

Translocation to a fragmented landscape: survival, movement, and site fidelity of Northern Bobwhites

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Abstract. Habitat fragmentation, degradation, and loss have taxed early-successional species including the Northern Bobwhite (*Colinus virginianus*) and numerous grassland obligate birds. Translocation is often applied to counteract the consequences of habitat fragmentation through the creation, reestablishment, or augmentation of wild populations for the purposes of conservation, biodiversity maintenance. However, the implementation of these techniques is often conducted without valid experimental designs and therefore lacks robust, empirical data needed to evaluate and advance the knowledge and application of translocation. Despite the increasing amount of habitat management applied to patches among fragmented landscapes, a paucity of source populations often limits natural (re)colonization. As such, translocation may serve as a surrogate to natural dispersal, but its efficacy among fragmented landscapes is uncertain. Few studies exist that have assessed site fidelity, movement, and survival of individuals following translocation among fragmented landscapes. Thus, we experimentally evaluated the efficacy of translocation using known-fate and multi-strata models to evaluate hypotheses of temporal, biological, and group effects on survival and movement of translocated and resident bobwhites. We did not detect differences in survival or movement between translocated and resident bobwhites, suggesting that movement of individuals to a fragmented habitat does not negatively influence these demographic attributes. Based on these data, we suggest that two site-specific criteria should be met prior to instituting translocation: habitat management should be conducted to ensure that quality habitat exists and the patch size should be a minimum of 600 ha of quality habitat (poorer sites may warrant even larger patches). Translocation is a viable conservation method for increasing abundance in patches when habitat quality is high but source populations are limited.

Key words: *Colinus virginianus*; habitat fragmentation; habitat quality; movement; multi-strata models; Northern Bobwhite; patch size; relocation; site fidelity; survival; translocation.

INTRODUCTION

Grassland and early-successional birds are a source of conservation concern because this group has been subject to precipitous population declines during recent decades (Sauer et al. 2008), more than other guilds of North American bird species (Askins 1993, Knopf 1994, Brennan and Kuvlesky 2005). Numerous species within this guild have been impacted (Vickery et al. 1992, 1994, Askins 1993), but the decline of Northern Bobwhites (*Colinus virginianus*; hereafter, bobwhites) is particularly concerning due to their historical prominence and socioeconomic value (Stoddard 1931, Brennan 1999, Burger et al. 1999). Fragmentation, degradation, or complete loss of habitat resulting from changing land-

use practices have reduced early-succession ecosystems (Brennan 1991, Church and Taylor 1992, Church et al. 1993, Roseberry and Sudkamp 1998, Brennan 1999, Peterson et al. 2002) and have negatively impacted survival of bobwhites and other grassland obligates (Roseberry 1993, Rollins and Carroll 2001, Burger 2002, Guthery and Lusk 2004). Due largely to limited dispersal capabilities, low-mobility species inhabiting fragmented systems often result in local populations being subject to low probabilities of recolonization and high risk of extirpation (Hanski and Gilpin 1991, Newman and Pilson 1997, Bijlsma et al. 2000, Frankham et al. 2004, Tallmon et al. 2004). Population viability among fragmented sites with small habitat patches (Johnson 2001) is uncertain, which is ostensibly linked to decreased survival (Vickery et al. 1992, Burger et al. 1994). Several species of grassland birds are intolerant of small patches, preferring to use larger patches (Herkert 1994).

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Although bobwhites have been studied extensively, population levels continue to decline throughout their distribution (Brennan 1991), with purported sharper declines during recent years (Sauer et al. 2008). Annual survival below that needed to maintain long-term population persistence, commonly observed throughout the bobwhite's range, is considered symptomatic of a landscape-level habitat fragmentation problem (Brennan 1991, Palmer and Wellendorf 2007, Terhune et al. 2007, Sisson et al. 2009). Research demonstrates the importance of habitat modification to increase demographic rates, including survival and reproduction, contributing to long-term population persistence (Stoddard 1931, Klimstra 1972, Roseberry and Klimstra 1984, Landers and Mueller 1986, Sisson et al. 2009). Escalating fragmentation forces bobwhites to utilize poorer quality and small, ephemeral patches, inhibiting dispersal by requiring larger movements to access other suitable habitat patches. This combination of factors increases mortality (Fies et al. 2002, Cook 2004, Folk 2006). Despite regional declines, research demonstrates that long-term, intensive habitat management maintains mean annual survival rates conducive to population stability and increase (Palmer and Wellendorf 2007, Terhune et al. 2007, Sisson et al. 2009). However, in cases where restored habitat patches are small or isolated, the probability of natural repopulation remains low. Translocating Northern Bobwhites prior to the breeding season is a nascent technique for replenishing native stocks where populations are absent or too low to respond following the implementation of other management techniques, such as habitat improvement (Terhune et al. 2005, 2006).

Translocation has become a common conservation option to fulfill biodiversity and restoration objectives by reducing the adverse effects associated with demographic and genetic bottlenecks (Griffith et al. 1989, Seddon et al. 2007). Movement of individuals to isolated or fragmented habitat may mitigate fragmentation effects by introducing novel alleles and potentially increasing reproductive output through effects of hybrid vigor (Tallmon et al. 2004). In addition, supplementation of *r*-selected species prior to the breeding season provides an opportunity to bolster fall abundance on a site by capitalizing on their high reproductive capability (Burger et al. 1995, Brennan 1999, Terhune et al. 2005, 2006). However, potentially adverse effects of translocation via direct (e.g., trap or transport stress) or indirect (e.g., dispersal, habitat acclimation) losses may preclude its utility for improving genetic diversity and establishing, reestablishing, or augmenting wild populations (Griffith et al. 1989, Wolf et al. 1996).

Among bobwhites, recent studies of translocation have created optimism for its utility. Results demonstrate that translocation of individuals to areas following substantial habitat improvements elicits a positive population response (Terhune et al. 2005, 2006). Despite these successes, when translocation was conducted prior

to the breeding season and among large, contiguous blocks of managed habitat (Terhune et al. 2005, 2006), the release of individuals to sites among fragmented landscapes has not been adequately investigated. Investigators and researchers have requested objective assessments of translocation using adequate study design(s) to empirically test hypotheses while advancing the knowledge and application of the technique (Griffith et al. 1989, Brennan 1999, Seddon et al. 2007). The efficacy of translocation is predicated on the survival at, and fidelity of individuals to, the release site. Thus, it is imperative to assess the effects of translocation on demographic parameters, principally survival and site fidelity, among fragmented landscapes prior to implementing translocation at larger scales. Here we compare survival, home range, and site fidelity between resident and translocated bobwhites following release to an isolated, fragmented site in southwest Georgia.

STUDY AREA

Translocation site

We conducted this study on a private property (1092 ha; Fig. 1) in Marion County near Tazewell, Georgia, USA (84°24'23.46" W, 32°21'39.07" N). This property is located near the fall line of the Piedmont physiographic region and is characterized by gradual rolling hills and sandy clay to clay type soils. The habitat is predominantly upland pine forests (59.1%); scattered fallow fields (12.0%); thinned hardwoods, interspersed hardwood hammocks, and drains (11%); hardwood-tupelo-dominated bottomland (9.5%); wildlife openings (3.5%), roads (2.5%); other (e.g., pasture, food plots, landscape; 1.3%); and water (1.2%). The upland pine forests contain moderate basal areas (BA = 6–9 m²/ha) consisting of longleaf (*Pinus palustris*), loblolly (*P. taeda*), and slash (*P. ellioti*) pines; upland pines were managed to promote an understory of early-succession vegetation. Typical habitat management included roller-chopping, mowing, prescribed burning, periodic timber thinning, hardwood management, supplemental feeding, fallow-field management, and cover-patch planting. Plantation staff managed mammalian nest predators at an equal rate throughout the study site.

Prior to onset of habitat management in 1996, the property was typical of the region: there was little farming, and the landscape was dominated by pasture (sod-forming grasses) and pine monocultures (BA > 19 m²/ha) enrolled in the Conservation Reserve Program (CRP), with an abundance of <0.25 bobwhites/ha. During 1996–2003, the landowner undertook extensive habitat improvements on the study site; however, modest increases in bobwhite population abundance were observed (2003 abundance: <0.75 bobwhites/ha). Following habitat management, this site maintained vegetation composition and structure similar to that of the bobwhite source sites. As a result of habitat management, we consider this property an "island" of well-managed bobwhite habitat surrounded by a matrix

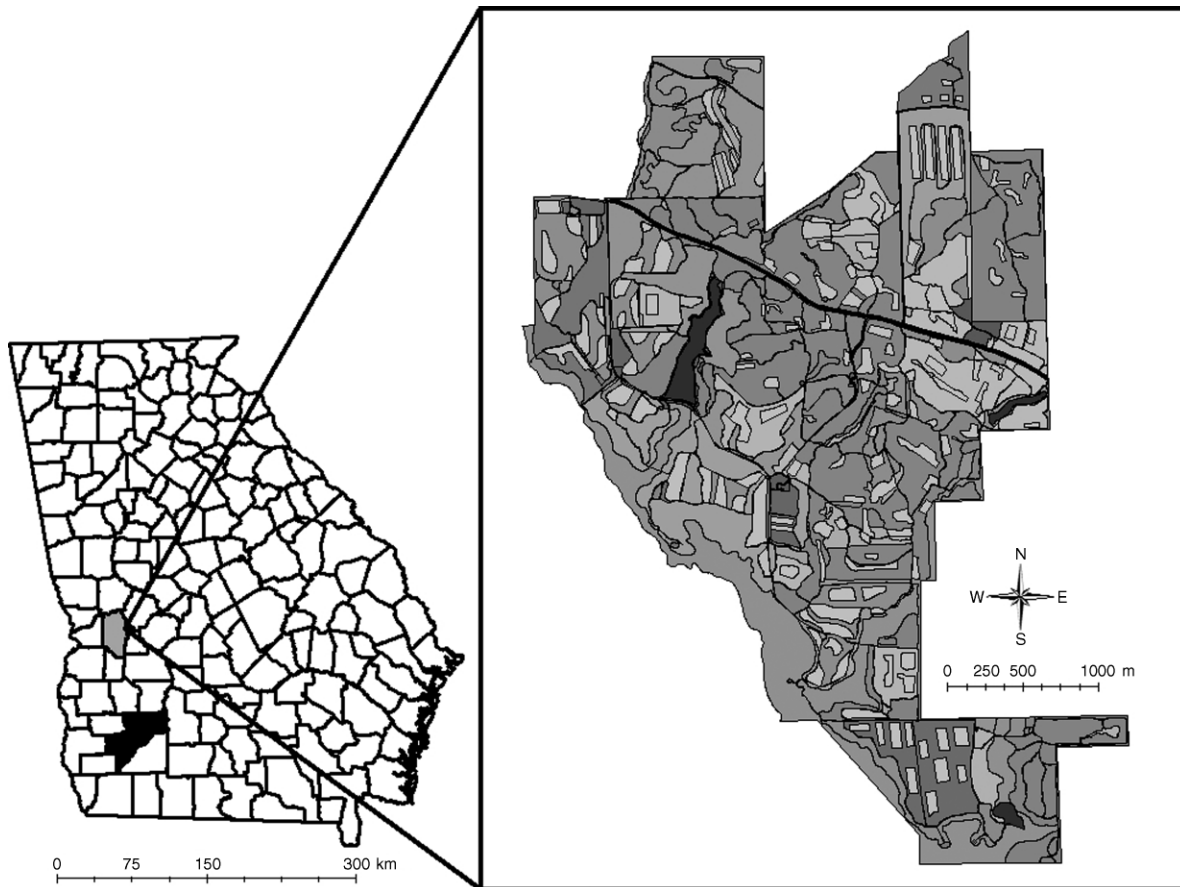


FIG. 1. The translocation study site on the right indicates, by shadings of different habitats, the general diversity of patch types, sizes, and edge. The map of Georgia (USA) on the left shows the position of the translocation study site in Marion County (gray); the source sites for translocated Northern Bobwhites were located in Baker and Dougherty counties (black).

of poorer quality landscapes (e.g., dense pine monocultures [CRP], pastureland, and late-succession hardwood forests). Landscape habitat composition (using a 5-mile [~ 11 km] buffer and 2001 GAP land cover data) surrounding the study site consisted of: upland pine (58.9%); hardwood (11.9%); pasture (5.3%); early succession (4.9%); agriculture/row crop (10.6%); wetland (4.3%); and other (e.g., roads, urban; 4.1%). Landscape patch metrics for early-succession habitat types included: edge density, ED (26.01 m/ha); mean patch edge, MPE (123.24 m); and contagion (<5), a unitless measure of homogeneity, which increases when a landscape becomes dominated by a single class. Low ED values reflect landscapes composed of a few big regions, whereas high values reflect more complex, more diverse landscapes with more edge.

Source sites

As source sites for individuals to be translocated, we selected three private properties (located ≤ 15 km apart) in Baker and Dougherty counties, southwest Georgia, USA. These properties lie within the Upper Coastal Plain physiographic region, and owners of each have

implemented intensive wild quail management. Additional descriptions of the source sites are available (see Yates et al. 1995, Terhune et al. 2005, 2006, 2007). Landscape habitat composition (using a 5-mile [~ 11 km] buffer and 2001 GAP land cover data) surrounding the source sites consisted of: upland pine (28.5%); hardwood (8.7%); pasture (3.4%); early succession (39.8%); agriculture/row crop (5.9%); wetland (5.6%); and other (roads, urban, and the like; 8.1%). Landscape patch metrics for early-succession habitat types at the source sites included: edge density, ED (150.75); mean patch edge, MPE (454.36); and contagion (>65).

METHODS

Capture and handling

We captured bobwhites during October–November (autumn trapping period) and January–March (spring trapping period), 2003–2005, using “walk-in” funnel traps (Stoddard 1931:442) baited with milo and cracked corn. We covered traps with brush (e.g., fresh-cut pine limbs) to minimize stress on captured birds and to conceal traps from predators. We captured and classified

all bobwhites (translocated and resident) by age and sex, and we weighed, leg-banded, and collected 10–15 feathers from the ventral and humeral feather tracts of each individual.

During the spring trapping season in 2003 and 2004, we radio-tagged each translocated bobwhite (≥ 132 g) and a subsample of the “resident” bobwhites (≥ 132 g) with a 6-g ($\leq 5\%$ of body mass) necklace-style radio-transmitter equipped with an activity switch (Holohil Systems, Carp, Ontario, Canada). We used necklace-style transmitters because they do not influence body mass dynamics or physiology of captive birds (Corteville 1998, Hernandez et al. 2004), nor do they inhibit survival of bobwhites in the wild (Palmer and Wellendorf 2007, Terhune et al. 2007, Holt et al. 2009).

We held translocated bobwhites overnight in vented transport boxes and we released them at random locations (using a stratified sampling schema with a GIS) within the defined core area (see Fig. 1) in groups of 8–12 individuals, not necessarily from the same covey. We released translocated bobwhites within 24 h of capture, and we did not provide water or feed other than that consumed in traps, prior to release. To avoid recapturing translocated birds, we did not conduct spring trapping in the core area following release.

We located radio-tagged individuals at least three times weekly during the breeding season (1 April–30 September) using the homing method (White and Garrott 1990, Kenward 2001). We approached birds within 25–50 m to minimize location and habitat classification errors, and we recorded all locations using a Geographical Information System (ArcGIS, version 9.2; ESRI 2007). When radio contact was lost, we systematically searched the study area within 5 km of the last known location, and we determined specific causes of mortality when possible, by evidence at the kill site and condition of the radio transmitter (Curtis et al. 1993).

The Georgia Department of Natural Resources (Social Circle, Georgia) approved capture and monitoring procedures outlined in this study for the source sites in Baker and Dougherty Counties (permit #29-WMB-03-280 and #29-WSF-04-200) and the release site in Marion County, Georgia (permit #29-WMB-00-105, #29-WMB-03-38, and #29-WMB-04-128). The University of Georgia Institutional Animal Care and Use Committee approved all procedures (2000–2002 IACUC approval numbers: A990028M1, A990028C1; 2003 extension: A200310109-0).

Statistical analysis

Survival.—We estimated survival rates of bobwhites in relation to temporal and biological (group) effects using the known-fate data type in program MARK (White and Burnham 1999). The known-fate model employs a binomial likelihood and permits incorporation of individual covariates (e.g., gender and age) delineated by groups (e.g., translocated, resident) to

evaluate their affect on survival. When biologically relevant, we constructed a priori candidate models incorporating additive effects and interactions using a logit-link function. We computed weekly survival across three intervals: two 2-day intervals and one 3-day interval, and we specified the appropriate interval length in program MARK to yield accurate estimates of survival.

We used an information-theoretic approach (Akaike 1973, Guisan 1977, Anderson et al. 2000, Burnham and Anderson 2002) to evaluate each set of candidate models and to test explicit hypotheses. We used Akaike’s information criterion adjusted for small sample bias and overdispersion, QAIC_c (Akaike 1973, Wedderburn 1974, Burnham and Anderson 2002) to compare each candidate model, and we considered the model with the lowest QAIC_c to be the best approximating model, given the data. We assessed model fit (using evaluation of residual plots and \hat{c}) derived from the most general model. We assessed the relative plausibility of each model in the set of candidate models using Akaike weights, w_i (Anderson et al. 2000, Burnham and Anderson 2002), where the best approximating model in the candidate set has the greatest Akaike weight. We used model averaging (Akaike 1974, 1978, Burnham and Anderson 2002) to obtain daily survival rates (DSR), and we derived monthly and seasonal survival from the product of weekly survival rates across the respective intervals. To provide additional inferential power and to allow direct comparison of covariates, we report beta coefficients, their standard errors, and 95% confidence intervals for variables of interest (e.g., group). We also report the derived estimates of DSR (with associated 95% CIs), allowing comparison to other studies.

We conducted two separate analyses with known-fate data to delineate: (1) temporal and (2) biological and grouping effects on survival. First, we examined a candidate set of temporal models, which included parameterizations for time via week, month, and year effects. We included models with no time dependence (constant survival), first- and second-order linear time trends within year, and models with constant or variable survival among years. To further evaluate the potential impact of translocation on survival, we included models (developed as an exploratory analysis; i.e., models were not developed a priori) where survival was constant across week (weeks 1–4) and month (months 1–4) and where survival varied between week and month.

We used the temporal-effects model with the lowest QAIC_c value as the basis for formulating an a priori candidate set of models to examine relevant biological and group effects on survival.

1. *Group.*—We compared two groups: translocated and resident bobwhites. Based on results from previous studies (Terhune et al. 2005, 2006), we hypothesized that survival between groups would not differ.

2. *Age.*—Cohorts (adult vs. subadult) often account for variation in survival (Roseberry and Klimstra 1984,

Pollock et al. 1989a, Terhune et al. 2007), based on the tenet that experience increases survival. Age has not been investigated in the context of translocation. We hypothesized that adult bobwhites would have higher survival rates than subadults, and we hypothesized that adult bobwhites would acclimate more quickly to their surroundings, and would be better at selecting optimal habitats. This would result in an interaction of age and group.

3. *Gender*.—A common source of variation in breeding season survival is differences between males and females (Roseberry and Klimstra 1984, Pollock et al. 1989a, Terhune et al. 2007). Male bobwhites, during the breeding season, exhibit a higher propensity to disperse and, in general, make larger movements (Cook 2004, Folk 2006), increasing their likelihood of mortality. We hypothesized that the combination of this tendency with translocation to an unfamiliar area would decrease male survival relative to female survival, as indicated by parameter estimates for the interaction between group and gender status.

4. *Source*.—We captured translocated bobwhites from three different sites during both 2003 and 2004. However, all three source sites were adjacent properties situated within a large block of quality habitat. Therefore we hypothesized that source would not explain additional variation in survival.

Home range, movement, and site fidelity.—We used multi-strata models in program MARK (White and Burnham 1999) to quantify movement among strata and fidelity to individual stratum. Multi-strata models simultaneously estimate apparent survival, resighting, and movement probabilities among strata (Hestbeck et al. 1991, Kendall and Nichols 2004). We delineated three strata based on translocation effort and the designated release area: stratum A was the core area (315 ha) where we released translocated bobwhites; stratum B (775 ha) was a buffer area immediately surrounding the core area (stratum A), but still on the study site property, and stratum C was completely off the study site. Because we estimated survival in the known-fate framework, we used the multi-strata model to assess movement, or transition probabilities; however, we modeled survival in the context of strata (A, B, and C) to gauge the effects of site-specific survivability relative to habitat quality among strata. We reduced the number of parameters by constraining capture probabilities ($p = 1$) to be equal across time, strata, or both time and strata, while allowing movement probabilities to remain time and stratum specific. We modeled movement (ψ) as constant, or as varying by group, age, or group and age. We estimated movements from strata i to j (i.e., movement from the original stratum to a different stratum or movement from a different stratum back to the original stratum) separately ($\psi_{A:B}$, $\psi_{B:C}$, $\psi_{A:C}$, $\psi_{B:A}$, and $\psi_{C:B}$). We fixed movements from $\psi_{C:A}$ to zero because there was little evidence in the data for this directional movement, especially early in the

breeding season, because no individuals were radio-tagged or released off the study site. We selected models using AIC_c , and we report model-averaged parameter estimates as described previously. To allow comparison of movements to those from other bobwhite translocation studies (Terhune et al. 2005), we additionally estimated the arithmetic center (A_c) of breeding-season home ranges for each individual and calculated the Euclidean distance from the A_c to the release and trap sites for translocated and resident bobwhites, respectively.

To allow comparison of home range size to that in other bobwhite studies, we computed kernel (95%, 50%) and minimum convex polygon (100%, 95%) home ranges using the ADEHABITAT package in R (Calenge 2006). To ensure that a representative number of points was used to generate each MCP, we excluded individuals with fewer than 25 telemetry locations (White and Garrott 1990, Kenward 2001). We estimated the smoothing parameter (h) for kernel home ranges in each year (h_{year}) of the study as the mean, least-squares cross-validation-derived h over all individuals where the algorithm converged (bivariate normal kernel; Kenward 2001).

RESULTS

During 2003–2004, we radio-located 136 (62 male, 74 female) resident and 127 (70 male, 57 female) translocated bobwhites, for a total of 8869 telemetry locations. We did not exclude from analysis translocated or resident bobwhites that died during the traditional 1-week censor period (Pollock et al. 1989b) immediately following release because we believed that those mortalities had relevant effects on the success of translocation.

Survival

The most parsimonious temporal-effects model included differences in survival among months for the duration of the season (Table 1); this “best” model was 2.6 times more likely than the next-best model. However, the second-best model, containing an additive effect of year, also received substantial support ($\Delta QAIC_c = 1.196$; Table 1). Several temporal models, including the null survival model (β_0), received moderate support, indicating that the variation in survival is probably attributable to factors other than, or in addition to, temporal effects. Our temporal analysis suggests that the first month following release explains the most variation in survival (Table 1), but the effect was positive ($\beta_{Mar} = 0.895$ [95% CI = 0.067–1.724]). The beta estimates for all other months overlapped zero, implying that these months did not adequately explain any additional variation in survival.

We used the most plausible temporal-effects model ($\beta_0 + \beta_1 Mar + \beta_2 Apr + \beta_3 May + \beta_4 Jun + \beta_5 Jul + \beta_6 Aug$) as the baseline model to evaluate hypotheses relative to biological and group effects on survival. The best

TABLE 1. Model selection results for examination of temporal factors affecting survival of resident and translocated Northern Bobwhites on Buck Creek Plantation, Marion County, Georgia, 2003–2004.

Model	Qdeviance	<i>K</i>	QAIC _c	ΔQAIC _c	<i>w_i</i>
$\beta_0 + \beta_1 \text{ Mar} + \beta_2 \text{ Apr} + \beta_3 \text{ May} + \beta_4 \text{ Jun} + \beta_5 \text{ Jul} + \beta_6 \text{ Aug}$	1419.0098	7	1433.0178	0.0000	0.5095
$\beta_0 + \beta_1 \text{ Mar} + \beta_2 \text{ Apr} + \beta_3 \text{ May} + \beta_4 \text{ Jun} + \beta_5 \text{ Jul} + \beta_6 \text{ Aug} + \beta_6 \text{ Yr}$	1418.9236	8	1434.9339	1.9161	0.1954
$\beta_0 + \beta_1 \text{ T} + \beta_2 \text{ TT}$	1430.4377	3	1436.4394	3.4216	0.0921
$\beta_0 + \beta_1 \text{ T}$	1433.8818	2	1437.8826	4.8648	0.0447
$\beta_0 + \beta_1 \text{ wk1}$	1434.1663	2	1438.1671	5.1493	0.0388
β_0	1436.3101	1	1438.3104	5.2926	0.0361
$\beta_0 + \beta_1 \text{ Yr} + \beta_2 \text{ T} + \beta_3 \text{ TT}$	1430.3319	4	1438.3348	5.3170	0.0357
$\beta_0 + \beta_1 \text{ wk1} + \beta_2 \text{ wk2} + \beta_3 \text{ wk3} + \beta_4 \text{ wk4} + \beta_5 \text{ wk5} + \dots + \beta_6 \text{ wk28}$	1381.5238	29	1439.6480	6.6302	0.0185
$\beta_0 + \beta_1 \text{ Mar} + \beta_2 \text{ Apr} + \beta_3 \text{ May} + \beta_4 \text{ Jun} + \beta_5 \text{ Jul} + \beta_6 \text{ Aug} + \beta_6 \text{ Yr} + \beta_7(\text{Yr} \times \text{Mar})$	1411.9855	14	1440.0154	6.9976	0.0154
$\beta_0 + \beta_1 \text{ Yr}$	1436.2412	2	1440.2420	7.2242	0.0138
Exploratory analysis					
$\beta_0 + \beta_1 \text{ Mar}$	1422.9358	2	1426.9366	0.0000	0.2878
$\beta_0 + \beta_1 \text{ wk1} + \beta_2 \text{ wk2} + \beta_3 \text{ wk3}$	1419.2986	4	1427.3014	0.3648	0.2398
$\beta_0 + \beta_1 \text{ Mar} + \beta_2 \text{ Apr}$	1421.5804	3	1427.5822	0.6456	0.2084
$\beta_0 + \beta_1 \text{ wk1} + \beta_2 \text{ wk2} + \beta_3 \text{ wk3} + \beta_4 \text{ wk4}$	1418.6413	5	1428.6456	1.7090	0.1225
$\beta_0 + \beta_1 \text{ Mar} + \beta_2 \text{ Apr} + \beta_3 \text{ May}$	1421.5020	4	1429.5049	2.5683	0.0797
$\beta_0 + \beta_1 \text{ Mar} + \beta_2 \text{ Apr} + \beta_3 \text{ May} + \beta_4 \text{ Jun}$	1421.3690	5	1431.3733	4.4367	0.0313
$\beta_0 + \beta_1 \text{ wk1} + \beta_2 \text{ wk2}$	1425.4225	3	1431.4242	4.4876	0.0305

Notes: Qdeviance is the deviance of the model adjusted for lack of fit. *K* is the number of parameters. QAIC_c represents Akaike's information criterion corrected for small sample bias and variance inflation (Burnham and Anderson 2002), and ΔQAIC_c is the relative change in QAIC_c from the smallest value or most parsimonious model; *w_i* is the model weight. In the models, T and TT represent a linear and quadratic time trend, respectively; wk, month (i.e., Mar, Apr, etc.), and Yr parameterize weekly, monthly, and annual variation in survival, and × indicates an interaction between factors.

approximating model from this analysis included an age effect on survival, but this model did not receive overwhelming support (Table 2). The best approximating model includes age, suggesting that age is an important parameter. However, we did not detect differences in survival among translocated (trans) and resident (model-averaged estimate: $\beta_{\text{trans}} = 0.002$ [95% CI = -0.491–0.487]) or adult ($\hat{S} = 0.432$ [95% CI = 0.015–0.848]) and juvenile ($\hat{S} = 0.312$ [95% CI = 0.127–0.587]) bobwhites (model-averaged estimate: $\beta_{\text{adult}} = 0.330$ [95% CI = -0.165–0.824]). The effect of gender on survival was minimal (model-averaged estimate: $\beta_{\text{male}} = 0.0481$ [95% CI = -0.198, 0.295]). Variation in monthly survival among translocated and resident bobwhites was also inconsequential (Fig. 2). Overall survival (mean, with 95% CI) was 0.406 (0.273–0.534) and 0.384 (0.265–

0.500) during 2003 and 0.383 (0.254–0.511) and 0.370 (0.247–0.494) during 2004 for translocated and resident bobwhites, respectively. The model including source as an explanatory additive effect did not substantially improve the temporal-only model (Table 2). Survival (mean, with 95% CI) among individuals from source site 1 ($\hat{S} = 0.382$ [0.134–0.632]), source site 2 ($\hat{S} = 0.311$ [0.095–0.560]), and resident individuals ($\hat{S} = 0.377$ [0.298–0.463]) was more similar than individuals translocated from source site 3 ($\hat{S} = 0.501$ [0.222–0.729]).

Multi-strata model analysis of survival (mean, with 95% CI) indicated that survival estimates among stratum A (0.380 [0.284–0.502]), B (0.334 [0.095–0.588]), and C (0.235 [0.006–0.558]) were not different, although the model including strata as an explanatory

TABLE 2. Model selection results for examination of group and biological factors affecting survival of Northern Bobwhites on Buck Creek Plantation, Marion County, Georgia, 2003–2004.

Model	Qdeviance	<i>K</i>	QAIC _c	ΔQAIC _c	<i>w_i</i>
Month + $\beta_7 \text{ Age}$	1416.030	8	1432.040	0.000	0.266
Month	1419.010	7	1433.018	0.978	0.163
Month + $\beta_7 \text{ Gender} + \beta_8 \text{ Age} + \beta_9(\text{Gender} \times \text{Age})$	1413.054	10	1433.069	1.029	0.159
Month + $\beta_7 \text{ Gender} + \beta_8 \text{ Age}$	1416.018	9	1434.031	1.991	0.098
Month + $\beta_7 \text{ Gender}$	1418.650	8	1434.660	2.620	0.072
Month + $\beta_7 \text{ Group}$	1418.948	8	1434.959	2.918	0.062
Month + $\beta_7 \text{ Group} + \beta_8 \text{ Age} + \beta_9(\text{Group} \times \text{Age})$	1415.284	10	1435.300	3.259	0.052
Month + $\beta_{7-9} \text{ Source}$	1416.079	10	1436.095	4.055	0.035
Month + $\beta_{7-9}(\text{Month} \times \text{Group})$	1408.544	14	1436.574	4.533	0.028
Month + $\beta_7 \text{ Group} + \beta_8 \text{ Gender}$	1418.593	9	1436.606	4.566	0.027
Month + $\beta_7 \text{ Group} + \beta_8 \text{ Gender} + \beta_9 \text{ Age} + \beta_{10}(\text{Gender} \times \text{Age})$	1415.184	11	1437.202	5.162	0.020
Month + $\beta_7 \text{ Group} + \beta_8 \text{ Gender} + \beta_9(\text{Group} \times \text{Gender})$	1417.382	10	1437.397	5.357	0.018

Notes: Model statistics are as defined in Table 1. In the models, Group refers to resident vs. translocated birds, Source refers to the site from which the birds came, and × indicates an interaction between factors.

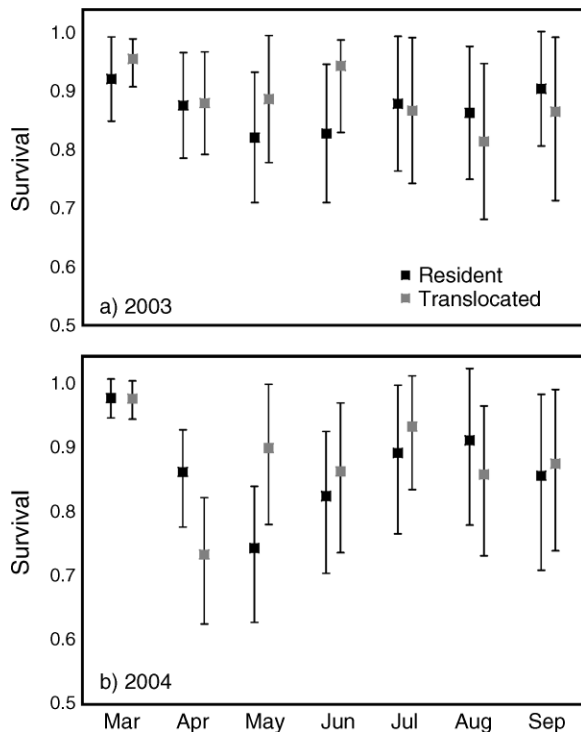


FIG. 2. Model-averaged monthly survival estimates (error bars represent 95% CI) for translocated and resident Northern Bobwhites located on Buck Creek Plantation, Marion County, Georgia, during 2003 and 2004.

variable received substantial support ($w_i = 0.448$; Table 3).

Home range, movement, and site fidelity

Home range size was similar among translocated and resident bobwhites but was generally larger during 2003 than 2004 (Table 4). Multi-strata model analyses indicated that movement was best explained by a location effect [$S(\cdot) \psi_{Strata}$; Table 3] with different transition or movement probabilities (ψ) occurring between different strata (= locations); see Table 5. Models receiving substantial support for explaining

movement of individuals included strata, and no single model lacking this parameter received a model weight ($w_i > 0$; Table 3). The addition of group, age, and gender as additive effects did not improve stratum-specific models. The best additive model included the group parameter, but this model received little relative support ($\Delta QAIC_c = 8.22$). A similar model excluding the group parameter, the strata-only model ($S(\cdot) \psi_{Strata}$), was ~66 times more plausible (Table 3).

Bobwhites moving off the core area (stratum A) tended to stay on the managed property (stratum B; $\psi_{A:B} = 0.06$) rather than dispersing off the property (stratum C; $\psi_{A:C} = 0.003$). Site fidelity of translocated individuals ($\psi_{A:A} = 0.934$) to the core area was similar to that of resident bobwhites ($\psi_{A:A} = 0.954$). Additionally, some individuals leaving the core area or dispersing off-site during one time interval returned to the study site upon subsequent intervals (Table 1).

Distances moved from the trap or release sites to the arithmetic center (A_c) of individual home ranges did not vary among translocated and resident bobwhites or among males or females (Fig. 3) within years; however, mean distance moved from release and trap sites was greater during 2004 than 2003 (Fig. 3). Most bobwhites (>60%) moved <500 m from their trap or release sites, but >15% of all translocated individuals moved >1000 m from their release site, compared to <8% of resident bobwhites moving this same distance (Fig. 4). Overall, movement (dispersal) did not differ among males and females (Figs. 3–5). Evaluation of mean minimum daily (MMD) movements revealed that larger daily movements occurred early in the breeding season (in March and early April) and immediately following release, but movement distance generally stabilized and fluctuated around 50 m for the duration of the season (Fig. 5).

DISCUSSION

Survival

Evaluation of hypotheses relative to group and gender indicate that their effects on survival were negligible, which was in accord with our a priori predictions. Survival estimates for translocated and resident bob-

TABLE 3. Model selection results for the estimation of Northern Bobwhite movement and stratum-specific survival (S) for radio-tagged individuals on Buck Creek Plantation, Marion County, Georgia, 2003–2004.

Model	Qdeviance	K	QAIC _c	ΔQAIC _c	w _i
S(·) ψ_{strata}	2189.126	7	2203.244	0.000	0.534
S(Strata) ψ_{strata}	2185.404	9	2203.595	0.351	0.448
S(·) $\psi_{strata+group}$	2183.018	14	2211.465	8.221	0.009
S(· + Group) $\psi_{strata+group}$	2185.767	13	2212.154	8.910	0.006
S(Strata + Group) $\psi_{strata+group}$	2181.268	17	2215.922	12.678	0.001
S(Group) $\psi_{strata+age}$	2181.480	17	2216.133	12.889	0.001
S(Group) $\psi_{strata+gender}$	2181.524	17	2216.178	12.934	0.001
S(Group) $\psi_{strata-group+age}$	2175.480	22	2218.471	15.227	0.000
S(Group) $\psi_{strata-group+gender}$	2173.820	22	2218.901	15.663	0.000

Notes: Model statistics are as defined in Table 1; ψ represents probability of movement (transition).

TABLE 4. Home range size calculated by minimum convex polygon (MCP) and kernel methods for Northern Bobwhites on Buck Creek Plantation, Marion County, Georgia, 2003–2004.

Year	Group	<i>n</i>	Locations, $\bar{x} \pm SD$	95% MCP (ha)	100% MCP (ha)	50% kernel (ha)	95% kernel (ha)
2003	Resident	46	43 \pm 25	22.635 (4.204)	33.503 (4.861)	5.338 (0.346)	23.661 (1.450)
	Translocated	42	45 \pm 23	18.889 (3.924)	25.376 (4.298)	4.151 (0.332)	18.623 (1.300)
2004	Resident	27	29 \pm 24	9.812 (1.098)	13.623 (1.560)	4.243 (0.281)	17.913 (1.050)
	Translocated	30	38 \pm 16	13.144 (3.404)	15.712 (3.724)	3.791 (0.282)	16.533 (1.050)
Pooled	Resident	73	37 \pm 21	17.892 (2.766)	26.150 (3.303)	4.933 (0.248)	21.535 (1.040)
	Translocated	72	42 \pm 18	16.495 (2.697)	21.349 (2.984)	4.001 (0.226)	17.752 (0.878)

Notes: Sample size (*n*) is the number of individuals; also shown is the number of telemetry locations per individual (mean \pm SD). Home range MCP and kernel estimates are means with SE in parentheses.

whites were similar during both years of this study; similar to those reported for other translocation studies (DeVos and Mueller 1989, Lui et al. 2000); and higher than those reported by Terhune et al. (2006), whose techniques were congruent with ours. Additionally, breeding season survival of translocated individuals was similar to estimates reported for long-term mark-recapture studies in which subsequent population levels remained stable to increasing (Palmer and Wellendorf 2007, Terhune et al. 2007). Variation in survival was best explained temporally with an additive effect of age. Although translocated adults tended to have higher survival than juveniles, suggesting a biological difference (>12%), the effect size did not substantiate this difference. However, small sample size, particularly among adults, and resulting standard errors may have

precluded the detection of a difference in our data. The source of translocated birds did not adequately explain additional variation in survival, despite one site (source site 3) having relatively high survival (>50%) when compared to the other two source sites (31% and 38%) and resident (37%) bobwhites. Notably, all three source sites were agricultural sites with similar management regimes and were located adjacent to extensively managed properties focused on benefiting bobwhites.

Using multi-strata analysis, we assessed differences in stratum-specific survival in addition to movement and site fidelity. Although we did not detect differences among strata, models including strata received substantial support. Whereas the difference in survival for

TABLE 5. Movement probability estimates derived from multi-strata model analyses using program MARK for translocated and resident Northern Bobwhites on Buck Creek Plantation, Marion County, Georgia, 2003–2004.

Movement direction	Estimate	SE	95% CI
Translocated			
$\psi_{A:A}$	0.9338	0.0177	0.8894–0.9611
$\psi_{A:B}$	0.0632	0.0174	0.0364–0.1072
$\psi_{A:C}$	0.0030	0.0016	0.0054–0.0116
$\psi_{B:A}$	0.0207	0.0215	0.0026–0.1446
$\psi_{B:B}$	0.9590	0.0298	0.8411–0.9904
$\psi_{B:C}$	0.0202	0.0208	0.0025–0.1400
$\psi_{C:A}$	0.0000		
$\psi_{C:B}$	0.0600	0.0352	0.0184–0.1783
$\psi_{C:C}$	0.9400	0.0426	0.8565–1.0000
Resident			
$\psi_{A:A}$	0.9540	0.0001	0.9537–0.9542
$\psi_{A:B}$	0.0460	0.0001	0.0457–0.0462
$\psi_{A:C}$	0.0000		
$\psi_{B:A}$	0.0228	0.0237	0.0029–0.1575
$\psi_{B:B}$	0.9546	0.0329	0.8259–0.9893
$\psi_{B:C}$	0.0226	0.0156	0.0049–0.0863
$\psi_{C:A}$	0.0000		
$\psi_{C:B}$	0.0500	0.0361	0.0117–0.1895
$\psi_{C:C}$	0.9500	0.0632	0.8261–1.0000

Notes: In the first column, ψ is the probability of movement (transition) between observation strata defined as: stratum A, target release site (core area); stratum B, off the target area but still within the managed study site; and stratum C, completely off the study site. For example, subscript A:B represents movement from A to B; A:A represents birds remaining in A.

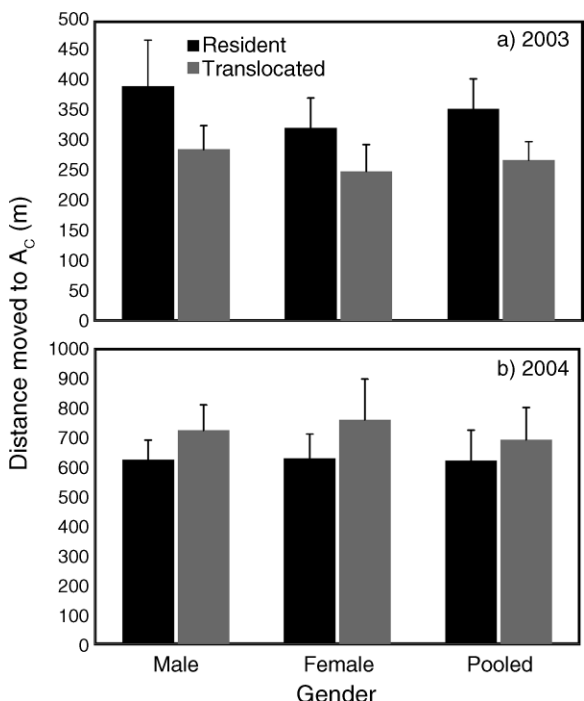


FIG. 3. Male and female mean distances moved (error bars represent 95% CIs) from release or trap site to the arithmetic center (A_C) of breeding-season home ranges for translocated and resident Northern Bobwhites located on Buck Creek Plantation, Marion County, Georgia, during 2003 and 2004.

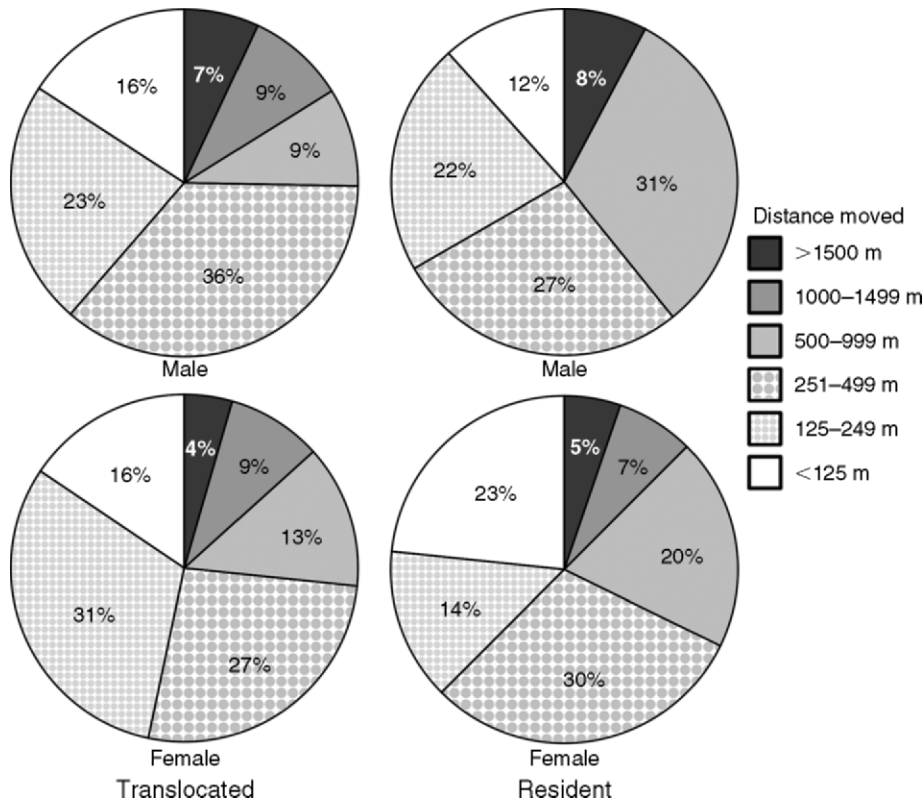


FIG. 4. Percentage of all individuals within a defined group (resident vs. translocated, by gender) for Northern Bobwhites located on Buck Creek Plantation, Marion County, Georgia, during 2003–2004. Movement is based on the distance a bird moved from release or trap sites to the arithmetic center (A_C) of its individual home range during the breeding season.

stratum A (core area) and B (periphery area) was only about 6% and that for strata B and C (off the study site) was about 8.5%, the difference in survival between strata A and C was approximately twice as large ($>14\%$). In general, stratum-specific survival declined as individuals moved away from the target release area. This declining gradient may be indicative of declining habitat quality. Intensive habitat management on the property occurred on the core area (stratum A) area, prior to the onset of the study, for seven years, in contrast to four years of management on the periphery area (stratum B); no management occurred off the study site (stratum C). Models including stratum-specific group effects did not receive substantial weight, suggesting that survival between translocated and resident bobwhites was not different, regardless of strata location. Despite the small number of individuals dispersing completely off the study site, probability of mortality increased substantially for individuals leaving the managed property. These results underscore the importance of habitat management in bobwhite survival, and they further corroborate the findings of previous research (Stoddard 1931, Klimstra 1972, Roseberry and Klimstra 1984, Landers and Mueller 1986, Sisson et al. 2009). Therefore, habitat management on recipient sites should

be a prerequisite for translocation to ensure adequate vegetative cover and to optimize the probability of survival for released individuals.

Home range, movement, and site fidelity

Differences in home range size between translocated and resident bobwhites were inconsequential; however, home range sizes during 2003 were generally larger than during 2004. Urban (1972) posited that habitat largely influences bobwhite mobility during the breeding season. Thus, the disparity observed in home range size may have been a result of either limited food resources or differences in habitat structure between years (Landers and Mueller 1986, Sisson et al. 2000). Anecdotal observations of reduced brood-field quality during 2003 suggested low productivity. Similarly, brood-field use during 2003 was considerably lower than in 2004. Food resources were more abundant during 2004 than 2003, due to consistent application of supplemental feed.

Breeding season dispersal is commonly reported among bobwhites, is generally considered an innate behavior, and is an important process from both an ecological and evolutionary perspective (Howard 1960, Clobert et al. 2001). Furthermore, movement probabil-

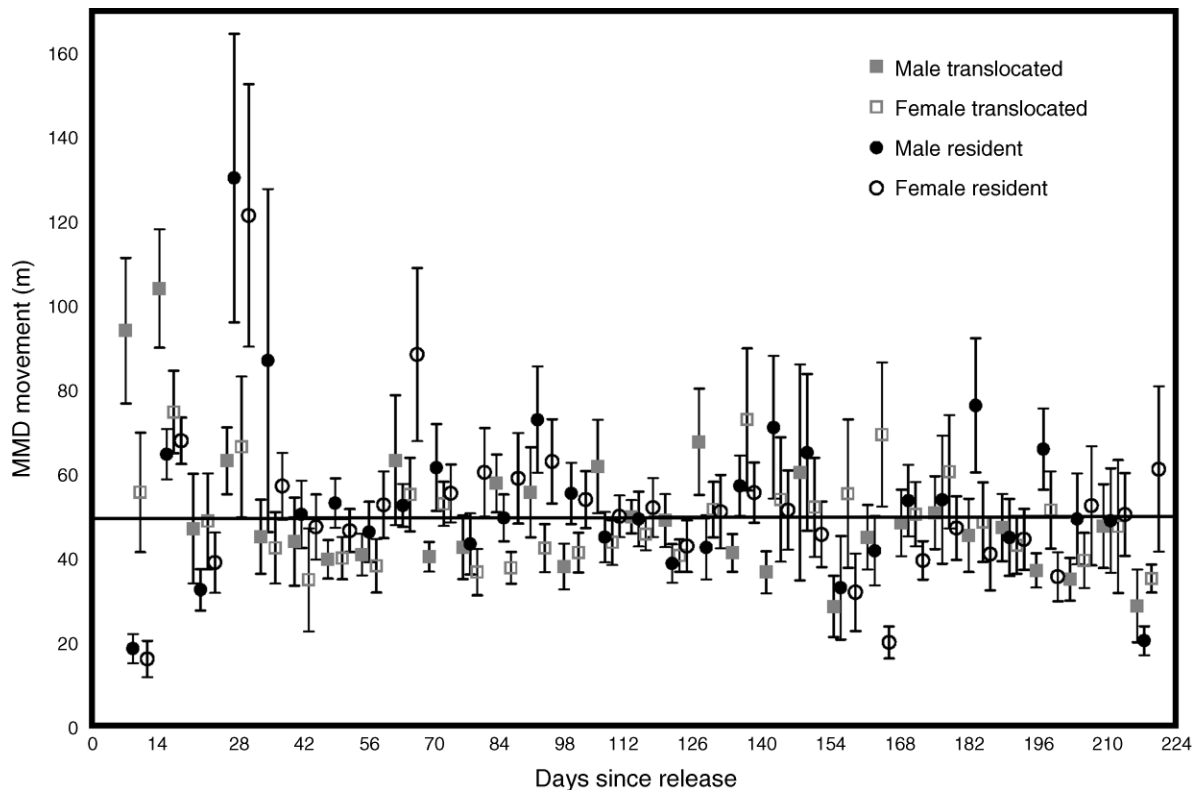


FIG. 5. Weekly mean minimum daily (MMD) movements (error bars represent 95% CI) delineated by gender for translocated and resident Northern Bobwhites located in Marion County, Georgia, during 2003–2004. The solid horizontal line represents the pooled MMD.

ities are useful for guiding management and conservation strategies (Spendelov et al. 1995). However, few studies have examined dispersal of bobwhites following translocation (Lui et al. 2002, Terhune et al. 2005). We evaluated dispersal and site fidelity using two metrics: (1) distance moved from the trap or release site to the arithmetic mean center (A_c) of individual home ranges and (2) estimation of transition probabilities using multi-strata models. Interestingly, distances moved from the release and trap sites to the A_c were lower in 2003 compared to 2004, in contrast to larger home ranges observed during 2003 relative to 2004. A_c distances for both groups in our study were considerably larger than those in other studies (Terhune et al. 2005). This may be attributable to different habitat characteristics among years (Urban 1972) or the presence and abundance of conspecifics, whereby individuals located on low-density sites would ostensibly be required to traverse greater distances to search and find suitable mates (Errington 1945, Urban 1972, Roseberry and Klimstra 1984, Townsend et al. 2003). Bobwhite densities reported by Terhune et al. (2005) were ≥ 3.71 birds/ha, whereas density in the present study was ≤ 1.24 birds/ha. However, more research is warranted to investigate the potential effects, if any, that density dependence and presence of conspecifics have on the efficacy of

translocation and movements of translocated individuals to sites of varying population densities.

Ecological advantages of site familiarity may influence site fidelity (Lande 1988, Clobert et al. 2001) and the overall success of translocation because translocated individuals would, in theory, be at a disadvantage compared to resident individuals. Site fidelity of translocated bobwhites to the core release area was moderately lower than that of resident bobwhites, but a majority of the individuals dispersing off the core area remained on the managed property. Less than 2% of all bobwhites (2.4% of translocated) permanently dispersed completely off the study site (i.e., >98% site fidelity). We did, however, lose radio contact with some individuals, and it is possible that these individuals dispersed off the study site. Approximately 16% of translocated individuals dispersed off the core area, compared to 8.5% of resident bobwhites. To have ensured 100% site fidelity of translocated bobwhites in this study, the property size would have had to be 1256 ha.

Although MMD distances moved were not different among groups or years, bobwhites exhibited larger MMD movements early in the breeding season. In particular, male translocated bobwhites had larger movements during the first two weeks post-release compared to their resident counterparts, and both male

and female resident bobwhites moved greater distances during weeks 4 and 5 post-capture (last week in April and first week in May). Larger movements observed early in the breeding season may have been a result of male-biased dispersal (Hood 1955, Smith et al. 1982) of translocated individuals following release; alternatively, this increased movement may be related to the natural behavior associated with covey breakup (Yoho and Dimmick 1972, Church and Taylor 1992, Roseberry 1993). Increased mobility during the early breeding season may be best explained by the natural tendency of individuals to search for mates or suitable nest sites (Townsend et al. 2003). Previous research suggests that increased movement negatively impacts survival (Cook 2004, Folk 2006); however, inclusion of movement in our survival analyses did not explain additional variation in survival. Stratum-specific and temporal effects were better explanatory variables. In our study, movements were generally smaller than those reported in other studies (Cook 2004, Folk 2006), but it is a well-accepted tenet that mobility of bobwhites is typically dictated by habitat quality and degree of fragmentation (Kabat and Thompson 1963, Fies et al. 2002, Townsend et al. 2003, Cook 2004). Intensive habitat management occurred for more than 4 years on our study site prior to translocation; thus an obvious, but important, consideration prior to instituting translocation is an assessment of habitat quality and subsequent implementation of habitat management where necessary.

Conservation implications

Conservation and management decisions should be driven by current and sound research. Translocation has become a common management tool in wildlife conservation for establishing, reestablishing, or augmenting existing populations (Griffith et al. 1989), but many translocations and reintroductions implemented to date have lacked scientific rigor (Seddon et al. 2007). Thus, improper study designs and the lack of sufficient empirical data collected have limited our ability to make valid inference for refining protocols and guiding conservation and management strategies.

The ultimate goal of translocation is to increase population abundance and reduce the risk of local population extinction; its efficacy is predicated on site fidelity and survival of the individuals being released to confer genetic and demographic benefits. In this study, we did not detect differences in survival or movement (dispersal) among translocated and resident bobwhites, supplanting the notion that translocation negatively influences survival and movement. In addition, salient stratum-specific survival estimates relative to managed and unmanaged habitat advocated the importance of quality habitat not only to the success of translocation, but also for population persistence. Taken collectively, both variation in survival and movement following release are probably better explained by site-specific

habitat conditions than by mechanisms germane to translocation of individuals.

Translocation is not a panacea for preservation or broadscale restoration of bobwhites and should not, by any means, be viewed as a substitute to habitat management or even a common management practice. Translocation, however, should remain a pragmatic conservation option instituted on a site-by-site basis, and decisions governing its implementation should take into account knowledge of the species' life history and ecology. This approach would ideally increase the efficacy of translocation and help to guide its role in conservation planning and management for the species of concern. Results from this study are directly applicable to bobwhites, but also may apply broadly to grassland obligate birds with limited mobility, e.g., Red-cockaded Woodpecker *Picoides borealis* (Carrie et al. 1999); Brown-headed Nuthatch *Sitta pusilla*, Henslow's Sparrow *Ammodramus henslowii*, and Bachman's Sparrow *Aimophila aestivalis* (J. Cox, unpublished data). This study augments our knowledge of translocation and helps to refine the translocation process as to the appropriate spatiotemporal scale for its successful application.

We believe that four primary mechanisms contributed to the success of translocation: (1) large target release area; (2) quality habitat on the release site; (3) an available source of wild bobwhites; and (4) timing of release. We propose that conservation strategies should primarily focus on habitat restoration and improvement, employing translocation only as a means to complement this strategy. As such, translocating individuals to establish or augment populations on areas where habitat has been recently restored and that have the potential to become source populations or connect disjunct and fragmented habitats would then optimize conservation of the species. Given adequate habitat management and a valid source of wild bobwhites, we also recommend translocating individuals 3–4 weeks prior (during March) to the breeding season to provide ample time to acclimate to their new surroundings, but not longer than 3–4 weeks prior to breeding season to reduce mortality, as observed during this study (Terhune et al. 2006). Because we did not experimentally investigate the time of release on the success of translocation, we cannot unequivocally relegate the benefit of translocation occurring during other periods (i.e., fall). Finally, we recommend (based on movement and dispersal data in this study) that release sites be as large as possible, but minimally should be ≥ 600 ha to reduce dispersal from managed habitat.

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