limitations along the glacial boundary benefited bobwhite populations where it occurred (e.g., small field sizes).

The 4 study sites (Fee, Peach, Wildcat, and Thurner) represented a gradient from agriculture- to forest-dominated landscapes (Table 1). Land-use at each study site was evaluated using National Land Cover Data (NLCD) within a 10-km buffer around the site centroids. Nesting habitat was considered to be any early successional herbaceous habitat (i.e., grassland/shrub, pasture/hay). The Fee site had the highest proportion of row crops and the lowest proportions of nesting habitat (11.0%) and forests. Wildcat and Thurner were intermediate along the agricultural-forest gradient and had 27.6 and 33.3% nesting habitat, respectively. Peach was the most forested site due to its location on the glacial boundary and also had the lowest proportion of row crops and the second lowest proportion of nesting habitat (28.2%). High proportions of row crops (range = 38.5–72.1%) and large field sizes (range = 7.6–12.6 ha) were considered indicators of reduced habitat connectivity at study sites; these areas were considered fragmented.

Row crop fields were predominantly in no-till soybeans, corn, and winter wheat. Forest composition varied with topography. Dry upland ridges supported communities dominated by shagbark (*Carya ovata*) and pignut hickory (*C. glabra*), and white (*Quercus alba*) and red oak (*Q. rubra*). Lower elevations and depressional areas were dominated by black walnut (*Juglans nigra*),

green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), and occasionally pin oak (*Quercus palustris*). Early successional land cover types in our study sites included fields enrolled in the Conservation Reserve Program (CRP), idle fields, fencerows, agricultural drainage ditches, and roadsides. Early successional grass fields were dominated by cool season grasses such as fescue (*Festuca* spp.) and forbs such as goldenrod (*Solidago* spp.) and Queen Anne's lace (*Daucus carota*). Small proportions of the study sites were in warm-season grass CRP fields, primarily planted with Indiangrass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), and partridge pea (*Chamaecrista fasciculata*). Early successional woody habitats included fencerows, ditches (< 50 m in width), and patches of advanced successional growth. Early successional vegetation included woody species such as blackberry (*Rubus allegheniensis*), black raspberry (*R. occidentalis*), trumpet creeper (*Campsis radicans*), poison ivy (*Toxicodendron radicans*), and Japanese honeysuckle (*Lonicera japonica*).

The long-term mean temperature for this region was 11.1 °C and the mean monthly temperature during the study period (Apr-Sep 2010–2011) was 20.2 °C (range 12.2–26.6 °C; NCDC 2011). The long-term mean annual precipitation was 1,102 mm and the mean monthly precipitation during the study period was 277 mm (range = 64–1,775 mm; NCDC 2011). The mean departure from normal during the study period was 97 mm (range = –64–528 mm; NCDC 2011). The 2010 breeding season began with the fourth driest April in Ohio history followed by the third wettest May and slightly below average rainfall through September (NCDC 2011). This area also experienced unprecedented rainfall in spring 2011 with amounts in April that were 285% of normal and the highest since 1882 (NCDC 2011).

METHODS

Data Collection

Bobwhites were continually captured and outfitted with radio transmitters during fall 2009 through summer 2011. Individuals were captured using baited funnel traps and targeted mist-netting (Wiley et al. 2012). Captured individuals were weighed, classified to age and sex (Rosene 1969), and banded with uniquely-numbered aluminum leg bands (size 3 or 3B) that included a phone number for band recoveries. Most individuals were also fitted with an Advanced Telemetry Systems (ATS, Isanti, MN, USA) radio transmitter with an 8-hr mortality sensor. Individuals were radiomarked during the 2010 field season with bib-mounted or necklace-style transmitters; zip-tie style necklace transmitters were used on individuals captured or recaptured after 1 September 2010. The switch to zip-tie attached transmitters significantly improved retention of radio transmitters during the 2011 breeding season and seemed to be the best compromise between transmitter weight and attachment durability. Radio transmitters (6.6 g) were placed only on individuals weighing > 150 g. All trapping, handling, and marking

procedures were consistent with guidelines approved by the Ohio State University Institutional Animal Care and Use Committee (# 2007A0228).

Individuals were tracked daily throughout spring dispersal (Apr-May) by homing to within 15–20 m with ATS or Telonics (Mesa, AZ, USA) receivers and a hand-held 3-element yagi antenna. A truck-mounted, null-peak system was used for triangulations when property access was restricted or to avoid disturbing spring wild turkey (*Meleagris gallopavo*) hunters. Global Positioning System (GPS) coordinates were recorded with handheld GPS units (Garmin, Olathe, KS, USA) in the field and later loaded into ArcMap 9.3 (ESRI, Redlands, CA, USA).

The dispersal period was defined by non-affiliation with coveys, long directional daily movements, and observed breeding activity. It concluded with earliest nest initiation dates and a cutoff date of 10 May was used for individuals whose dispersal termination was uncertain. Individuals were assumed to have initiated breeding activity, unless movement patterns or nesting indicated otherwise, even if a nest for that individual had not yet been found. Individuals that died after 1 April while still associated with their winter covey were excluded from analyses. Individuals captured after 1 April while not associated with a covey were excluded from distance analyses because they may have already dispersed. Individuals that lost their transmitters, died during dispersal, or with which radio contact was lost were excluded from distance analysis because they did not have equal opportunity to complete movement during the period. We searched for radio-marked individuals in the area surrounding their last known location for at least 2 hrs with a truck-mounted, whip-antenna and periodic scans with a truck-mounted, null-peak system when radio contact was lost. Attempts to relocate individuals were discontinued after failing to find birds for 3 consecutive days. Missing individuals could have been lost due to transmitter failure or because they dispersed outside our search area. Radio contact was most likely lost due to transmitter failure rather than an inability to relocate dispersing individuals.

Analyses

Locate III was used to calculate location points from triangulations (Nams 2006). Telemetry locations were analyzed using Hawth's Tools in ArcMap 9.3 (Beyer et al. 2010). Dispersal distances were measured by the net Euclidean distance moved between start and end dates of dispersal. A modified method for classifying dispersal behavior was used as described by Townsend et al. (2003) and used in other bobwhite dispersal studies (Fies et al. 2002). Dispersers were defined as birds that moved > 2x the diameter of their mean home-range size. Non-dispersing bobwhites traveled < 1 home-range diameter and intermediate movements (> 1 to < 2 home-range diameters) were classified as a home range shift. The Townsend et al. (2003) method uses a somewhat arbitrary winter home-range diameter of 1 km. Spring dispersal was classified by comparing dispersal movements to a population-specific mean home range for radio-marked

Table 2. First phase of spring dispersal analysis and ranked models evaluating the influence of design variables on dispersal distances of radio-marked northern bobwhite at 4 study sites in southwestern Ohio during 2010–2011.

| Model ^a | k ^b | AIC ^c | AIC _c ^d | ΔAIC _c ^d | w _i ^e |
|--------------------|----------------|------------------|-------------------------------|--------------------------------|-----------------------------|
| SEX + AGE | 4 | 192.10 | 192.79 | 0.00 | 0.20 |
| AGE | 3 | 192.45 | 192.85 | 0.07 | 0.19 |
| Null | 2 | 193.37 | 193.57 | 0.78 | 0.13 |
| SEX * AGE | 5 | 192.85 | 193.90 | 1.12 | 0.11 |
| SEX | 3 | 193.76 | 194.17 | 1.38 | 0.10 |
| YEAR + AGE | 4 | 194.19 | 194.88 | 2.10 | 0.07 |
| YEAR + SEX + AGE | 5 | 194.06 | 195.11 | 2.32 | 0.06 |
| YEAR | 3 | 194.72 | 195.13 | 2.34 | 0.06 |
| YEAR + SEX | 4 | 195.33 | 196.02 | 3.23 | 0.04 |
| YEAR + SEX * AGE | 6 | 194.73 | 196.23 | 3.44 | 0.04 |
| YEAR * SEX * AGE | 9 | 197.30 | 200.70 | 7.91 | 0.00 |

^a HRESW = average proportion of early successional woody vegetation in covey home ranges.

^b Number of parameters included in models. All models included an intercept and a random effect of covey affiliation.

^c AIC = Akaike Information Criterion.

^d AIC_c = Akaike Information Criterion adjusted for small sample sizes.

^e w_i = Akaike weight.

coveys at the study sites during October–March 2010 and 2011 (26.1 ha, 0.58-km diameter; Janke and Gates 2013).

There were 104 radio-marked bobwhites during the 2010 and 2011 breeding seasons. Six bobwhites were not included in any analyses because they were associated with coveys after death or last known location. Twenty-four individuals were excluded from dispersal analyses

because they were either marked after covey break-up, died during the dispersal period, or were not relocated during the dispersal period. Dates of covey break-up and dispersal distances were compared between years with analysis of variance and linear regression using program R (R Development Core Team 2012). Influences of sex, age, and dispersal distances of individuals on survival during spring dispersal were evaluated with known-fates analysis in Program MARK (White and Garrott 1999).

Sixty-three individuals used in our analyses were members of 29 individual coveys. Linear mixed models with covey as a random effect were used to first examine effects of year, age, and sex (with 2-way interactions) on dispersal distance. The distribution of dispersal distances was heavily right-skewed so the dependent variable was log_n-transformed before analysis. Estimated means and confidence intervals were back-transformed (antilog) for graphical presentation of results. Information theoretic methods (Burnham and Anderson 2002) were used to evaluate 11 null and candidate models that included combinations of these covariates (Table 2). Covariates from the top-ranked model in the first step were added to evaluate a second set of 16 candidate models that included the null model, and combinations and interactions of habitat covariates including study site and proportional composition of early successional woody and grass habitats within covey home ranges before the dispersal period (Table 3). All models were specified *a priori* and included a constant intercept term and the random effects variable (covey). Effects (singly and in combination) of sex, age, year, study site, early successional woody and grassland habitat composition of covey home ranges were tested on dispersal distance with a minimum number of

Table 3. Final candidate model set for spring dispersal analysis and ranked models evaluating the influence of habitat and design variables on dispersal distances of radio-marked northern bobwhite at 4 study sites in southwestern Ohio during 2010–2011.

| Model ^a | k ^b | AIC ^c | AIC _c ^d | ΔAIC _c ^d | w _i ^e |
|------------------------------------|----------------|------------------|-------------------------------|--------------------------------|-----------------------------|
| SEX + AGE | 4 | 192.10 | 192.79 | 0.00 | 0.24 |
| Null | 2 | 193.37 | 193.57 | 0.78 | 0.16 |
| HRESW + SITE | 6 | 192.44 | 193.94 | 1.16 | 0.13 |
| SITE | 5 | 192.90 | 193.95 | 1.17 | 0.13 |
| HRESW | 3 | 193.93 | 194.34 | 1.55 | 0.11 |
| SITE + SEX + AGE | 7 | 192.81 | 194.84 | 2.06 | 0.09 |
| HRESW + SEX + AGE | 5 | 193.80 | 194.86 | 2.07 | 0.08 |
| HRESW + SITE + SEX + AGE | 8 | 193.55 | 196.21 | 3.43 | 0.04 |
| HRGRASS + SEX + AGE | 5 | 201.39 | 202.45 | 9.66 | 0.00 |
| HRGRASS + HRESW + SITE | 7 | 201.03 | 203.06 | 10.28 | 0.00 |
| HRGRASS | 3 | 202.74 | 203.14 | 10.36 | 0.00 |
| HRGRASS + SITE | 6 | 202.25 | 203.75 | 10.96 | 0.00 |
| HRGRASS + HRESW | 4 | 203.17 | 203.86 | 11.07 | 0.00 |
| HRGRASS + HRESW + SEX + AGE | 6 | 202.64 | 204.14 | 11.35 | 0.00 |
| HRGRASS + HRESW + SITE + SEX + AGE | 9 | 201.28 | 204.68 | 11.89 | 0.00 |
| HRGRASS + SITE + SEX + AGE | 8 | 202.10 | 204.77 | 11.98 | 0.00 |

^a HRESW = average proportion of early successional woody vegetation in covey home ranges; HRGRASS = average proportion of early successional herbaceous vegetation in covey home ranges.

^b Number of parameters included in models. All models included an intercept and a random effect of covey affiliation.

^c AIC = Akaike Information Criterion.

^d AIC_c = Akaike Information Criterion adjusted for small sample sizes.

^e w_i = Akaike weight.

Table 4. Dispersal classifications and mean movements for radio-marked northern bobwhites in southwestern Ohio during spring 2010 and 2011. Dispersal classifications were based on the average covey home-range size for the preceding winters (26.1 ha, 0.58 km diameter; Janke and Gates 2013).

| Year | Total | | Non-disperser | | Range shift | | Disperser | |
|--------|----------|-----------------------|---------------|-----------------------|--------------|-----------------------|--------------|-----------------------|
| | <i>n</i> | Distance ^a | <i>n</i> (%) | Distance ^a | <i>n</i> (%) | Distance ^a | <i>n</i> (%) | Distance ^a |
| 2010 | 34 | 1.98 ± 1.00 | 14 (41.2) | 0.30 ± 0.06 | 6 (17.6) | 0.88 ± 0.07 | 14 (41.2) | 4.13 ± 1.00 |
| 2011 | 32 | 1.09 ± 0.52 | 14 (43.8) | 0.32 ± 0.08 | 9 (28.1) | 0.71 ± 0.05 | 9 (28.1) | 2.66 ± 0.52 |
| Pooled | 66 | 1.55 ± 0.58 | 28 (42.4) | 0.31 ± 0.06 | 15 (22.7) | 0.78 ± 0.06 | 23 (34.8) | 3.65 ± 1.30 |

^a Mean distance ± 95% confidence interval (km).

candidate models. It was hypothesized that early successional woody habitat would facilitate (i.e., increase) dispersal while higher proportions of early successional herbaceous habitats would inhibit movements by providing nesting habitat near where birds wintered.

The package *lme4* in Program R (R Development Core Team 2012) was used to fit candidate models. Support for each model was compared based on Akaike Information Criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2.0$ were considered to have equivalent support (Burnham and Anderson 2002). The difference between AIC_c from the best model and all other models (ΔAIC_c) and Akaike weights (w_i) was used to identify the relative support for each candidate model.

RESULTS

Results are based on 66 bobwhites (females = 30, males = 36) in 29 coveys during the 2010 and 2011 breeding seasons. Observed dispersal periods for individual birds ranged from 4 April to 26 May and lasted a mean of 21.0 ± 1.94 days (range = 7-35 days) for the sample population. There were no differences between years for date of covey break-up ($F = 0.23$, $P = 0.634$) or length of the dispersal period ($F = 2.435$, $P = 0.124$), and radio-marked individuals were pooled across years for survival analyses. There was no evidence of differences in survival associated with dispersal distance. Survival models for age, sex, age*sex, and dispersal distance all ranked lower than the null model and had $\Delta AIC_c > 2$.

The mean dispersal distance for all individuals was 1.55 km (Table 4). We classified 28 (42.4%) individuals as non-dispersers, 15 (22.7%) as having a range shift, and 23 (34.8%) as dispersers. Non-dispersers averaged net movements of 0.31 km, range shifts averaged 0.78 km, and dispersal distances averaged 3.56 km.

The 2 highest-ranked candidate models for design variables were within 2 ΔAIC_c units of the null model (Table 2), offering no statistical support for differences in dispersal among age, sex, classes, or years. However, mean values differed substantially among age-sex classes (Fig. 1) and the regression coefficients were significant for age ($P = 0.038$) and not significant ($P = 0.073$) for sex. Adult females dispersed the shortest mean distance, followed in increasing order by adult males, juvenile females, and juvenile males (Table 5, Fig. 1).

Top candidates were within 2 ΔAIC_c units of the null model (Table 3) but did contain significant variable coefficients. The highest ranked model included covariates for sex and age and was the only one to rank above the null. The third ranked model contained variables for study site and the proportion of early successional woody habitat in covey home ranges (HRESW). The coefficient for HRESW was highly significant ($P = 0.006$) and indicated dispersal distance declined with increasing amounts of early successional woody habitat in covey home ranges (Figs. 2, 3). Mean dispersal distance was greater on the Peach site ($P = 0.073$) and did not differ among the other 3 sites (Fig. 4). The Thurner site had the lowest proportion of dispersing individuals (27.3%; Table 6) and the lowest mean dispersal distances (0.58 km; Fig. 4). The Thurner and Wildcat sites had intermediate values but were more similar to the Peach site which had the highest proportion of dispersing individuals (44.4%) and the highest mean dispersal distances (2.84 km). Proportion of grass within covey home ranges had no relationship to dispersal distance ($P > 0.91$; Table 3).

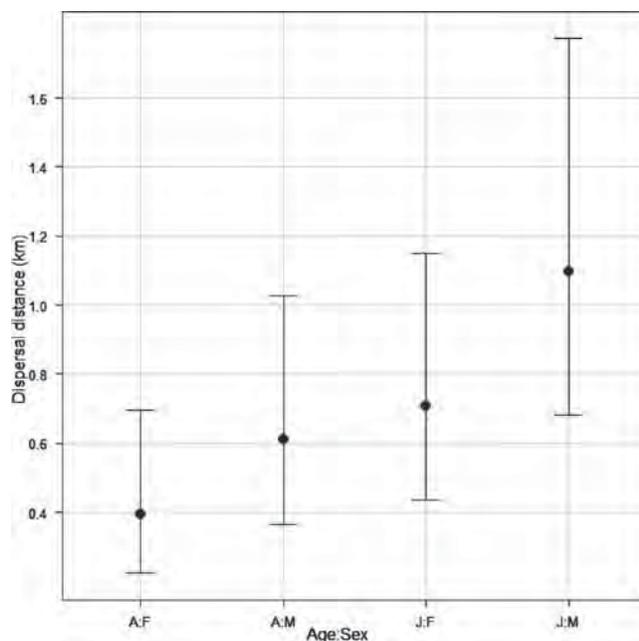


Fig. 1. Mean spring dispersal distances with 95% confidence intervals for radio-marked bobwhites in southwestern Ohio during 2010 and 2011 based on age (A = adult, J = juvenile) and sex (F = female, M = male).

Table 5. Mean dispersal distances \pm 95% confidence intervals (km) and dispersal classification percentages for radio-marked northern bobwhites in southwestern Ohio during spring 2010 and 2011.

| | <i>n</i> | Dispersal classification (%) ^a | | | Distance (km) | |
|----------|----------|---|------|------|-----------------|------------|
| | | ND | RS | D | Mean | Range |
| Female | | | | | | |
| Juvenile | 21 | 23.8 | 38.1 | 38.1 | 1.82 \pm 1.17 | 0.03–11.49 |
| Adult | 9 | 100.0 | 0.0 | 0.0 | 0.29 \pm 0.09 | 0.07–0.42 |
| Pooled | 30 | 46.7 | 26.7 | 26.7 | 1.36 \pm 0.85 | 0.03–11.49 |
| Male | | | | | | |
| Juvenile | 20 | 25.0 | 30.0 | 45.0 | 2.21 \pm 1.29 | 0.06–11.09 |
| Adult | 16 | 56.3 | 6.3 | 37.5 | 1.08 \pm 0.72 | 0.18–6.13 |
| Pooled | 36 | 38.9 | 19.4 | 41.7 | 1.71 \pm 0.80 | 0.06–11.09 |
| Pooled | | | | | | |
| Juvenile | 41 | 24.4 | 34.1 | 41.5 | 2.01 \pm 0.86 | 0.03–11.49 |
| Adult | 25 | 52.0 | 4.0 | 44.0 | 0.79 \pm 0.48 | 0.07–6.13 |
| Pooled | 66 | 34.8 | 22.7 | 42.4 | 1.55 \pm 0.58 | 0.03–11.49 |

^a ND = non-dispersal; RS = range shift; D = dispersal.

The longest spring dispersal distance documented was for a radio-marked bobwhite during this study. One juvenile male made an initial spring dispersal movement of 3.80 km that ended on 10 May 2010 after which he was observed to be paired with a female. He then made a second movement of 13.87 km, an apparent second breeding season dispersal during 19–24 May 2010 after which he settled and was heard whistling. This bird traveled a net distance of 18.9 km from initial spring location before his transmitter failed on 7 June 2010.

DISCUSSION

Dispersal can rescue declining populations or re-establish them after extinction events (Howard 1960) but dispersing individuals must often traverse unfamiliar areas where their survival is at risk (Bélíchon et al. 1996). Dispersal may be particularly important for states like Ohio that are on the northern periphery of the bobwhite range where populations are in decline and extirpation of local populations is common (Williams et al. 2003). Early bobwhite research reported individuals

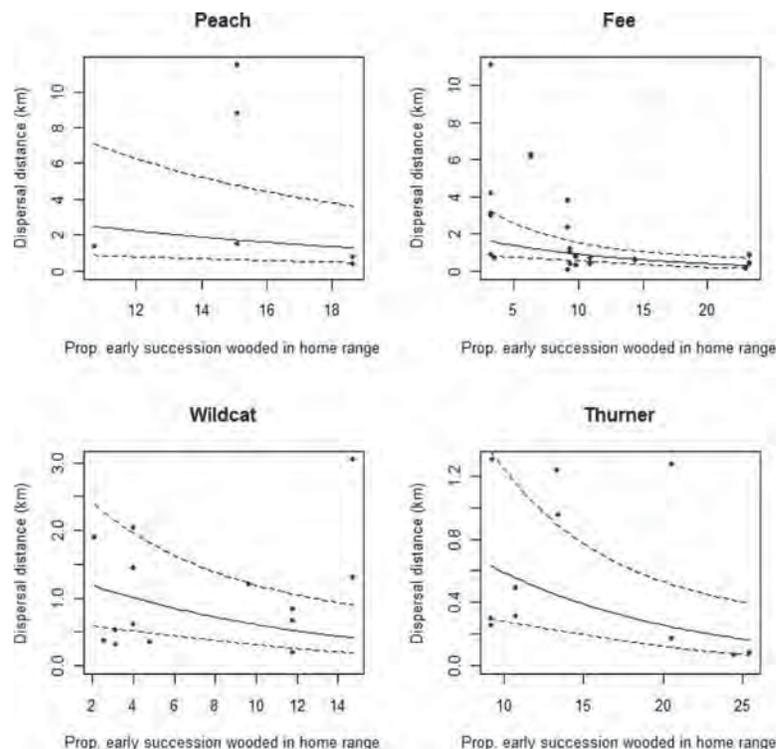


Fig. 2. Spring dispersal distances with 95% confidence intervals versus the proportion of early successional woody habitat in winter home ranges by study site for radio-marked bobwhites in southwestern Ohio during 2009–2011.

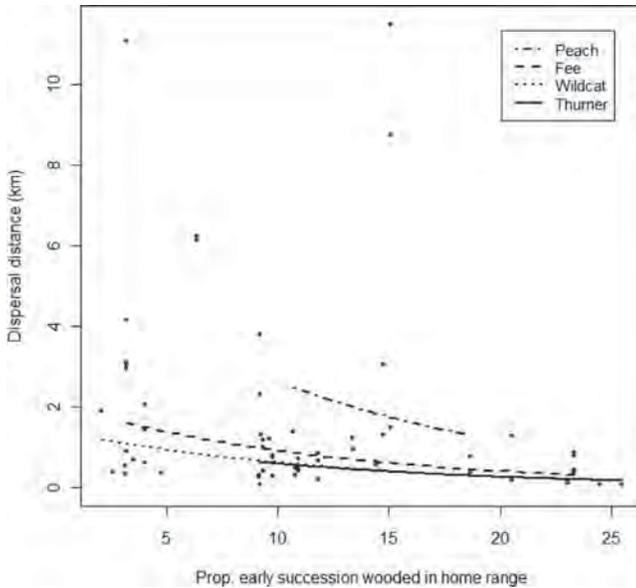


Fig. 3. Spring dispersal distances versus the proportion of early successional woody habitat in winter home ranges by study site for radio-marked bobwhites in southwestern Ohio during 2009–2011.

were relatively sedentary (Lehmann 1946, Murphy and Baskett 1952, Lewis 1954). These studies generally used capture-mark-recapture methods that were limited by study site boundaries, low recovery of marked individuals, and anecdotal or opportunistic reporting of longer dispersal movements. Studies that use radiotelemetry provide more complete evaluations of spring movements and dispersal (White and Garrott 1999).

Our results provide additional evidence that bobwhites are highly mobile and regularly travel long distances during spring (Fies et al. 2002, Townsend et al. 2003, Cook et al. 2006). Radio-marked individuals traveled farther between nonbreeding and breeding season ranges compared to those in other bobwhite populations (Fies et al. 2002, Townsend et al. 2003, Cook et al. 2006).

Proportions of individuals classified as range shifts and dispersers during our study (Table 4) were comparable to other bobwhite populations (Fies et al. 2002, Townsend et al. 2003, Cook et al. 2006). Our criteria were based on winter home range diameters observed in our population (Janke and Gates 2013); only Cook et al. (2006) used a biologically-based dispersal criterion. Only 19% (not 35%) of individuals in our study population would have been classified as dispersers if we used the 1-km cutoff proposed by Townsend et al. (2003). Individuals in our study classified as dispersers after Townsend et al. (2003) dispersed further on average (5.23 km) than those in other bobwhite populations. Bobwhite breeding habitats on our study areas were often separated from winter ranges by croplands or other areas devoid of suitable nesting habitat. Thus, it may have been necessary for individuals in our study to move long distances to find mates or suitable nesting habitat (Fies et al. 2002).

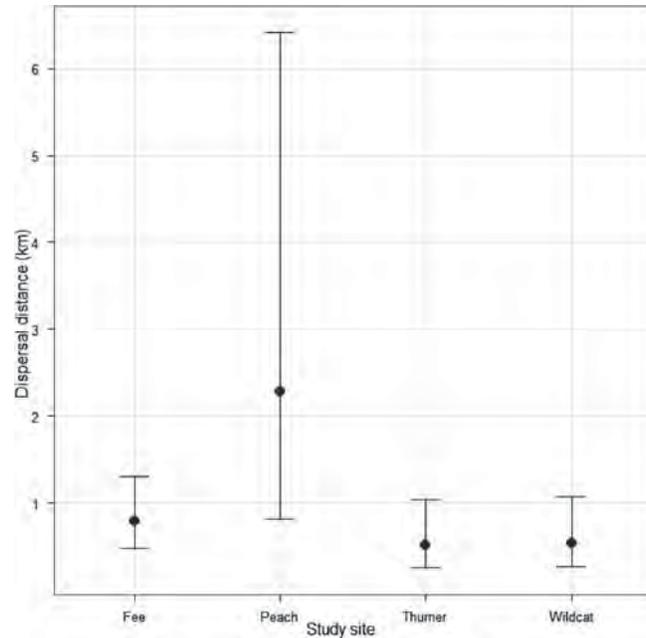


Fig. 4. Mean spring dispersal distances with 95% confidence intervals by study site for radio-marked bobwhites in southwestern Ohio during 2009–2011.

Studies have found that both translocated and resident bobwhites had strong site fidelity and small dispersal movements in areas receiving active bobwhite management (Liu et al. 2002; Terhune et al. 2006, 2010). The dispersal proportions and distances during these studies (Liu et al. 2002; Terhune et al. 2006, 2010) are considerably lower than those from other bobwhite dispersal studies (Fies et al. 2002, Townsend et al. 2003, Cook et al. 2006, this paper). Translocation management targets areas that cannot be reached by natural dispersal, have low population densities, and typically occur in areas with managed habitat. Habitat management seems to have dramatic influences on dispersal behavior and underscores the importance of evaluating bobwhite populations in the array of landscapes found in its range, especially those that receive limited management.

Average distances and proportions of range shifts and dispersals (Table 4) may have been higher except for above average spring rainfall during our study, especially during 2011 (NCDC 2011). High rainfall and flooding during spring can negatively affect bobwhite survival (Applegate et al. 2002) or delay covey break-up diminishing length of the dispersal period (Roseberry and Klimstra 1984). April 2011 had the highest amount of precipitation in the past 129 years and May 2011 was the sixth wettest in Ohio history. The study areas received rainfall amounts that were 285% of normal in April 2011 and 147% of normal in May 2011. There was no evidence of differences between years for date of covey break-up or dispersal distances, but the comparison may be constrained by high rainfall during May 2010 which may have limited dispersal.

Table 6. Dispersal classification percentages and average distances for radio-marked northern bobwhite based on study sites in southwestern Ohio during spring 2010 and 2011.

| Study site | <i>n</i> | Percent at study site | | |
|------------|----------|-----------------------|-------------|-----------|
| | | Non-disperser | Range shift | Disperser |
| Fee | 32 | 40.6 | 28.1 | 31.3 |
| Thurner | 11 | 63.6 | 9.1 | 27.3 |
| Peach | 9 | 33.3 | 22.2 | 44.4 |
| Wildcat | 14 | 35.7 | 21.4 | 42.9 |

Age and sex of dispersing individuals were the best predictors of spring dispersal distances for bobwhite in Ohio; this was the only model to rank above the null (Table 3). Juveniles and males in our study traveled furthest during spring dispersal (Fig. 1). Juvenile-biased dispersal is common for avian species and is an adaptation to avoid inbreeding with related individuals (Howard 1960). The juvenile-biased dispersal during our study supports results from other bobwhite dispersal studies (Urban 1972, Smith et al. 1982, Fies et al. 2002, Townsend et al. 2003). Density-dependence within breeding habitats may also bias juvenile dispersal, particularly if dominant adults keep them from preferred breeding areas (Murphy and Baskett 1952, Howard 1960). Female-biased dispersal is the pattern displayed by most avian species but male-biased dispersal is occasionally reported especially for species with polygamous breeding systems (Greenwood and Harvey 1982, Curtis et al. 1993). Other bobwhite studies have documented male-biased dispersal (Hood 1955, Urban 1972, Terhune et al. 2010) while others documented female-biased dispersal (Fies et al. 2002) or no sex-specific differences (Smith et al. 1982, Townsend et al. 2003, Cook et al. 2006, Terhune et al. 2010). Our results for sex-specific dispersal distances support the conclusions of Clarke et al. (1997) that dispersal biases tend to be facultative and should not be assumed to be an unvarying species characteristic.

We hypothesized that early successional woody habitats with generally linear arrangements (i.e., fence-rows, ditches, riparian) would facilitate dispersal by providing travel corridors. Cook et al. (2006) reported early successional habitats had negligible effect on dispersal probabilities for radio-marked bobwhites in Georgia but both early successional herbaceous and woody vegetation were included in this category. We separated early succession herbaceous and woody habitat types because we suspected they may differentially affect dispersal. We found that dispersal distances declined with amounts of early succession woody habitat in covey home ranges (Figs. 2, 3).

Woody vegetation provides year-round benefits to bobwhites by providing cover from predators and thermal extremes. Vegetation structure of woody habitat can also create preferred foraging conditions by shading sod-forming grasses and patches of bare ground (Collins et al. 2009). Woody habitats were preferred by coveys at our study sites during the nonbreeding season (Janke and Gates 2013) and this may have continued during spring

despite the need for bobwhites to find suitable nesting areas provided by early succession herbaceous habitats. Nest sites (i.e., habitat patches and nesting substrates) may be sufficient in our study areas to not limit reproduction as they do for bobwhite populations in arid regions (Rader et al. 2011).

MANAGEMENT IMPLICATIONS

Bobwhites in Ohio do not appear to be dispersal-limited yet they have failed to expand their range into historically-occupied areas. Gates et al. (2012) found that bobwhite metapopulations in southwestern Ohio were not producing sufficient individuals to rescue local populations or to recolonize historically-populated areas, despite their dispersal capabilities. Dispersal rates were also too low to compensate for high mortality rates in these areas (Gates et al. 2012). Trap and transplant programs in Ohio should focus on providing quality bobwhite habitat within the dispersal range of extant populations. Target areas should contain early successional woody habitats and in proximity to extant populations to connect locally isolated subpopulations and, if successful, supplement extant populations. We recommend areas within 0.73-1.41 km (50th to 75th percentiles of dispersal distances) of existing populations in southwestern Ohio be targeted to avoid creating isolated subpopulations. Habitat management will likely be necessary to create conditions that support sufficiently high survival rates to allow populations to produce surplus individuals.

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