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Effects of Sex, Age, and Habitat on Northern Bobwhite Spring Dispersal Patterns

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Information on northern bobwhite (*Colinus virginianus*) dispersal patterns is crucial for implementing effective management strategies. Researchers have examined bobwhite dispersal, but information on how habitat affects dispersal patterns is lacking. We examined the effects of habitat, sex, and age on bobwhite spring dispersal patterns in a southern Georgia agricultural landscape during 2002-2003. Of 101 birds used in our analyses, 29.7% (4.6 SE) dispersed an average of 1,835m (194 SE). We fit 9 logistic regression models to predict bobwhite dispersal probability. The selected best model (Akaike weight $[\omega]$ = 0.58) included age, proportions of closed-canopy pine within winter home ranges (CCPN), and an age*CCPN interaction term. Adults with higher proportions of closed-canopy pine within their winter home range were more likely to disperse (β = 0.18, 0.06 SE). Because of greater experience, adults may perceive habitat differently than juveniles, which could influence adult tendency to disperse. However, a significant portion of birds from both age classes will likely disperse every spring, regardless of habitat quality. Although dispersal may allow bobwhite populations to persist in fragmented landscapes, efforts to increase bobwhite populations at the local scale are hindered if emigration exceeds immigration. Therefore, it is important to consider landscape quality and management unit size when determining which areas are most likely to respond to management and the proper management strategy needed to achieve bobwhite population objectives.

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Key words: age, closed-canopy pine, *Colinus virginianus*, dispersal, Georgia, habitat, metapopulation, northern bobwhite, scale, sex

Introduction

Information on northern bobwhite dispersal patterns is crucial for implementing effective management strategies. Site-specific management will always be an important component of any effort to increase bobwhite populations, but management strategies aimed at increasing bobwhite populations on a regional scale must consider landscape level aspects of bobwhite ecology in order to be effective (Brady et al. 1993, Roseberry 1993, Burger 2002, Fies et al. 2002). Areas on the landscape with the greatest potential to respond positively to management need to be identified so that management efforts can be implemented in an efficient and effective manner (Roseberry and Sudkamp 1998, Schairer et al. 1999). Most of the landscapes in which bobwhites exist are highly fragmented; therefore, an understanding of the role of metapopulation processes in regulating regional populations is critical for management programs designed to increase bobwhite populations. The development of spatially explicit population models has been advocated (Burger 2002, Fies et al. 2002) and may be particularly valuable because these models allow managers to predict the possible effects of large-scale management strategies (Conroy et al. 1995, Dunning et al. 1995). All of these endeavors will require information on dispersal rates and distances and how factors such as sex, age and habitat affect these parameters. Dispersal information would also be useful for site-specific management. Knowledge of immigration/emigration ratios for management units and how these ratios may be affected by management unit size and the surrounding landscape will be useful in predicting population response to different management strategies. It

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would be particularly useful to know if and to what degree emigration would decrease as habitat quantity/quality changed on a management unit.

Several studies have examined bobwhite mobility/dispersal (e.g., Stoddard 1931, Duck 1943, Loveless 1958, Kabat and Thompson 1963, Urban 1972, Smith et al. 1982, Fies et al. 2002, Townsend et al. 2003, Terhune et al. 2006). However, most of the early efforts relied on recoveries of leg-banded individuals. Large sample sizes are required to estimate dispersal distances using these techniques (Paradis et al. 1999). Also, these studies likely underestimated dispersal distances because detection probabilities (recovery rates) generally decline with increasing dispersal distance (Koenig et al. 1996). Radio-telemetry provides an opportunity to more accurately detect dispersal and estimate dispersal distances. However, many telemetry studies also likely underestimate dispersal distances because birds that leave the study area are often censored from analysis. Recent studies of bobwhite dispersal (Fies et al. 2002, Townsend et al. 2003) have produced more accurate estimates of dispersal distances and rates because they were conducted using radio-telemetry without study area boundary constraints. However, these studies did not examine the effect of habitat on dispersal patterns. The effects of habitat configuration and composition on bobwhite dispersal patterns may have profound management consequences.

We quantified bobwhite spring dispersal (rate and distance) and examined the effects of sex, age, and habitat on spring dispersal. Although bobwhites may move long distances during any time of the year, most dispersal events occur in the spring prior to the breeding season (Fies et al. 2002, Townsend et al. 2003, Folk 2006). We defined spring dispersal as a permanent movement from a winter range to a breeding range.

Study Area

We conducted this study on a 133 km^2 area in western Laurens County, Georgia. This fragmented landscape, typical of the modern southeastern USA, was comprised of row-crops (13%), pasture/hayfields (12%), closed canopy pine plantations (23%), hardwoods/mixed stands (33%), and early successional habitat (10%). Most crop fields were planted in cotton (*Gossypium hirsutum*), but some were planted in peanuts (*Archis hypogaea*), corn (*Zea mays*), or soybeans (*Glycine max*). A few fields were planted in winter wheat (*Triticum aestivum*) or rye (*Secale cereale*). Pastures and hayfields were dominated by bermudagrass (*Cynodon dactylon*) and/or bahiagrass (*Paspalum notatum*). Closed-canopy pine plantations were planted stands of either loblolly (*Pinus taeda*) or slash pine (*P. elliotii*) that had reached canopy closure and had little to no vegetation in the understory. Areas classified as early successional were dominated by weeds and/or short brush. These included abandoned fields, herbaceous strip-cover that either bordered or passed through the interior of crop fields (habitats provided by the Georgia Bobwhite Quail Initiative, Georgia Department of Natural Resources 1999), planted pines / clearcuts that had not reached canopy closure, hedgerows, and fencerows. We created a computerized (vector) habitat map of the study area by referencing U.S. Geological Survey 1993 Digital Orthophoto Quarter Quadrangles (DOQQ) in ArcView® (Environmental Systems Research Institute, Inc., Redlands, California). Although the photographs were 10-years old, we verified land cover types through infield ground truthing using Global Positioning System equipment.

Methods

We captured bobwhites during January 2002-April 2002 and November 2002-April 2003 using wire walk-in funnel traps (Stoddard 1931) baited with cracked corn. Captured bobwhites weighing >140g were banded, equipped with a 6.4-6.9 g pendant-style (necklace) radiotransmitter and released at the trap site. We determined sex and age (juvenile and adult) using techniques of Rosene (1969). All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on

Table 1: Spring dispersal rates and distances for 101 radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

		Dispersal Rate (%)			Dispersal Distance (m)		
		n	Rate	SE	n	Mean	SE
Female	Juvenile	35	25.7	7.5	9	2,184	341
	Adult	15	26.7	11.8	4	2,150	790
	Pooled	50	26	6.3	13	2,173	319
Male	Juvenile	35	34.3	8.1	12	1,339	203
	Adult	16	31.3	12	5	2,146	575
	Pooled	51	33.3	6.7	17	1,576	230
Pooled	Juvenile	70	30	5.5	21	1,701	204
	Adult	31	29	8.3	9	2,148	442
	Pooled	101	29.7	4.6	30	1,835	194

the Use of Wild Birds in Research (American Ornithologists' Union 1988) and those of the University of Georgia, Institutional Animal Care and Use Committee (IACUC Protocol No. A2003-10109-0).

We located bobwhites 4-7 times per week during the breeding season (15 April-15 September) by homing (White and Garrott 1990) to within 25-50 m. Locations prior to the breeding season were obtained 3-5 times per week. When radio contact was lost, we systematically searched from vehicles for lost birds within 5 km of their last known location. We plotted locations onto aerial photos and later transferred to a Geographic Information System format using ArcView®.

We detected spring dispersal using the vectored dispersal detection technique (Kenward 2001) in RANGES V (Kenward and Hodder 1996). This technique tests if n new locations are outside the distribution of all previous N locations in a single direction. The detector begins by calculating the arithmetic mean center (Ac) of the first N = 3 locations and buffers this center by the upper confidence limit of distances of points to the Ac for a selected α level (we used α = 0.05). It then calculates the Ac of the next n = 3 locations and constructs a line (vector) through the two Ac points. If all of the orthogonal distances of the n points along the vector are outside of the confidence limit of the first N locations, then dispersal is flagged. If not, N incrementally increases by 1 and the routine begins again. We considered the first n location that was part of a set of n = 3 locations where dispersal was flagged to be the first date of dispersal. To determine when dispersal ended, we treated the last breeding season location as the first winter location (and *vice versa*) and considered the n that was part of a set of n = 3 where dispersal was flagged to be the last date of dispersal. Dispersal was not detected "in reverse" for a few dispersers. This was likely due to the fact that the distances of breeding season locations to their Ac were generally much greater than the distances of winter locations to their Ac. When this occurred, dispersal locations were considered to be part of the breeding season location set. Dispersal distance was determined by measuring the distance between the Ac of winter locations and the Ac of breeding season locations for each disperser.

We employed several additional decision rules

Table 2: Ranking of candidate models used to predict spring dispersal of radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

Model	K[a]	**Log Likelihood**	QAICc[b]	**Δ QAICc**	**Akaike Weight**
Age + CCPN[c] + Age*CCPN	4	-56.64	113.72	0.00	0.58
Null Model	1	-61.44	116.72	2.56	0.16
Sex	2	-61.12	117.75	4.03	0.08
Age	2	-61.44	118.35	4.63	0.06
Age + ERSC[d] + Age*ERSC	4	-59.62	119.27	5.55	0.04
CCPN + ERSC	3	-60.79	119.28	5.56	0.04
Sex + Age	3	-61.11	119.86	6.15	0.03
Global Model	8	-55.61	120.13	6.41	0.02
Sex + Age + Sex*Age	4	-61.09	122.00	8.28	0.01

[a] Number of parameters included in models. All models include an intercept, [b] Akaike Information Criterion adjusted for overdispersion and small sample size, [c] CCPN = proportion of closed-canopy pine within the winter home range, [d] ERSC = proportion of early successional habitat within the winter home range.

and techniques in our dispersal analysis. Whenever dispersal was detected, we calculated the Ac for all pre-dispersal (winter) locations and the Ac for all post-dispersal (breeding season) locations and buffered the centers by their respective 95% confidence limits. If the circles overlapped or if any post-dispersal location was within the pre-dispersal confidence limit circle, dispersal was rejected because we wished to adhere to the unidirectional definition of dispersal. The possibility of dispersal being detected on that particular set of n locations was then eliminated by setting a minimum distance to winter trap site for dispersal to be detected that was greater than the distance of the first n location to the trap site and the routine was repeated. Bobwhites trapped after 30 March (three days before the earliest recorded dispersal date, 2 April) were excluded from analysis because they could have already dispersed. Of the bobwhites not classified as dispersers, those that died or were censored prior to 19 May (the latest recorded date of dispersal) were excluded from analysis because they may not have had an opportunity to disperse. Of the bobwhites classified as dispersers, those that died before 16 days (the greatest number of days recorded between the initial date of an erroneous dispersal detection and a subsequent return) had elapsed since the initial dispersal date were also excluded from analysis because these birds may not have had time to return. Bobwhites are known to make long distance movements following nest failure (Urban 1972, Fies et al. 2002). We did not consider these to be dispersal events because those birds were already on their breeding range. To minimize the possibility of detecting these movements as dispersal events, dispersal detected after 19 May (the earliest recorded date of nest incubation) was not considered to be dispersal.

We used the animal movements extension (Hooge and Eichenlaub 1997) designed for ArcView® to calculate fixed kernel winter home ranges (Worton 1989) with a 95% isopleth requiring ≥20 locations to calculate home ranges. For bobwhites that dispersed, we only used pre-dispersal locations. For non-dispersers, we used locations collected before 15 April. We estimated ”pseudo home ranges” for birds with less than 20 winter locations by calculating the Ac for the locations that we did have and then buffering this point to create a 14.52

ha (average winter home range size) circle. We intersected home ranges with the habitat map of the study area using the ArcView® Geoprocessing Wizard to determine the proportions of home ranges composed of different habitat types.

We examined the effects of several covariates on spring dispersal probability using an information-theoretic approach. We developed an *a priori* set of 9 candidate models, based on literature review, our knowledge of bobwhite biology, and field observations. The model set included the effects of sex (coded Female = 0, Male = 1), age (Juvenile = 0, Adult = 1), proportions of closed-canopy pine plantations (CCPN) and early successional habitat (ERSC) within the winter home range, a sex*age interaction term, and terms for interactions between age and habitat covariates. We considered ERSC to be the most beneficial habitat and CCPN to be the most deleterious habitat for bobwhites in the landscape in which we were working (Lewis 1999, Parnell 2002, Cook 2004). Other habitat types were not considered because we viewed CCPN and ERSC as most likely to affect dispersal probability and we wished to minimize the number of models, thereby reducing the possibility of spurious results (Anderson and Burnham 2002). We included interactions between age and habitat because adults may perceive habitat quality differently due to their greater experience. We also included a null (intercept only) model in the candidate set. We used logistic regression (SAS PROC LOGISTIC; SAS Institute, Inc. 2002) to produce likelihood and parameter estimates for each model. We then calculated QAIC$_c$ (AIC corrected for small sample sizes and overdispersion) values and QAIC$_c$ weights for each model (Burnham and Anderson 2002). We assessed model fit using the Hosmer and Lemeshow (1989) goodness-of-fit statistic ($\hat{C}$).

We plotted model predicted dispersal probabilities with 95% confidence intervals over the range of habitat levels observed in the data for each age to evaluate the relationship of predicted dispersal probability over the range of our data. Model predicted dispersal probabilities were calculated using:

$$\text{Dispersal probability} = e^{ln(\hat{\pi})}/(1 + e^{ln(\hat{\pi})}),$$

where $\hat{\pi}$ is the model estimated logit.

Results

We radio-tagged 202 bobwhites from 39 coveys. We used 101 bobwhites in our dispersal analysis. Of these, 29.7% (4.6 SE) were classified as dispersers and mean dispersal distance was 1,835 m (194 SE) (Table 1). We excluded 8 birds from analysis because they were trapped after 30 March. We excluded 2 because they were classified as dispersers, but died before 16 days had elapsed since the initial dispersal date. We excluded 91 because they died or were censored prior to 19 May. Of these, 4 were censored during the dispersal period because radio contact was lost and not regained. Although transmitter failure could have caused the loss of radio contact, we may have been unable to find these birds because they dispersed beyond our search area. Therefore, we may have underestimated the dispersal rate and mean dispersal distance. If we did underestimate, we think that the underestimation was slight because only 4 birds were censored during this period. The selected best model ($\omega = 0.58$) for predicting spring dispersal included age, CCPN, and an age*CCPN interaction term (Table 2). This model fit the data ($\hat{C} = 0.15$). Age interacted with within winter home range proportions of CCPN ($\beta = 0.18$, 0.06 SE; Table 3). The null model was the next best model ($\omega = 0.16$). All other models performed poorly, ranking lower than the null model. Over the range of proportions of CCPN within winter home ranges (0-28%), predicted adult dispersal probability increased as the proportion of CCPN within the winter home range increased (Figure 1). Conversely, predicted juvenile dispersal probability decreased as the proportion of CCPN within the winter home range increased (Figure 2). However, confidence intervals for predicted dispersal probabilities were quite large for both age classes.

Discussion

Our results suggest that habitat may affect dispersal rates and this effect may vary by age. The

Table 3: Logistic regression parameter estimates of the selected best model (Age + CCPN + Age*CCPN) for predicting spring dispersal of radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

Parameter	**Coefficient**	**SE**	**LCI**[a]	**UCI**[b]
Intercept	-0.51	0.3	-1.1	0.07
Age	-1.14	0.66	-2.43	0.14
CCPN	-0.08	0.05	-0.18	0.01
Age*CCPN	0.18	0.06	0.05	0.3

[a] Lower 95% C.I. limit, [b] Upper 95% C.I. limit.

selected best model indicated that dispersal probability varied according to an interaction between age and proportions of closed-canopy pine within winter home ranges. Adults with greater proportions of closed-canopy pine within their winter home range were more likely to disperse. Because of greater experience, adults may perceive habitat differently from juveniles, which could influence adult tendency to disperse. Surprisingly, model predictions suggested that juvenile dispersal probability may decrease with increasing proportions of within winter home range closed canopy pine. Juveniles could perceive closed-canopy pine as quality woody cover. There is evidence that closed-canopy pine plantations are especially deleterious to bobwhite survival (Parnell 2002, Cook 2004); therefore, they may serve as an ecological trap to juveniles. However, we suggest that predictions based on this model be interpreted cautiously. We did not test this model with independent data. Although the age*CCPN interaction was statistically significant, confidence intervals for predicted dispersal probabilities were quite broad; therefore, the magnitude of the effect remains uncertain. Because of this and the apparently negligible effect of early successional habitat on dispersal probability, it is likely that a significant portion of birds from both age classes could disperse every spring, regardless of habitat quality. However, only 16% of birds in this study had winter home ranges comprised of >50% early successional habitat (range 2-82%). At higher proportions, early successional habitat may have a greater effect on dispersal probability. Although this is the first study to report an age-habitat interaction effect on bobwhite dispersal probability, other researchers have suggested that habitat affects bobwhite dispersal patterns. Urban (1972) reported that sizeable weed areas within winter home ranges tended to prevent bobwhites from shifting their home ranges. Duck (1943) attributed a shift from fall to winter ranges by bobwhites to a change in habitat preference. Of course, differences in matrix habitat may affect dispersal distances as well (Turner et al. 2001, pg. 220). Puckett et al. (1995) reported that distances from capture site to first nest for bobwhites were over four times greater on areas without herbaceous filter strips (beneficial habitats) versus areas with them. Fies et al. (2002) proposed an inverse relationship between dispersal distances of bobwhites and inter-patch connectivity which is supported by reports that mobility is lower on areas managed intensively for bobwhites (Loveless 1958, Smith et al. 1982, Terhune et al. 2006) and greater on areas containing marginal habitat (Kabat and Thompson 1963, Fies et al. 2002, this study). The effect of habitat on bobwhite dispersal probability may not be responsible for lower mobility on managed areas. We detected little effect of early successional habitat on dispersal probability. Perhaps bobwhites disperse in all landscapes, but dispersal distances vary according to inter-patch connectivity.

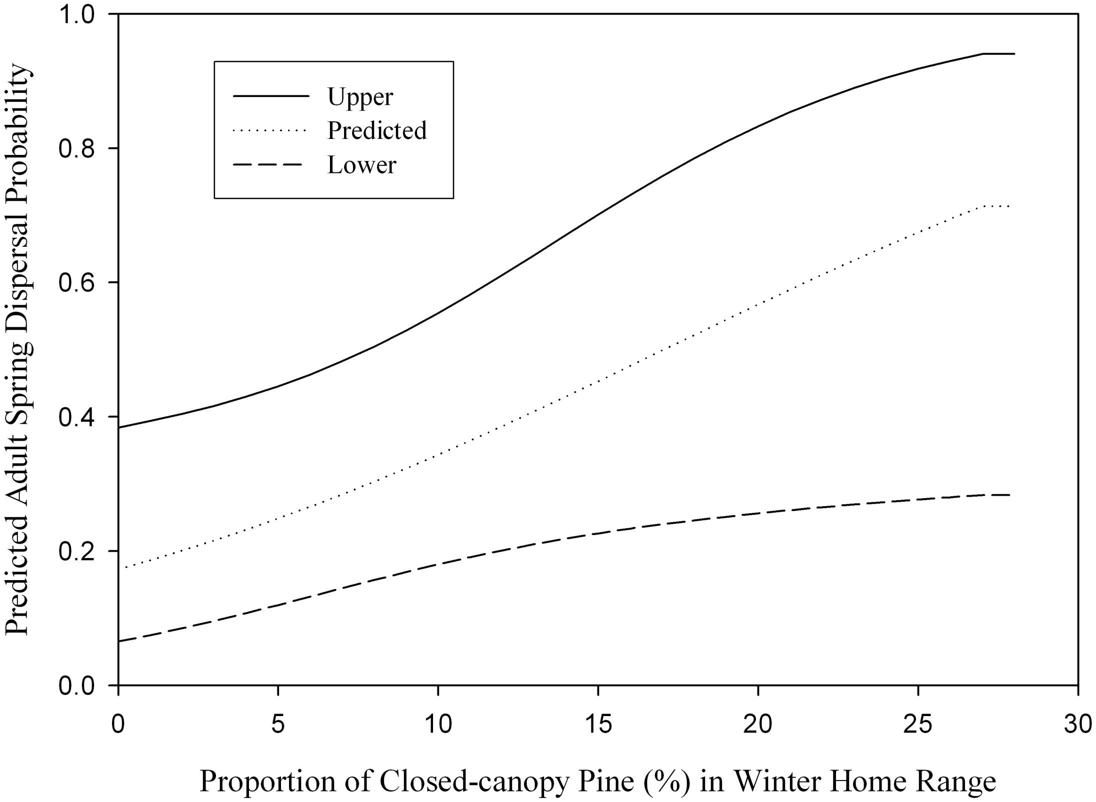

Figure 1: Predicted spring dispersal probability for adult bobwhites with 95% confidence intervals based on the selected best logistic regression model (Age + CCPN + Age*CCPN) for predicting spring dispersal of radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

Dispersers may be exposed to greater predation risk due to increased movement (Ambrose 1972, Smith 1974) and because dispersers inhabit space where they are unfamiliar with cover and food resources (Clark et al. 1993, Jacquot and Solomon 1997, Yoder et al. 2005). Researchers have reported that survival rates of dispersed bobwhites are either identical to or even greater than that of non-dispersed bobwhites (Townsend et al. 2003, Cook 2004, Mike Fies, Virginia Dept. of Game and Inland Fisheries, unpublished data). However, mortality that occurs during dispersal (transience) has yet to be examined. Dispersers may experience increased mortality during transience, especially in a hostile landscape matrix (Fahrig 2001). Examining the effect of daily movement rate on bobwhite survival, Folk (2006) reported that individuals that moved >890m in a day were twice as likely to be killed as birds that did not move at all. Although not directly measured in that study, the finding does suggest that bobwhite transience survival may be quite low in some landscapes. More research is needed to determine bobwhite mortality during transience and how this may be affected by matrix habitat composition and configuration.

Management Implications

Although dispersal may allow bobwhite populations to persist in fragmented landscapes, efforts to increase populations at the local scale (e.g. public wildlife management areas) are hindered if emigration greatly exceeds immigration. Our results suggest that habitat features may influence dispersal probability. However, the magnitude of the ef-

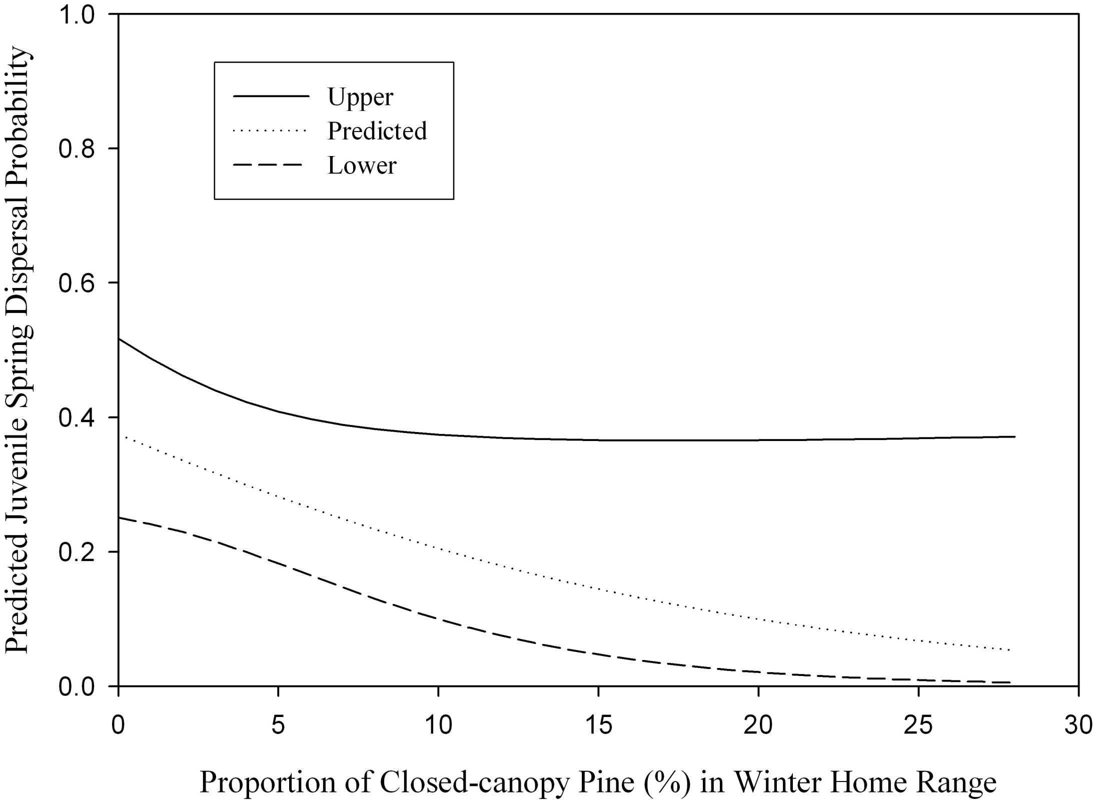

Figure 2: Predicted spring dispersal probability for juvenile bobwhites with 95% confidence intervals based on the selected best logistic regression model (Age + CCPN + Age*CCPN) for predicting spring dispersal of radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

fect of closed-canopy pine plantations on dispersal probability is uncertain and the amount of early successional habitat within winter home ranges appeared to have little effect on dispersal probability. It is likely that a significant portion of birds will disperse every spring, regardless of habitat quality on a management unit. Therefore, it is important to consider surrounding landscape quality and management unit size when determining which areas are most likely to respond to management and the proper management strategy needed to achieve bobwhite population objectives. Lower surrounding landscape quality (amount of and proximity to suitable habitat) will likely result in lower immigration rates. Smaller management unit size will likely result in lower immigration and higher emigration because birds on the management unit and surrounding areas that disperse will be less likely to form breeding ranges on the management unit. Because bobwhites are known to select for early successional habitat, immigration should increase as the amount of early successional habitat increases on an area. However, surrounding landscape quality and management unit size will still affect immigration rates. As surrounding landscape quality and management unit size decrease, managers must increase the intensity of their management to achieve bobwhite population objectives. On many areas in the modern landscape, managers may have to adopt an "all out" management strategy to offset losses to emigration and achieve bobwhite populations large enough to support hunting. This type of strategy would include converting all available acreage to bobwhite habitat and, in some cases, adopting practices that may be considered controversial (e.g. predator control). Not adopting this type of management strategy may lead to unrealized objectives in many cases. Finally, the greater mobility reported in this and similar studies conducted in fragmented landscapes (Kabat and Thompson 1963, Fies et al. 2002) compared to the lower mobility reported by studies conducted on areas of contiguous habitat (Loveless 1958, Smith et al. 1982, Terhune et al. 2006) strongly suggests that bobwhites disperse greater distances in fragmented landscapes. How exactly metapopulation theory fits bobwhites has yet to be determined, but many metapopulation principles are almost certainly applicable given the relatively low mobility of the species and the fact that it often inhabits fragmented landscapes (Burger 2002, Fies et al. 2002). In these fragmented landscapes, both dispersal rates and distances will determine the rates of emigration and immigration between populations and ultimately the long term viability of regional populations (Hanski 1999). Fies et al. (2002) recommended that areas of suitable habitat should be located within a "yet-to-be-defined critical dispersal distance." More information on how landscape attributes affect bobwhite dispersal patterns and transience survival is needed before this distance can be defined.

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