NORTHERN BOBWHITE BREEDING SEASON DISPERSAL, HABITAT USE, AND SURVIVAL IN A SOUTHEASTERN AGRICULTURAL LANDSCAPE

by

MERRILL PATRICK COOK

(Under the direction of John P. Carroll)

ABSTRACT

Most biologists agree that changes in land use that have reduced the quantity and quality of early successional habitat are primarily responsible for the decline of the northern bobwhite (*Colinus virginianus*). The decline of the bobwhite in Georgia led to the development of the Bobwhite Quail Initiative (BQI), a state-funded program designed to increase bobwhite populations by providing early successional habitat around crop fields. I examined dispersal, habitat use, and survival in a landscape with a relatively large number of crop fields enrolled in the BQI program. Both adults and broods used BQI habitats and the presence of BQI habitats had a positive effect on adult survival during the breeding season. However, the effect was highly variable suggesting that the effect is likely contingent upon other habitats, particularly closed-canopy pine. Management strategies aimed at increasing bobwhite populations on a regional level in the Southeast should consider the large-scale management of pine stands a high priority.

INDEX WORDS: Bobwhite Quail Initiative, *Colinus virginianus,* Dispersal, Georgia, Habitat use, Northern bobwhite, Survival

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

During the past three decades, northern bobwhite (*Colinus virginianus*) (hereafter bobwhite) populations have declined throughout most of their distribution (Brennan 1991, Church *et al.* 1993, Sauer *et al.* 2000, Burger 2002). In the southeastern U.S.A., bobwhite populations declined by 66% during 1966 to 1999 (Sauer *et al.* 2000). There is concern not only because bobwhites are declining, but because the decline of this valuable game bird may negatively impact rural economies due to lost hunting opportunities and associated revenue (Burger *et al.* 1999). Furthermore, the bobwhite is considered an indicator of habitat quality for many other early successional species (Church *et al.* 1993).

There have been many reasons proposed for this decline including increases in avian and mammalian predators (Rollins and Carroll 2001), introduction of the fire ant (*Solenopsis invicta*) (Allen *et al.* 1993, Allen *et al.* 1995, Brennan 1993, Pedersen *et al.* 1996), and increased use of pesticides in agricultural practices (Percival *et al.* 1973, Palmer *et al.* 1998). However, most biologists consider the major cause of this decline to be loss of the early successional habitat upon which bobwhites depend for nesting, brood-rearing and foraging (Brennan 1991, Brennan 1993, Palmer *et al.* 1998, Rollins and Carroll 2001, Burger 2002). Agricultural landscapes once supported high densities of bobwhite in the Southeast by providing this habitat as a by-product of agricultural management (Brennan 1991). Weeds and grasses were abundant in crop fields, fallow patches, burned woodlots and linear habitats, such as field edges, fencerows and hedgerows that separated small fields.

Large amounts of farmland in the Southeast have been lost in recent decades. In Georgia, 27.6% of cropland was converted to other uses during 1982-1997 (United States Department of Agriculture – Natural Resources Conservation Service, Natural Resources Inventory *http://www.nrcs.usda.gov/technical/NRI/1997/summary_report/*). In addition to losses as a result of urbanization and other land uses, much farmland has been converted to pine plantations, typically planted in loblolly pine (*Pinus taeda*). Although the total amount of pine has remained stable, pine plantation acreage increased from 2.8 to 6.1 million acres in Georgia during 1972-1997 and 32% of this increase was due to the conversion of agricultural land (Thompson and Thompson 1997). The conversion of agricultural land to pine plantations in the Southeast has been encouraged by the Conservation Reserve Program (CRP). There has also been a reduction in the use of fire as a forestry management tool (Brennan *et al.* 1998). As a result of these trends, the modern southeastern landscape contains increased acreage of closed-canopy pine plantations devoid of herbaceous vegetation in the understory.

Besides reducing available habitat, pine plantations create a hostile matrix through or around which bobwhites must cross to move between patches of suitable habitat and may function as an ecological trap (Lewis 1999, Parnell 2002). Bobwhites may cross through these stands or flush into them while escaping predators because they perceive them to be quality woody cover. The proximate cues that bobwhites use may not be linked to ultimate rewards in modern landscapes (Taylor and Burger 2000). For example, Lewis (1999) and Parnell (2002) found a disproportionate number of bobwhite mortality locations (locations where radio-transmitters of dead birds were retrieved) in closed-canopy pine plantations. However, it is uncertain that these areas were where the actual mortality occurred. The birds may have been killed in adjacent habitats and then carried to the pine stands where they were eaten by the predators. Therefore, the landscape effects of differing proportions of closed-canopy pine stands and the adjacency of these stands with other habitats on bobwhite survival need to be examined.

The loss of farmland has been accompanied by intensification in the management of remaining farmland (Burger 2002). Today, crop fields are more intensively managed through the use of herbicides and insecticides that eliminate weeds and the insects that chicks need in their diet for early growth (Palmer 1995). Fallow fields and weedy field edges are rare. Field sizes have been increased to accommodate larger equipment and irrigation systems (Brennan 1991). The introduction of exotic forage grasses, most notably bermudagrass (*Cynodon dactylon*), has also likely had a negative impact (Burger 2002, Burkhart 2004). Bermudagrass is an aggressive, invasive species which quickly out-competes native vegetation in open areas. It forms a dense mat-like ground cover which may negatively impact bobwhite chicks by impeding movements and causing higher temperatures at the ground level resulting in thermal stress (Burkhart 2004).

The long-term decline of the bobwhite population led the Georgia Department of Natural Resources and the Georgia General Assembly to develop the Bobwhite Quail Initiative (BQI) in 1999. The goal of the BQI is to increase or at least stabilize bobwhite populations in Georgia by providing bobwhite habitat in privately owned row crop agriculture fields. BQI offers financial incentives to landowners who are willing to manage land in such a way to provide bobwhite habitat. The amount of the incentive depends upon how much and what type of habitat is provided. Landowners must maintain a minimum amount of habitat over the contract period (3 years) to receive payment. The BQI is a state-funded pilot program that is designed to adapt its management strategies to new research findings (GA DNR 1999, Hamrick 2002).

BQI habitats are intended to mimic those provided in past agricultural systems by:

1) establishing 10-20 meter wide linear herbaceous field borders encircling crop fields
2) establishing 10-20 meter wide linear strips of herbaceous vegetation through crop field interiors (weedrows)
3) establishing 20-40 meter wide linear strips of herbaceous vegetation centered on drainage ditches through crop field interiors (filter strips)
4) fallowing patches adjacent to crop fields
5) planting spring crops into residue left from winter crops or weeds (conservation tillage); and
6) thinning and/or burning pine stands that are adjacent to crop fields enrolled in the BQI program.

Among these, the most common practice has been the establishment of linear habitats (field borders, filter strips, and weedrows). The establishment of linear habitats may be the most practical and efficient method to increase bobwhite habitat in modern agricultural systems because they are easily incorporated into crop fields, minimize reduction in productive crop acreage and can be economically feasible for farmers to establish (Puckett *et al.* 2000, Hamrick 2002). Several researchers have advocated their use to improve habitat conditions in crop fields (e.g. Stoddard 1931, Rosene 1969, Exum *et al.* 1982, Puckett *et al.* 2000). Hamrick (2002) found that bobwhite abundance was greater on crop fields enrolled in the BQI program than on fields with no linear habitats. In North Carolina, Bromley *et al.* (2002) also found higher numbers of bobwhites on fields with field borders. Also in North Carolina, Puckett *et al.* (1997, 2000) found that bobwhites were attracted to crop fields with filter strips and that bobwhites on filter strip areas had smaller home ranges and a higher nest production rate.

Other species with similar habitat requirements as the bobwhite benefit from linear habitats in agricultural systems. Grassy roadsides are preferred nesting habitat for ring-necked pheasant (*Phasianus colchicus*) (Warner and Joselyn 1986) and gray partridge (*Perdix perdix*) (Carroll and Crawford 1991). The establishment of conservation headlands (field edges excluded from herbicide and pesticide treatments) has been reported to increase ring-necked pheasant, gray partridge and red-legged partridge (*Alectoris rufa*) brood survival and size in Great Britain (Rands 1985, 1986*b*, Potts 1986, Sotherton and Robertson 1990, Sotherton 1991). Also in Great Britain, field edges with greater nesting cover increased gray and red-legged partridge populations (Rands 1986*a*, 1987). California quail (*Callipepla californica*) in Nevada preferred field borders to all other habitat types year-round for feeding, loafing, escape and brood-rearing cover (Stinnett and Klebenow 1986).

Although bobwhites may benefit from linear habitats in agricultural systems, the evidence is not conclusive. Although studies have found higher bobwhite abundance on farms with linear habitats (e.g. Bromley *et al.* 2002, Hamrick 2002), it is unknown if the increased abundance was a result of an increase in survival and/or reproductive success or a result of increased immigration. Although Puckett *et al.* (1997) found that bobwhites had increased nest production on areas with filter strips, low sample size precluded testing for survival differences between bobwhites that used filter strips and those that did not. Oakley *et al.* (2002) reported that pen-raised bobwhites on farms with buffer strips had lower survival than those on farms without buffer strips. Although pen-raised bobwhite survival in the wild is known to be poor and their use in a survival study is of suspect utility, such results suggest that more research on the value of linear habitats for bobwhites is needed. If there is an effect of these habitats on bobwhite populations, knowing which parameters are being affected and the magnitude of the effect would be useful in determining the utility of these habitats.

The primary objective of this study was to examine movements, habitat use, and survival of bobwhites in a southeastern landscape containing a mixture of agriculture and forestry. My goal was to determine which habitats bobwhites used and the effect of particular habitats on bobwhite survival. I was most interested in the potential use and benefit of linear habitats provided by the BQI program. Finally, as a result of recent discussion regarding the importance of bobwhite dispersal information in landscape-level management for the species, I also examined this aspect of bobwhite ecology (Burger 2002, Fies *et al.* 2002, Townsend *et al.* 2003).

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CHAPTER 2

NORTHERN BOBWHITE BREEDING SEASON DISPERSAL

INTRODUCTION

The decline of northern bobwhite (*Colinus virginianus*) (hereafter bobwhite) populations during the past three decades has been well documented (Brennan 1991, Church *et al.* 1993, Sauer *et al.* 2000, Burger 2002). Site-specific management will always be a crucial component of any effort to increase bobwhite populations, but management strategies aimed at increasing bobwhite populations at a regional level 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 will 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 and therefore an understanding of the possible role that metapopulation processes play in regulating regional populations may be critical for management programs designed to increase bobwhite populations. The development of spatially explicit population models (SEPMs) has been advocated (Burger 2002, Fies *et al.* 2002) and may be particularly valuable because these models can 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 these parameters are affected by factors such as sex, age and habitat.

Information on dispersal is needed not only for landscape level management of bobwhites, but also for a better understanding of the ecology and evolution of the species. It is crucial for understanding population dynamics (Caizergues and Ellison 2002), especially for species inhabiting fragmented landscapes (Fies *et al.* 2002). Furthermore, knowledge of dispersal patterns may allow us to better understand the proximate and ultimate causes of dispersal (Lidicker and Stenseth 1992).

Although a great deal of research has been undertaken on bobwhite dispersal, 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 since 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. In addition, these studies are often conducted on areas managed specifically for quail where dispersal distances are likely lower than on areas of marginal habitat (Urban 1972, Fies *et al.* 2002). The most recent studies (i.e. Fies *et al.* 2002, Townsend 2003) have likely produced more accurate estimates of bobwhite dispersal because they were conducted using radio-telemetry and without study area boundary constraints. However, these studies did not examine the potential impact of habitat configuration on dispersal patterns. I quantified bobwhite breeding season dispersal rate and distance, and examined the effects of sex, age and habitat on dispersal patterns in a fragmented landscape typical of the modern southeastern U.S. without study area boundary constraints. I defined breeding season dispersal as a permanent movement from a winter range to a breeding range.

METHODS

Study Area

I conducted my study on a 133 km^2 area in western Laurens County, Georgia. This landscape was comprised of a mixture of intensive agriculture (26%) and woodland (56%). Most of the crop fields were planted in cotton. The other annual crops planted were peanuts, corn, and soybeans. A few fields were planted in wheat or rye during the winter. I 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 photos were 10 years old, I correctly classified all habitat types using field reconnaissance and ground truthing of unfamiliar areas with GPS equipment.

For this study, only two habitats were considered (Table 2.1). Early-successional (ERSC; 10% of study area) consisted of areas dominated by weeds and/or short brush and included abandoned fields, fallow strips that either encircled or passed through the interior of crop fields, young planted pines, hedgerows, fencerows, and young clearcuts. Closed-canopy pine (CCPN; 23% of study area) were stands of either loblolly or slash pine that had reached canopy closure and therefore had little to no vegetation in the understory. I considered ERSC to be beneficial habitat that would be desirable to bobwhites and CCPN to be a deleterious habitat (Lewis 1999, Parnell 2002).

Capture and Telemetry

I 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 were banded, equipped with a 6.4-6.9 g pendant-style (necklace) radiotransmitter and released at the trap site. I determined sex and age (juvenile and adult) using standard techniques. All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on 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).

I located bobwhites on foot using homing techniques (White and Garrott 1990). I approached within 25-50m; therefore, I could accurately identify the location of each bird on the base map and correctly classify habitat. Individual bobwhites were located 4-7 times per week during the breeding season (15 April-15 September). Prior to the breeding season, bobwhites were located 3-5 times per week. All bobwhite locations were plotted onto aerial photos and later entered into a GIS format using ArcView®

Dispersal Detection and Analysis

I detected breeding season dispersal using the vectored dispersal detection technique (Kenward 2001) in RANGES V (Kenward and Hodder, 1996). The technique tests if n new locations are outside the distribution of all previous N locations in a single direction. In RANGES V, 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 (I used $\alpha = 0.05$). 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 increments up by 1 and the routine begins again. I 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, I 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.

I employed several additional decision rules and techniques in my dispersal analysis. I wanted to adhere to the unidirectional definition of dispersal. Whenever dispersal was detected, I 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 confidence limits ($\alpha = 0.05$). If the circles overlapped or if any post-dispersal location was within the pre-dispersal confidence limit circle, dispersal was rejected. 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. Also, bobwhites 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. 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 classified as dispersers, those that died or were censored 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). I did not consider these to be dispersal events because those birds, by definition, were already on their breeding range. To minimize the possibility of detecting these events as dispersal events, dispersal detected after 19 May (the earliest recorded date of nest incubation) was not considered to be dispersal.

I 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, only pre-dispersal locations were used. For non-dispersers, I used only locations collected before 15 April.

I examined the effects of several covariates on dispersal probability and dispersal distance using an information-theoretic approach. I developed two *a priori* sets of candidate models based on literature review and my knowledge of bobwhite biology. My model set for dispersal probability included the effects of sex (coded F=0, M=1), age (J=0, A=1), proportions of CCPN and ERSC habitat within the winter home range, a sex*age interaction term, and terms for interactions between age and habitat covariates. Other habitat types were not considered because the two habitats I used were viewed as the most likely to have an effect on dispersal probability and I wished to keep the number of models low, thereby reducing the possibility of spurious results (Anderson and Burnham 2002). I included interactions between age and habitat because adults may perceive the quality of habitats differently having already experienced at least one breeding season and two winters. When habitat covariates were missing for a particular bird (i.e. when not enough winter locations were collected to estimate its home range), I substituted the values with the means of all non-missing values. My model set for dispersal distance included the effects of sex, age, and a sex*age interaction term. Although habitat likely influences dispersal distance (Åberg *et al.* 1995, Turner *et al.* 2001:200, Fies *et al.* 2002), no habitat variables were included in this model set because the exact dispersal path was unknown. Year was not included in either model set because I had no reason, biological or otherwise, to suspect that year would have an effect on either dispersal tendency or distance (Burnham and Anderson 2002). I used the PROC LOGISTIC (logistic regression; dispersal probability) and PROC REG (linear regression; dispersal distance) procedures in SAS (SAS version 8.2) to produce parameter estimates and Akaike's Information Criterion (AIC) for each model. I then calculated AIC_c (AIC corrected for small sample sizes) values, AIC_c weights, model-averaged parameter estimates and unconditional standard errors for each parameter (Burnham and Anderson 2002).

RESULTS

I captured and radio-tagged 202 (99 female, 103 male; 58 adult, 144 juvenile) bobwhites from 39 coveys. There were 101 bobwhites used in dispersal analysis. Of these, 29.7% were classified as dispersers and mean dispersal distance for all bobwhites was 1835m (SE=194) (Table 2.2).

My best approximating model (ω=0.38) for dispersal probability showed that dispersal probability varied among individuals relative to interactions between age and proportions of CCPN and ERSC habitat within winter home ranges (Table 2.3). The model that best described variation in dispersal distance (ω=0.41) included only sex as an effect. However, the next 3 best models in the dispersal probability model set and all other models in the dispersal distance model set were within 2 ΔAIC_c units of the best models indicating substantial empirical support of these models as well (Burnham and Anderson 2002:70-72). The last two models describing variation in dispersal probability were >2 but still within 10 ΔAIC_c units of the best model indicating at least a reasonable level of support (Anderson *et al.* 2001).

The proportion of ERSC habitat within the winter home range seemed to have a moderate negative effect on dispersal probability ($\beta = -1.16$, SE = 1.39), whereas CCPN seemed to have very little effect ($\beta = 0.87$, SE = 4.72) (Table 2.4). However, our best approximating model showed that age interacts with ERSC ($\beta = -3.29$, SE = 2.11) and CCPN ($\beta = 15.34$, SE = 9.36), such that adults with higher proportions of ERSC habitat within their winter home range were less likely to disperse and those with more CCPN were more likely to disperse. The second best model suggested that males were more likely to disperse, but this sex effect was slight ($\beta = 0.35$, SE = 0.44). There appeared to be very little effect of age ($\beta = -0.05$, SE = 0.47) and a sex*age interaction ($\beta = 0.09$, SE = 0.59). Males appeared to disperse somewhat shorter distance than females ($\beta = -594.91$, SE = 382.20) and adults seemed to disperse somewhat farther than juveniles ($\beta = 441.90$, SE = 417.75).

DISCUSSION

Dispersal in birds is usually reported to be female-biased (Greenwood 1980, Greenwood and Harvey 1982, Clark *et al.* 1997) and female-biased dispersal has been identified in several Galliformes, including Ruffed Grouse (*Bonasa umbellus*) (Small and Rusch 1989), Black Grouse (*Tetrao tetrix*) (Caizergues and Ellison 2002), Blue Grouse (*Dendragapus canadensis*) (Hines 1986), Spruce Grouse (Boag and Schroeder), Willow Ptarmigan (*Lagopus lagopus*) (Smith 1997) and Lesser Prairie Chicken (*Tympanuchus pallidicinctus*) (Giesen 1998). Greenwood's (1980) hypothesis to explain female-biased dispersal in birds states that the phenomenon results from monogamy, the typical mating system of birds, and also from resource defense mating systems. Males typically defend territories; therefore, they benefit from remaining near a familiar area where they can better compete for resources. Conversely, females benefit from moving so that they can choose the best mates and/or resources. However, this hypothesis does not adequately explain female-biased dispersal in some Galliformes (Martin and Hannon 1987, Caizergues and Ellison 2002). Female Willow Ptarmigan (Martin and Hannon 1987) and Spruce Grouse (Nugent and Boag 1982) defend territories and female-biased dispersal has been identified in both these species. Furthermore, female-biased dispersal has been detected in grouse species that exhibit all mating system types (Caizergues and Ellison 2002) and dispersal is male-biased in Grey Partridge, a species which exhibits a monogamous mating system (Potts 1986).

In discussing this and other topics relative to the northern bobwhite there are several caveats that make interpretation of research studies difficult. Among studies there have been considerable differences in field methods, dispersal detection, and data analyses. Most of the studies of bobwhite mobility have been conducted using banding techniques. Even the recent telemetry studies of bobwhite movement have used quite different methods to identify dispersal and to analyze data. Comparisons made below should be viewed within this context.

Previous researchers have suggested that bobwhite movements are either male-biased (Hood 1955, Loveless 1958, Kabat and Thompson 1963, Smith *et al.* 1982) or not affected by sex (Stoddard 1931:176, Simpson 1976). More recently, Fies *et al.* (2002) found that male juveniles dispersed at a rate greater than any other sex/age group. Townsend *et al.* (2003) reported that females were less likely to disperse than males. Male-biased dispersal in bobwhites would not be in contradiction to Greenwood's (1980) hypothesis since the species exhibits a polygamous mating system (Curtis *et al.* 1993) and is generally non-territorial (Fies *et al.* 2002). However, my results suggest that there may be some female bias in bobwhite dispersal. Although sex did not have an overall great effect on dispersal, I found that mean dispersal distance of juvenile females was greater than that of juvenile males. If juveniles did not disperse during autumn, then breeding season dispersal of juveniles would be natal dispersal, dispersal from birth site to breeding site. For most avian species, it is during natal dispersal when females move greater distances (Gauthreaux 1978, Greenwood and Harvey 1982). Although I could not determine if juveniles had already dispersed the preceding autumn, there is evidence that autumn dispersal does not occur in bobwhites. Agee (1957) reported that coveys often formed winter ranges within 100 yards of their hatching site, and Urban (1972) also found no major dispersal during autumn. However, Duck (1943), Lehman (1946) and Loveless (1958) all noted definite shifts to winter home ranges. Autumn natal dispersal is known to occur in Ruffed Grouse (Small and Rusch 1989). Therefore, the possible natal dispersal of bobwhites in autumn should be examined more closely.

Dispersal of juveniles is common in many avian species (Clark *et al.* 1997) and is thought to reduce competition between parents and offspring (Liberg and von Schantz 1985) and possibly inbreeding (Howard 1960). However, we found that adults were just as likely to disperse during spring. Townsend *et al.* (2003) also found that dispersal rates did not differ by age, but juvenile dispersal distances were greater than those of adults. Smith *et al.* (1982) and Fies *et al.* (2002) also reported greater juvenile dispersal distances and in these studies juveniles were more likely to make extensive movements. In my study, adult dispersal distances were slightly higher than those of juveniles. Certainly, these conflicting results could be in part due to differences in methods used. However, Urban (1972) noted that differences in habitat composition and dispersion among study areas may explain the differences in bobwhite mobility among studies.

My best approximating model demonstrated that dispersal probability varied among individuals relative to interactions between age and proportions of closed-canopy pines and early successional habitat within their winter home ranges. Adults with higher proportions of early successional habitat in their winter home range were less likely to disperse and those with more closed-canopy pines were more likely to disperse. Perhaps adults, having already experienced at least one breeding season, had low reproductive success in areas associated with closed-canopy pine or high reproductive success in early successional habitat in previous year(s) and these experiences influenced their tendency to disperse. Adults had also experienced at least two winters. It is possible that these adults had been exposed to either high within-covey mortality in the vicinity of closed-canopy pines or low within-covey mortality in early successional habitat and these experiences could have also influenced their tendency to disperse.

Bobwhite dispersal has been considered an innate behavior (Howard 1960), but my finding of an age-habitat interaction effect on dispersal tendency suggests that proximate environmental factors can affect dispersal patterns. Some evidence of a genetic basis for individual differences in dispersal exists for Spruce Grouse (Keppie 1980, Schroeder and Boag 1988, Keppie and Towers 1992), but the role that genetics plays in determining dispersal tendencies is not clear (Cockburn 1992). Caizergues and Ellison (2002) noted that even if genetics play a role, environmental factors could still affect which individuals disperse. Urban (1972) also found that habitat influenced which bobwhites dispersed during spring. In his study, 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 habitat and in particular matrix habitat may affect dispersal distances as well (Turner *et al.* 2001:220). Åberg *et al.* (1995) found that matrix quality had a strong effect on dispersal distances of Hazel Grouse (*Bonasa bonasia*). Puckett *et al.* (1995) reported that distances from capture site to first nest for bobwhites were over four times greater on areas without 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. This is supported by the findings that mobility is lower on areas managed intensively for bobwhites (Loveless 1958, Smith *et al.* 1982) and higher on areas containing marginal habitat (Kabat and Thompson 1963). In this study, bobwhite mobility was also higher than that found on intensively managed areas and more similar to studies of bobwhite mobility in marginal habitat (e.g. Kabat and Thompson 1963, Fies *et al.* 2002, Townsend *et al.* 2003). Dispersal rates and distances documented in one landscape are likely not applicable to other landscapes, especially ones differing in matrix quality (Åberg *et al.* 1995). Therefore the development and implementation of SEPMs and other models using bobwhite dispersal information will need to be a landscape-specific exercise.

How traditional metapopulation theory fits bobwhites exactly has yet to be determined (Burger 2002), but many of the metapopulation principles are almost certainly relevant considering the relatively low mobility of the species and the fact that it often inhabits fragmented landscapes (Fies *et al.* 2002). In these fragmented landscapes, local population viability is likely affected by interactions with other populations (Roseberry 1993). 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 dispersal mortality is needed before this distance can be defined.

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Table 2.1. Proportions of closed-canopy pine and early-successional habitat within the winter home ranges of 101 radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

			n	Mean	SE	95% C.I.
Closed-canopy Pine	**Adult**	**Disperser**	9	0.069	0.019	0.032 – 0.107
		Non-disperser	22	0.044	0.007	0.030 – 0.058
	Juvenile	**Disperser**	21	0.044	0.010	0.024 – 0.063
		Non-disperser	49	0.049	0.007	0.034 – 0.063
	Pooled	**Disperser**	30	0.051	0.009	0.033 – 0.069
		Non-disperser	71	0.047	0.005	0.037 – 0.058
Early Successional	**Adult**	**Disperser**	9	0.255	0.034	0.188 – 0.322
		Non-disperser	22	0.350	0.037	0.279 – 0.422
	Juvenile	**Disperser**	21	0.287	0.033	0.222 – 0.353
		Non-disperser	49	0.294	0.027	0.241 – 0.346
	Pooled	**Disperser**	30	0.278	0.025	0.228 – 0.327
		Non-disperser	71	0.311	0.022	0.268 – 0.354

Table 2.2. Breeding season dispersal rates and distances for 101 radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

		Dispersal Rate		**Dispersal Distance (m)**			
		n	**% Dispersal**	**n**	**Mean**	**SE**	**95% C.I.**
Female	**Juvenile**	35	25.7	9	2184	341	1516 - 2852
	Adult	15	26.7	4	2150	790	602 - 3698
	Pooled	50	26.0	13	2173	319	1548 - 2798
Male	**Juvenile**	35	34.3	12	1339	203	941 - 1737
	Adult	16	31.3	5	2146	575	1019 - 3273
	Pooled	51	33.3	17	1576	230	1125 - 2027
Pooled	**Juvenile**	70	30.0	21	1701	204	1301 - 2101
	Adult	31	29.0	9	2148	442	1282 - 3014
	Pooled	101	29.7	30	1835	194	1455 - 2215

Table 2.3. Candidate models used to evaluate dispersal rate and dispersal distance of radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003. All models include an intercept term.

	Model	**AIC$_c$**	**Δ AIC$_c$**	**Model Weight**	**K[3]**
Dispersal Rate	Age*CCPN[1] + Age*ERSC[2]	125.05	0.00	0.38	3
	Sex	126.36	1.31	0.20	2
	Sex*Age	126.99	1.94	0.14	2
	Age	127.01	1.96	0.14	2
	ERSC + CCPN	128.28	3.23	0.08	3
	Sex + Age	128.49	3.44	0.07	3
Dispersal Distance	Sex	419.08	0.00	0.41	2
	Sex + Age	420.34	1.26	0.22	3
	Age	420.41	1.33	0.21	2
	Sex*Age	421.05	1.97	0.15	2

[1] CCPN = proportion of closed-canopy pine within the winter home range.

[2] ERSC = proportion of early successional habitat within the winter home range.

[3] Number of parameters included in models.

Table 2.4. Model-averaged estimates, unconditional standard errors, and confidence intervals of effects on dispersal rate and dispersal distance for radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

	Parameter	**β**	**SE**	**LCI[3]**	**UCI[4]**
Dispersal Rate	Intercept	-0.87	0.33	-1.52	-0.22
	Sex	0.35	0.44	-0.51	1.21
	Age	-0.05	0.47	-0.98	0.88
	Sex*Age	0.09	0.59	-1.07	1.24
	CCPN[1]	0.87	4.72	-8.38	10.11
	Age*CCPN	15.34	9.36	-3.00	33.68
	ERSC[2]	-1.16	1.39	-3.88	1.57
	Age*ERSC	-3.29	2.11	-7.43	0.85
Dispersal Distance	Intercept	1982	337	1320	2643
	Sex	-595	382	-1344	154
	Age	442	418	-377	1261
	Sex*Age	373	523	-657	1403

[1] CCPN = proportion of closed-canopy pine within the winter home range.

[2] ERSC = proportion of early successional habitat within the winter home range.

[3] Lower 95% C.I. limit.

[4] Upper 95% C.I. limit.

CHAPTER 3

NORTHERN BOBWHITE BREEDING SEASON HABITAT USE

INTRODUCTION

The decline of northern bobwhite (*Colinus virginianus*) (hereafter bobwhite) populations during the past three decades has been well documented (Brennan 1991, Church *et al.* 1993, Sauer *et al.* 2000, Burger 2002). In the southeastern U.S.A., bobwhite populations declined by 66% during 1966-1999 (Sauer *et al.* 2000). Although many reasons have been proposed for the decline, most biologists consider the major cause to be a reduction in the quantity and quality of bobwhite habitat through loss of farmland, intensification in the management of remaining farmland, and intensified timber management (Brennan 1991, Brennan 1993, Palmer *et al.* 1998, Rollins and Carroll 2001, Burger 2002).

The decline of the bobwhite population led the Georgia Department of Natural Resources and the Georgia General Assembly to develop the Bobwhite Quail Initiative (BQI) in 1999. The goal of the BQI is to increase or at least stabilize bobwhite populations in Georgia by providing different types of bobwhite habitat mainly in privately owned row crop agricultural fields. BQI offers financial incentives to landowners that are willing to provide habitat beneficial to bobwhites. There are many BQI management practices but the most commonly adopted practice has been the establishment of 10-20 meter wide linear strips of herbaceous vegetation. These are usually in the form of field borders which encircle fields. Others are established in the interior of fields (weedrows and filter strips) (GA DNR 1999).

Although use or avoidance of habitats alone does not necessarily infer relative quality of habitats (Van Horne 1983), knowledge of habitat use patterns is important in determining the value of habitats and the efficacy of management decisions (Alldredge *et al.* 1998). For example, BQI habitats may be potentially beneficial to bobwhites, but if these habitats tend to be avoided or are not available to bobwhites, then the management is of little use. Additionally, potentially negative habitats, such as closed-canopy pine stands and areas dominated by bermudagrass, could function as ecological traps (Gates and Gysel 1978) if bobwhites use them and have higher mortality rates. Therefore, I examined habitat use by bobwhites during the breeding season in a southeastern agricultural landscape where BQI habitats were present.

METHODS

Study Area

I conducted my study on a 133 km^2 area in western Laurens County, Georgia (Figure 3.1). This area was chosen because land uses and habitats there were typical of the southeastern U.S. and because of the relatively large numbers of fields enrolled in the BQI program. I 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 photos were 10 years old, I correctly classified all habitat types using field reconnaissance and ground-truthing unfamiliar areas using GPS equipment. I produced two maps (one for each year) to reflect any changes in the landscape that occurred during the course of the study.

I delineated eight habitat types for my study (Table 3.1). Most of the crop fields on my study area were planted in cotton, but there were also peanuts, corn, and soybeans. The mean size of crop fields was 9.55 ha (SE=0.69). Small sample size required that I combine some habitats for brood habitat analysis. From the original classification, I produced maps that contained only five habitats for analysis of brood habitat use. CCPN and HRWD were combined into one category: woodland (WOOD). FALL, SCRB and SBFA were combined into one category: early successional (ERSC).

Capture and Telemetry

I 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 were banded, equipped with a 6.4-6.9 g pendant-style (necklace) radiotransmitter and released at the trap site. All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on 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).

I located bobwhites on foot using homing techniques (White and Garrott 1990). I approached birds to within 25-50m to minimize location and habitat classification errors. Individual bobwhites were located 4-7 times per week during the breeding season. I assumed that birds were nesting if they were in the same location on 2 consecutive days and placed flagging within 10 m of the potential nest. I confirmed nesting once they were away from the nest to avoid nest desertion and recorded the nest location. Nests were monitored daily. If a nest was successful, the resulting brood was located 2-4 times per day until the 14th day post-hatch. All bobwhite locations were plotted onto aerial photos and later entered into a GIS format using ArcView®.

Habitat Selection

I used the animal movements extension (Hooge and Eichenlaub 1997) designed for ArcView® to calculate fixed kernel home ranges (Worton 1989) with a 95% isopleth, requiring ≥20 locations to calculate individual home ranges (DeVos and Mueller 1993) and >11 locations for brood home ranges (Taylor *et al.* 1999). I selected the defaults option which uses *ad hoc* calculation of a smoothing parameter. Brood home ranges were calculated for the 14-day post-hatch (pre-fledging) period only. For bobwhites that dispersed, I used only locations collected after the last date of dispersal until 15 September; and for non-dispersers, locations collected during 15 April – 15 September were used.

I examined 2nd and 3rd order habitat selection (Johnson 1980) for individual (adult and juvenile) bobwhites and broods using compositional analysis (CA) (Aebischer *et al.* 1993). Second order availability was defined individually for each brood and individual. I first generated 2 sets of 30 random distances from a normal distribution based on the mean and standard deviation of distances from nests (broods) or traps (individuals) to the arithmetic center (*Ac*) of the corresponding locations using the RANNOR function in SAS (SAS Institute version 8.2). Random points were generated at each of these distances and at random bearings from each nest or trap. I generated another 2 sets of 30 random numbers in the same manner based on the mean and standard deviation of home range sizes for broods and individuals. I then buffered each point to create polygons (random home ranges). The size of each polygon was determined randomly based on the random numbers generated from the mean and standard deviation of home range sizes. The average habitat proportions within these polygons was calculated and considered to be second order availability. Second order use was defined as the proportions of each habitat type within home ranges. I defined 3rd order availability as the proportion of each habitat type within home ranges and use as the proportion of individual radio-locations within each habitat type. Prior to analysis, I replaced zero values for use with the value 0.000001 which was one order of magnitude less than the smallest recorded non-zero proportion (Aebischer *et al.* 1993). When a habitat was not available for use, I replaced missing values in each log-ratio with the mean of all non-missing values for the respective log-ratio (Aebischer *et al.* 1993). All analyses were conducted using SAS (SAS version 8.2).

I also examined 2nd and 3rd order selection for broods and individuals with a distance-based approach using Euclidean distances (DA) (Conner and Plowman 2001, Conner *et al.* 2003). In order to determine 3rd order selection, I generated 1,000 random points from a uniform distribution within each brood and individual home range. I divided the average distance of actual locations to each habitat type (use) by the average distance of the respective random points to each habitat type (availability) for each sampling unit and then averaged these to create a mean vector of ratios. To determine second order selection, I generated 1,000 random points within each of the "random home ranges" of each brood and individual (30,000 for each sampling unit). The average distance of the within home range random points to each habitat type (use) was divided by the average distance of random home range points to each habitat type (availability) for each sampling unit. The resulting values were then averaged to create another mean vector of ratios. Similar to compositional analysis, I used MANOVA to test for overall nonrandom habitat use. Specifically, I tested if the mean vector of ratios differed significantly from a vector of ones. Given a significant overall model effect, I ranked habitats according to relative use, using pair-wise *t*-tests testing if the difference between each habitat type mean ratio and all other mean ratios was equal to zero. All analyses were conducted using SAS (SAS version 8.2).

I did not test for effects of year, sex, or age on habitat use. I had no reason to suspect that year or sex would have any effect on habitat use. I did think that adults may perceive the quality of habitats differently, having already experienced at least one breeding season and two winters (see Chapter 2), and therefore possibly use habitats differently. However, sample size constraints would have precluded separate analysis if an effect had been detected.

RESULTS

I captured and radio-tagged 202 (99 female, 103 male; 58 adult, 144 juvenile) bobwhites from 39 coveys over the entire duration of the study. For home range estimation and habitat selection analysis, I used 18 broods and 92 individuals.

Habitat Selection

Habitat use analysis using CA revealed overall nonrandom habitat use by broods and individuals at both the 2nd order (broods: $\lambda = 0.41$, $P = 0.01$; individuals $\lambda = 0.56$, $P < 0.0001$) and 3rd order (broods: $\lambda = 0.19$, $P < 0.0001$; individuals $\lambda = 0.45$, $P < 0.0001$). In order of most to least relative selection, individuals used SCRB most at the 2nd order followed by BQI, HRWD, CROP, TURF, SBFA, FALL and CCPN (Table 3.2, Figure 3.2). SCRB received the greatest relative use by individuals at the 3rd order as well followed by HRWD, BQI, SBFA, FALL, CCPN, TURF and CROP (Table 3.2). In order of most to least relative selection, broods used ERSC, WOOD, CROP, BQI and TURF at the 2nd order; however, at the 3rd order, relative use of BQI was greatest followed by ERSC, WOOD, TURF and then CROP (Table 3.3, Figure 3.3).

At the 2nd order, the MANOVA used in analysis of Euclidean distances detected overall nonrandom habitat use only for individuals (broods: $\lambda = 0.54$, $P = 0.11$; individuals: $\lambda = 0.22$, $P < 0.0001$), but overall nonrandom habitat use was detected for both broods and individuals at the 3rd order (broods: $\lambda = 0.41$, $P = 0.03$; individuals $\lambda = 0.47$, $P < 0.0001$). No further analysis of brood 2nd order selection was conducted (Conner and Plowman 2001:287). Individual within home range locations were relatively closest to CROP followed by BQI, SBFA, TURF, FALL, SCRB, HRWD, and CCPN (Table 3.4, Figure 3.4). Individual locations were relatively closest to SBFA followed by TURF, FALL, BQI, CROP, HRWD, CCPN, and SCRB (Table 3.5). At the 3rd order, pair-wise comparisons revealed that brood habitat use was relatively greatest for ERSC followed by CROP, TURF, BQI and then WOOD (Table 3.6, Figure 3.5).

DISCUSSION

Habitat selection

At the 2nd order level of selection, our findings that adult bobwhites used BQI, scrub, and hardwood more than expected is similar to results of other studies. Previous studies have reported higher selection of woody habitats similar to the scrub category (Taylor and Burger 2000, Smith 2001, Szukaitis 2001). Individuals probably incorporated scrub into their home ranges because of its value as escape cover (Stoddard 1931), safe travel corridors (Taylor and Burger 2000), and protection from weather extremes (Johnson and Guthery 1988). Although, hardwoods are not generally thought of as quality bobwhite habitat, other researchers have also reported disproportionate use of hardwoods (Lewis 1999, Parnell 2002). Many of the hardwood stands in my study area contained a dense shrub layer, especially near the edges. Therefore, hardwoods likely provided similar structural characteristics and benefits as scrub and may provide useful hard mast crops. Selection of BQI habitats suggests that these areas likely provide travel corridors and safe feeding areas due to their linear shape, vegetative composition, and interspersion with other habitats.

My finding avoidance of closed canopy pines is consistent with the results of other studies in Louisiana (Bell *et al.* 1985) and in Mississippi (Fuller 1994). However, at another site in Georgia, closed canopy pine was neither preferred nor avoided (Lewis 1999, Parnell 2002). Given that the structural characteristics of fallow and scrub/fallow should be attractive to bobwhites, avoidance of these habitats is surprising. The fallow fields in my study area may not have provided the best structure because most of them were recently abandoned crop fields that had a long history of intense management that reduced native weed-seed banks. I noticed that when individuals did use fallow fields, they remained near the edges of the fields that bordered woody cover; therefore, home ranges tended to incorporate fallow habitat, but not a large area of it. Additionally, BQI habitats were structurally similar to fallow habitat, but tended to border woody habitat. Reasons for the low use of scrub/fallow, usually clear-cuts or long-abandoned crop fields, are unknown. Besides containing an abundance of weeds, this habitat also contained a high amount of woody cover.

The highest ranked habitats at the 2nd order of individual habitat selection were also used disproportionately at the 3rd order level of selection. However, except for closed canopy pines, there was a shift in avoided habitats. Crop fields and turf/grass received intermediate use at the 2nd order, but were avoided at the 3rd order. Individuals likely incorporated these two habitats within their home ranges because they are generally associated with other open habitats that are selected. Although the habitats were within home ranges, they were rarely used because they were of little value for food or cover. Other researchers have also reported the avoidance of crop fields (Lewis 1999, Parnell 2002), and habitats dominated by sod-forming exotic forage grasses (Szukaitis 2001). I agree with the findings by Szukaitis (2001) that bobwhites avoid areas dominated by exotic forage grasses because of their dense structure and lack of bare ground which impedes movement.

Brood habitat selection also varied at the different orders of selection. The most notable difference is that BQI was avoided at the 2nd order, but was ranked highest in use at the 3rd order. One possibility is that BQI is so rare on the landscape that broods simply do not find them unless these areas are very close to the nest. When broods do have BQI habitat in their home range, it then becomes a valuable habitat. However, BQI was ranked high for 2nd order adult habitat use and there is anecdotal evidence that bobwhites exhibit at least some selection of brood range prior to choosing a nest site (Szukaitis 2001). Therefore, a more likely explanation is the spatial arrangement of BQI habitats is the reason for the low ranking of BQI at the 2nd order. At the second order level of selection, use of BQI necessitates a much higher use of crop fields because all linear BQI habitats either encircle or cross through the interiors of these crop fields. Therefore, broods using BQI habitats tend to incorporate a large proportion of crop fields within their home range, but rarely use the core of the fields. Indeed, crop field habitat was ranked lowest at the 3rd order of selection. Given that one of the main goals of the BQI program is to increase the amount of brood-rearing habitat in farmed landscapes of Georgia, disproportionate use of BQI by broods is an important finding and provides further evidence that the BQI program is providing useful habitat.

In contrast to low use of crops by broods in this study, Smith (2001) reported that broods used crop fields extensively and attributed this use to crops in his study having structural characteristics similar to early seral stage plant communities. Differences in crop type and/or availability of other habitats are likely responsible for these differences. The crops planted on Smith's (2001) study area were either corn or soybeans; conversely, most fields in my study were planted in cotton. Cotton is more intensively managed and likely provides very poor brood habitat. I observed two broods that used corn fields almost exclusively, but there was no observed use of cotton by broods.

Bermudagrass was avoided by broods at both levels of selection, likely due to its structural characteristics. Burkhart (2004) found that bermudagrass impeded the mobility of young chicks. Additionally, he found that patches of bermudagrass could form "heat traps" where temperatures exceed 39 C, the temperature at which Guthery *et al.* (2001) determined to be a critical threshold for heat dissipation.

CA and DA analysis of habitat

In contrast to Conner *et al.* (2003), there were some differences in results from the 2 types of habitat use analysis. Bingham *et al.* (2004) reported that CA may be more prone to Type I error. If true, this could explain why overall nonrandom habitat use for broods was detected at the second order level of selection with CA, but not with DA. However, there were also differences in relative habitat use from the two methods. Additionally, because the statistical procedures used in both techniques are similar, differences between the two methods can be attributed mostly to inherent differences in the way that the two methods measure habitat use (Conner *et al.* 2003).

Formulating reasons for the different results obtained from CA and DA is difficult. Spatial arrangement of habitats likely has a large effect on both the actual habitat use patterns of animals and the results obtained from the two methods. The most notable difference was the high ranking of scrub with CA and a low ranking with DA at the second order. Scrub on the study area was composed of both block (e.g. mid-seral clearcuts) and linear patches (e.g. hedgerows). Bobwhites use this habitat mostly for escape cover, therefore would not necessarily need a high amount of it within their home range. I noticed a tendency of bobwhites to use the latter more than the former, likely because the linear scrub patches are spread throughout the range and in close proximity to feeding areas and other habitats. I suspected that DA would reveal higher use of scrub and CA would reveal low use because bobwhites should select areas that have scrub in close proximity to other habitats but in general avoid large patches of the habitat. However, the opposite occurred. Therefore, there must be some other unknown landscape attributes affecting the results of the 2 methods. I believe that researchers examining habitat use with any method should consider the effect of the spatial arrangement of habitats on their results. An investigation of how landscape metrics such as patch size, patch size variability, and perimeter-area ratios affect habitat use analyses is needed.

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Table 3.1. Descriptions and relative proportions of cover types in western Laurens County, Georgia, U.S.A. where habitat use of radio-marked bobwhites was assessed during 2002-2003.

Cover Type	**Description**	**% of Study Area**
BQI	Linear habitats provided by BQI. These included field borders, filter strips, and weedrows.	0.27
CCPN	Closed-canopy stands of either loblolly pine. or slash pine.	23.36
CROP	Commercial row-crop fields. Most fields were planted in cotton. Other crops included corn, soybeans, and peanuts.	13.39
FALL	Fallow areas dominated weeds and grasses with very little to no woody vegetation. Included young planted pines.	5.01
HRWD	Fallow areas dominated by weeds and grasses with very little to no woody vegetation.	32.97
SBFA	Scrubland/fallow areas dominated by a mixture of shrubs, young trees, weeds and grasses.	3.24
SCRB	Scrubland areas dominated by shrubs and/or young trees including hedgerows and fencerows.	1.74
TURF	Included all pasture/hay land and other areas dominated by bermudagrass.	12.37
OTHR	Category that included residential areas, buildings, open water and other areas excluded from all analyses.	7.64

Table 3.2. Mean (± 1 SE) log ratio differences using compositional analysis for 2nd and 3rd order habitat selection of adult northern bobwhites (n = 92) in Laurens County, Georgia, USA, May – August, 2002-2003.

2nd Order	**BQI[1]**	**CCPN**	**CROP**	**FALL**	**HRWD**	**SCRB**	**SBFA**	**TURF**	**Rank[2]**
BQI		**2.89 ± 0.54***	0.32 ± 0.31	**1.36 ± 0.48***	0.04 ± 0.29	-0.49 ± 0.30	0.47 ± 0.39	0.41 ± 0.42	6
CCPN	**-2.89 ± 0.54***		**-2.57 ± 0.52***	**-1.53 ± 0.62***	**-2.85 ± 0.43***	**-3.38 ± 0.50***	**-2.42 ± 0.46***	**-2.47 ± 0.45***	0
CROP	-0.32 ± 0.31	**2.57 ± 0.52***		**1.04 ± 0.36***	-0.28 ± 0.32	**-0.81 ± 0.29***	0.15 ± 0.37	0.10 ± 0.43	4
FALL	**-1.36 ± 0.48***	**1.53 ± 0.62***	**-1.04 ± 0.36***		**-1.32 ± 0.43***	**-1.85 ± 0.41***	-0.89 ± 0.53	-0.95 ± 0.51	1
HRWD	-0.04 ± 0.29	**2.85 ± 0.43***	0.28 ± 0.32	1.32 ± 0.43*		-0.53 ± 0.26	0.43 ± 0.34	0.37 ± 0.32	5
SCRB	0.49 ± 0.30	**3.38 ± 0.50***	**0.81 ± 0.29***	**1.85 ± 0.41***	0.53 ± 0.26		**0.96 ± 0.37***	**0.90 ± 035***	7
SBFA	-0.47 ± 0.39	**2.42 ± 0.46***	-0.15 ± 0.37	0.89 ± 0.53	-0.43 ± 0.34	**-0.96 ± 0.37***		-0.05 ± 0.44	2
TURF	-0.41 ± 0.42	**2.47 ± 0.45***	-0.10 ± 0.40	0.95 ± 0.51	-0.37 ± 0.32	**-0.90 ± 0.35***	0.05 ± 0.44		3

[1] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - Agricultural fields. FALL - Fallow area. HARD – Hardwoods. SCRB - Scrub. SBFA - Scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass.

[2] Higher ranks indicate higher selection relative to other habitat types. Calculated by totaling number of positive values within row.

[*] *t*-test, $P \leq 0.05$).

Table 3.2. (cont.) Mean (± 1 SE) log ratio differences using compositional analysis for 2^{nd} and 3^{rd} order habitat selection of adult northern bobwhites (n = 92) in Laurens County, Georgia, USA, May – August, 2002-2003.

3^{rd} Order	**BQI[1]**	**CCPN**	**CROP**	**FALL**	**HRWD**	**SCRB**	**SBFA**	**TURF**	**Rank2**
BQI		**1.42 ± 0.38***	**3.57 ± 0.46***	**1.25 ± 0.39***	-0.10 ± 0.34	-0.64 ± 0.39	0.37 ± 0.40	**1.97 ± 0.42***	5
CCPN	**-1.42 ± 0.38***		**2.15 ± 0.53***	-0.17 ± 0.49	**-1.52 ± 0.36***	**-2.07 ± 0.42***	**-1.05 ± 0.48***	0.54 ± 0.43	2
CROP	**-3.57 ± 0.46***	**-2.15 ± 0.53***		**-2.31 ± 0.48***	**-3.66 ± 0.44***	**-4.21 ± 0.51***	**-3.19 ± 0.45***	**-1.60 ± 0.49***	0
FALL	**-1.25 ± 0.39***	0.17 ± 0.49	**2.31 ± 0.48***		**-1.35 ± 0.39***	**-1.90 ± 0.41***	**-0.88 ± 0.37***	0.71 ± 0.46	3
HRWD	0.10 ± 0.34	**1.52 ± 0.36***	**3.66 ± 0.44***	**1.35 ± 0.39***		-0.55 ± 0.30	0.47 ± 0.37	**2.06 ± 0.40***	6
SCRB	0.64 ± 0.39	**2.07 ± 0.42***	**4.21 ± 0.51 ***	**1.90 ± 0.41***	0.55 ± 0.30		**1.02 ± 0.36***	**2.61 ± 0.46***	7
SBFA	-0.37 ± 0.40	**1.05 ± 0.48***	**3.19 ± 0.45***	**0.88 ± 0.37***	-0.47 ± 0.37	**-1.02 ± 0.36***		**1.59 ± 0.50***	4
TURF	**-1.97 ± 0.42***	-0.54 ± 0.43	**1.60 ± 0.49***	-0.71 ± 0.46	**-2.06 ± 0.40***	**-2.61 ± 0.46***	**-1.59 ± 0.50***		1

[1] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - Agricultural fields. FALL - Fallow area. HARD – Hardwoods. SCRB - Scrub. SBFA - Scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass.

[2] Higher ranks indicate higher selection relative to other habitat types. Calculated by totaling number of positive values within row.

[*] *t*-test, $P \leq 0.05$).

Table 3.3. Mean (± SE) log ratio differences using compositional analysis for 2nd and 3rd order habitat use by radio-tagged northern bobwhite broods (n = 18) in Laurens County, Georgia, USA, May – August, 2002-2003.

2nd Order		**BQI**[1]	**CROP**	**ERSC**	**TURF**	**WOOD**	**Rank**[2]
	BQI		**3.93 ± 0.78***	0.56 ± 0.44	**2.94 ± 0.61***	**1.97 ± 0.59***	4
	CROP	**-3.93 ± 0.78***		**-3.38 ± 0.94***	-0.99 ± 1.02	-1.96 ± 1.06	0
	ERSC	-0.56 ± 0.44	**3.38 ± 0.78***		**2.39 ± 0.76***	**1.41 ± 0.46***	3
	TURF	**-2.94 ± 0.61***	0.99 ± 1.02	**-2.39 ± 0.76***		-0.97 ± 0.86	1
	WOOD	**-1.97 ± 0.59***	1.96 ± 1.06	**-1.41 ± 0.46***	0.97 ± 0.86		2
3rd Order							
	BQI		-0.19 ± 0.30	**-0.95 ± 0.42***	1.01 ± 0.87	-0.29 ± 0.49	1
	CROP	0.19 ± 0.30		-0.75 ± 0.43	1.21 ± 0.84	-0.10 ± 0.49	2
	ERSC	**0.95 ± 0.42***	0.75 ± 0.43		**1.96 ± 0.62***	**0.66 ± 0.30***	4
	TURF	-1.01 ± 0.87	-1.21 ± 0.84	**-1.96 ± 0.62***		**-1.30 ± 0.54***	0
	WOOD	0.29 ± 0.49	0.1 ± 0.54	**0.66 ± 0.30***	**1.30 ± 0.54***		3

[1] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CROP - Agricultural fields. ERSC - Early successional habitat, dominated shrubs, young trees, grasses, and/or weeds. TURF - Areas dominated by bermudagrass. WOOD - All woodland stands.

[2] Higher ranks indicate greater selection relative to other habitat types. Calculated by totaling number of positive values within row.

[*] *t*-test, $P \leq 0.05$.

Table 3.4. Results from distance-based analysis of 2nd order individual habitat use: mean differences (± 1 SE) between the ratios of distance of home range random points (used) and landscape random points (available) to each habitat type for individual bobwhites (n = 92) in Laurens County, Georgia, USA, May – August, 2002-2003.

	BQI[1]	**CCPN**	**CROP**	**FALL**	**HRWD**	**SCRB**	**SBFA**	**TURF**	**Rank**[2]
BQI		**-0.90 ± 0.12***	0.03 ± 0.06	**-0.18 ± 0.06***	**-0.54 ± 0.06***	**-0.23 ± 0.07***	-0.12 ± 0.07	**-0.17 ± 0.08***	6
CCPN	**0.90 ± 0.12***		**0.93 ± 0.12***	**0.71 ± 0.13***	0.36 ± 0.12	**0.67 ± 0.12***	**0.78 ± 0.11***	**0.73 ± 0.11***	0
CROP	-0.03 ± 0.06	**-0.93 ± 0.12***		**-0.21 ± 0.06***	**-0.57 ± 0.09***	**-0.26 ± 0.06***	**-0.15 ± 0.07***	**-0.20 ± 0.08***	7
FALL	**0.18 ± 0.06***	**-0.71 ± 0.13***	**0.21 ± 0.06***		**-0.36 ± 0.08***	-0.04 ± 0.06	0.07 ± 0.08	0.01 ± 0.09	3
HRWD	**0.54 ± 0.06***	-0.36 ± 0.12	**0.57 ± 0.09***	**0.36 ± 0.08***		**0.31 ± 0.09***	**0.42 ± 0.08***	**0.37 ± 0.10***	1
SCRB	**0.23 ± 0.07***	**-0.67 ± 0.12***	**0.26 ± 0.06***	0.04 ± 0.06	**-0.31 ± 0.09***		0.11 ± 0.08	0.06 ± 0.08	2
SBFA	0.12 ± 0.07	-0.78 ± 0.11	**0.15 ± 0.07***	-0.07 ± 0.08	**-0.42 ± 0.08***	- 0.11 ± 0.08		-0.05 ± 0.08	5
TURF	**0.17 ± 0.08***	**-0.73 ± 0.11***	**0.20 ± 0.08***	-0.01 ± 0.09	**-0.37 ± 0.10***	-0.06 ± 0.08	0.05 ± 0.08		4

[1] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - Agricultural fields. FALL - Fallow area. HARD – Hardwoods. SCRB - Scrub. SBFA - Scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass.

[2] Higher ranks indicate higher selection relative to other habitat types. Calculated by totaling number of negative values within row.

[*] *t*-test, $P \leq 0.05$).

Table 3.5. Results from distance-based analysis of 3rd order individual habitat use: mean differences (± 1 SE) between the ratios of distance of radiolocations (used) and home range random points (available) to each habitat type for individual bobwhites (n = 92) in Laurens County, Georgia, USA, May – August, 2002-2003.

	BQI[1]	**CCPN**	**CROP**	**FALL**	**HRWD**	**SCRB**	**SBFA**	**TURF**	**Rank[2]**
BQI		**-0.08 ± 0.03***	-0.02 ± 0.02	0.01 ± 0.03	-0.05 ± 0.07	-0.28 ± 0.28	**0.07 ± 0.03***	0.03 ± 0.03	4
CCPN	**0.08 ± 0.03***		**0.06 ± 0.03***	**0.08 ± 0.03***	0.03 ± 0.06	-0.19 ± 0.28	**0.15 ± 0.04***	**0.11 ± 0.04***	1
CROP	0.02 ± 0.02	**-0.06 ± 0.03***		0.02 ± 0.03	-0.03 ± 0.07	-0.26 ± 0.28	**0.09 ± 0.03***	0.05 ± 0.03	3
FALL	-0.01 ± 0.03	**-0.08 ± 0.03***	-0.02 ± 0.03		-0.06 ± 0.08	-0.28 ± 0.28	**0.07 ± 0.03***	0.03 ± 0.03	5
HRWD	0.05 ± 0.07	-0.03 ± 0.06	0.03 ± 0.07	0.06 ± 0.08		-0.23 ± 0.29	0.12 ± 0.08	0.09 ± 0.08	2
SCRB	0.28 ± 0.28	0.19 ± 0.28	0.26 ± 0.28	0.28 ± 0.28	0.23 ± 0.29		0.35 ± 0.29	0.31 ± 0.28	0
SBFA	**-0.07 ± 0.03***	**-0.15 ± 0.04***	**-0.09 ± 0.03***	**-0.07 ± 0.03***	-0.12 ± 0.08	-0.35 ± 0.29		-0.04 ± 0.03	7
TURF	-0.03 ± 0.03	**-0.11 ± 0.04***	-0.05 ± 0.03	-0.03 ± 0.03	-0.09 ± 0.08	-0.31 ± 0.28	0.04 ± 0.03		6

[1] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - Agricultural fields. FALL - Fallow area. HARD – Hardwoods. SCRB - Scrub. SBFA - Scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass.

[2] Higher ranks indicate higher selection relative to other habitat types. Calculated by totaling number of negative values within row.

*t-test, $P \leq 0.05$).

Table 3.6. Results from distance-based analysis of 3rd order brood habitat use: mean differences (± 1 SE) between the ratios of distance of radiolocations (used) and home range random points (available) to each habitat type for bobwhite broods (n = 18) in Laurens County, Georgia, USA, May – August, 2002-2003.

	BQI[1]	**CROP**	**ERSC**	**TURF**	**WOOD**	**Rank**[2]
BQI		0.13 ± 0.07	**0.22 ± 0.10***	0.006 ± 0.06	-0.06 ± 0.10	1
CROP	-0.13 ± 0.07		0.09 ± 0.14	-0.12 ± 0.09	-0.19 ± 0.13	3
ERSC	**-0.22 ± 0.10***	-0.09 ± 0.14		-0.22 ± 0.12	-0.28 ± 0.18	4
TURF	-0.006 ± 0.06	0.12 ± 0.09	0.22 ± 0.12		-0.07 ± 0.10	2
WOOD	0.06 ± 0.10	0.19 ± 0.13	0.28 ± 0.18	0.07 ± 0.10		0

[1] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CROP - Agricultural fields. ERSC - Early successional habitat, dominated shrubs, young trees, grasses, and/or weeds. TURF - Areas dominated by bermudagrass. WOOD - All woodland stands.

[2] Higher ranks indicate greater selection relative to other habitat types. Calculated by totaling number of negative values within row.

[*] *t*-test, $P \leq 0.05$.

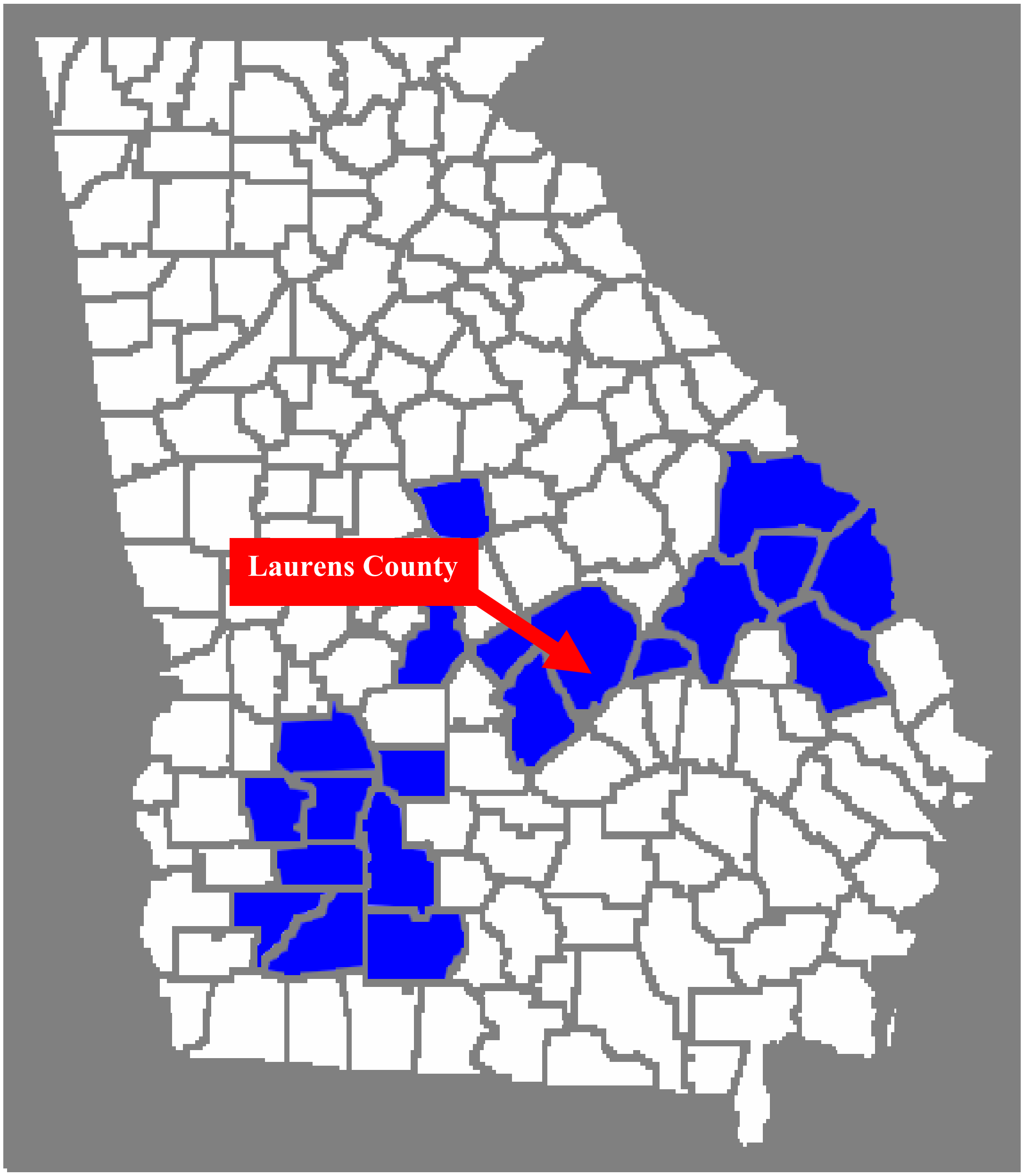

Figure 3.1. Map of Georgia, USA by county. Bobwhite Quail Initiative counties are shaded. This research was conducted in Laurens County.

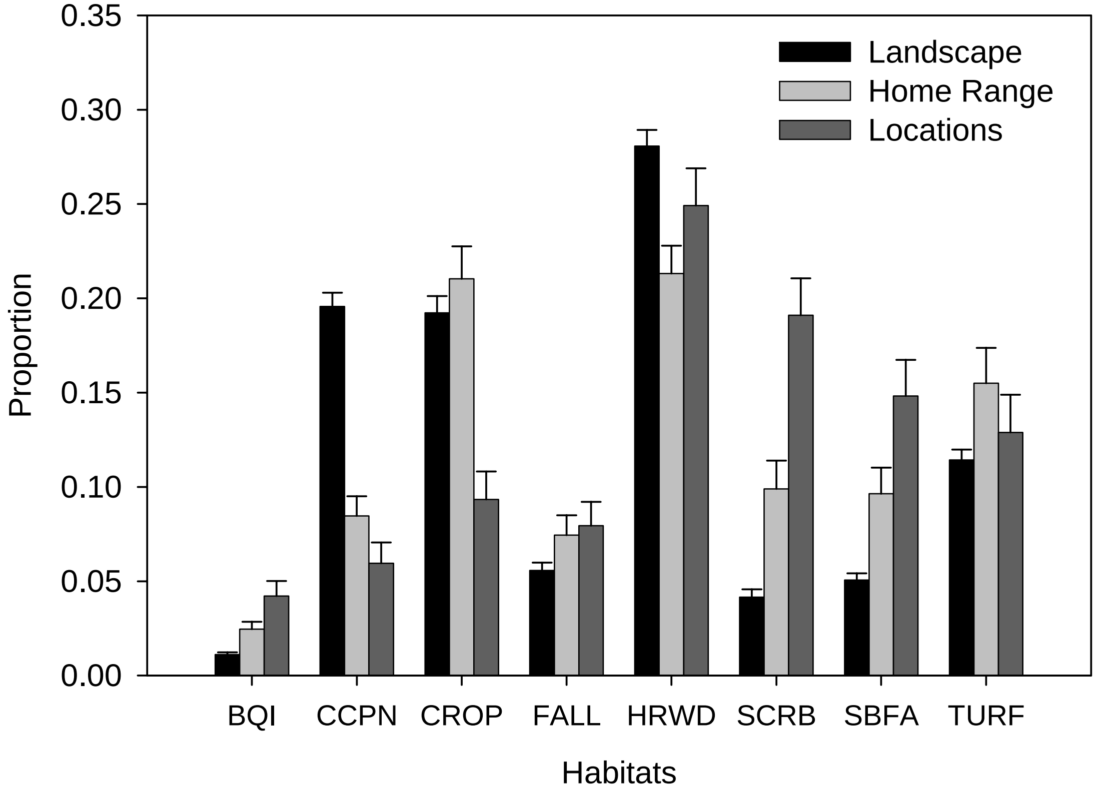

Figure 3.2. Mean (± SE) landscape, home range, and location level habitat proportions for adult northern bobwhites (n = 92) in Laurens County, Georgia, USA, May – August, 2002-2003. BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - Agricultural fields. FALL - Fallow area. HARD – Hardwoods. SCRB - Scrub. SBFA - Scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass.

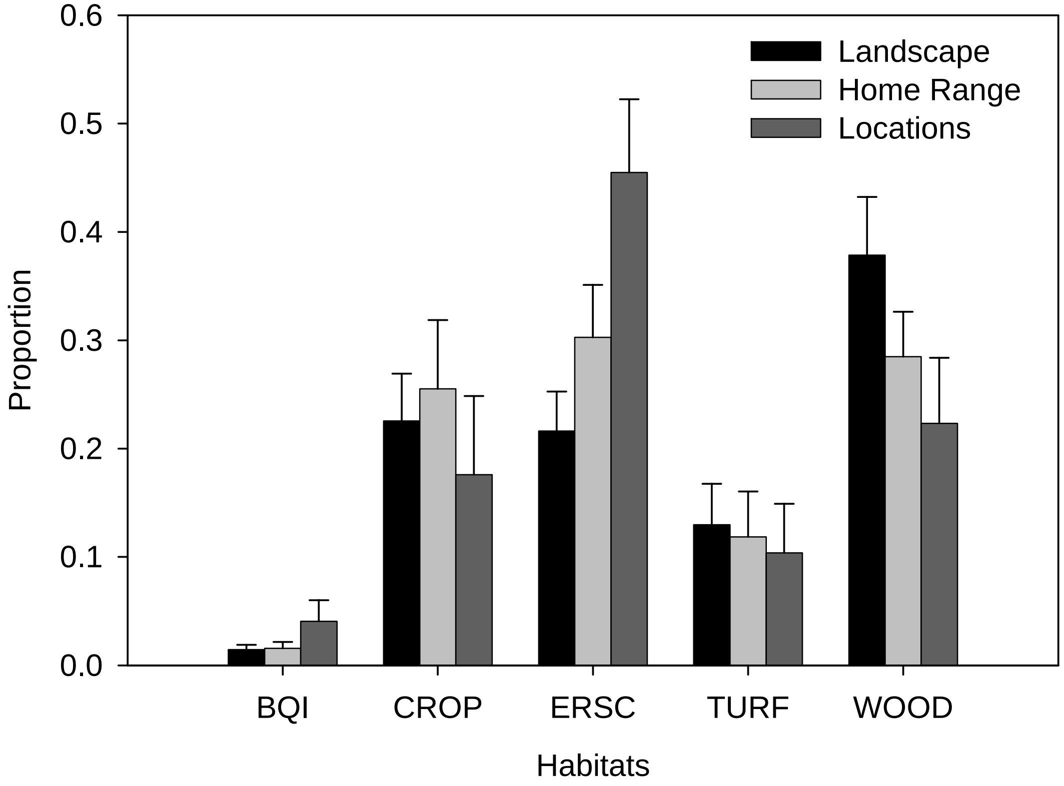

Figure 3.3. Mean (± SE) landscape, home range, and location level habitat proportions for northern bobwhite broods (n = 18) in Laurens County, Georgia, USA, May – August, 2002-2003. BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CROP - Agricultural fields. ERSC - Early successional habitat, dominated shrubs, young trees, grasses, and/or weeds. TURF - Areas dominated by bermudagrass. WOOD - All woodland stands.

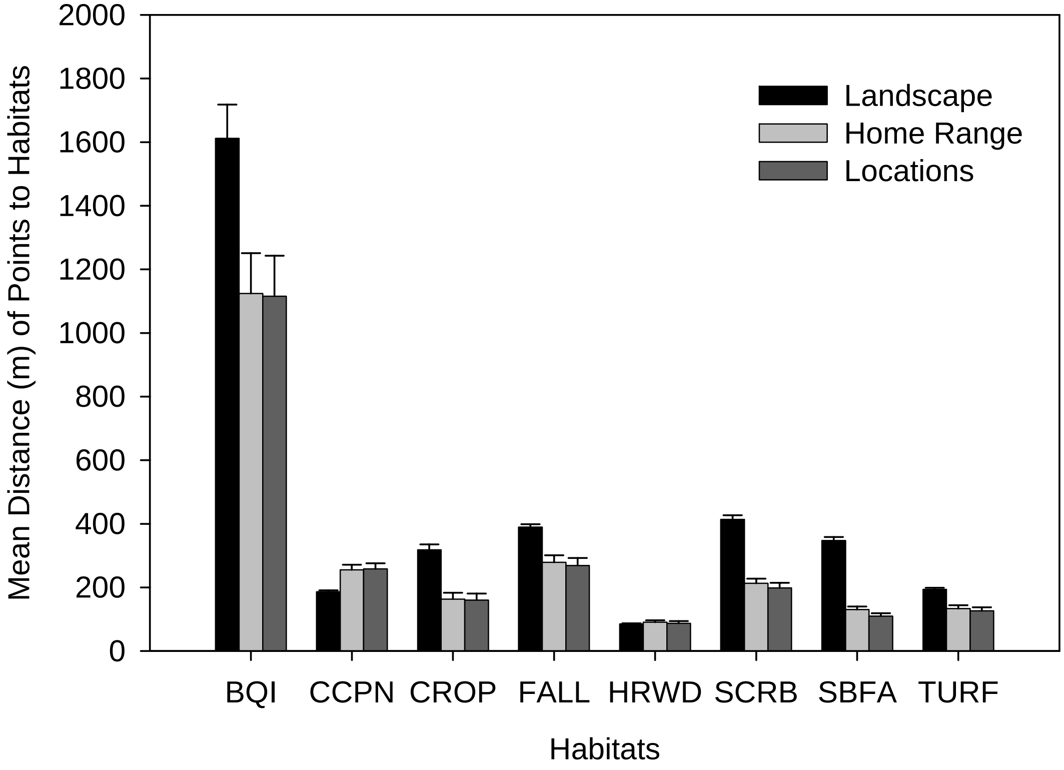

Figure 3.4. Mean (± SE) distances of landscape-level random points, within home range random points, and actual locations to habitat types for adult northern bobwhites (n = 92) in Laurens County, Georgia, USA, May – August, 2002-2003. BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - Agricultural fields. FALL - Fallow area. HARD – Hardwoods. SCRB - Scrub. SBFA - Scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass.

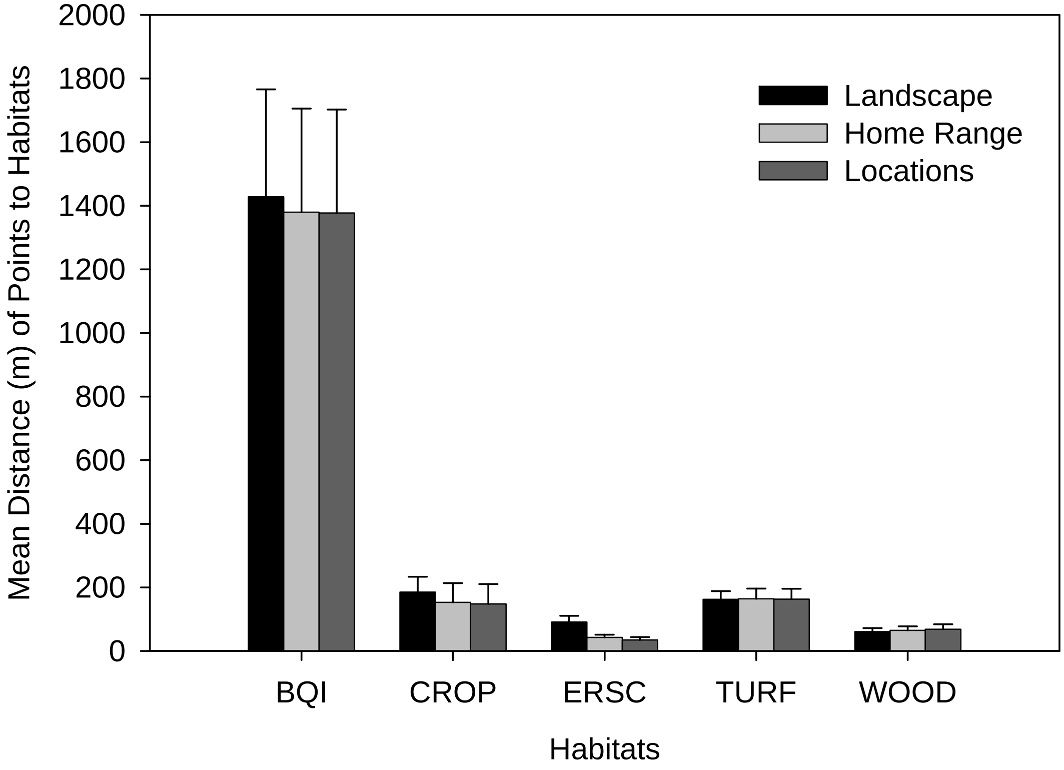

Figure 3.5. Mean (± SE) distances of landscape-level random points, within home range random points, and actual locations to habitat types for northern bobwhite broods (n = 18) in Laurens County, Georgia, USA, May – August, 2002-2003. BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CROP - Agricultural fields. ERSC - Early successional habitat, dominated shrubs, young trees, grasses, and/or weeds. TURF - Areas dominated by bermudagrass. WOOD - All woodland stands.

CHAPTER 4

NORTHERN BOBWHITE BREEDING SEASON SURVIVAL

INTRODUCTION

The decline of northern bobwhite (*Colinus virginianus*) (hereafter bobwhite) populations has been attributed mainly to changes in land use that have degraded bobwhite habitat (Brennan 1991, Burger 2002). Most researchers that have examined bobwhite-habitat relationships have inferred the value of habitats based on their use or associated bobwhite abundance. Several studies have reported higher abundance of bobwhites where linear habitats are present in agricultural ecosystems. For example, Hamrick (2002) found that bobwhite abundance was greater on crop fields enrolled in Georgia's Bobwhite Quail Initiative (BQI) program (GA DNR 1999), a program aimed at providing habitat mainly in the form of linear habitats on crop fields, than on fields with no linear habitats. Similar results have been observed in North Carolina (Puckett *et al.* 2000, Bromley *et al.* 2002). Although these findings suggest that bobwhites are attracted to linear habitats in agricultural systems, the evidence that these habitats benefit populations is not conclusive. These studies could not ascertain if the observed differences were a result of an increase in survival and/or reproductive success or a result of temporarily increased immigration. If there is an effect of these habitats on bobwhite populations, knowing which parameters are being affected and the magnitude of the effect would be useful in determining the utility of these habitats. Although knowledge of habitat use patterns is important in determining the value of habitats and the efficacy of management decisions (Alldredge *et al.* 1998), use or avoidance of habitats alone does not necessarily infer relative quality of habitats (Van Horne 1983). To increase bobwhite populations on a regional level, we must determine how specific habitat attributes affect demographic parameters, such as survival, and distinguish these effects from changes in local population distributions (Taylor *et al.* 1999).

Information on how other factors affect survival would also be useful in both the management of bobwhite populations and understanding the ecology of the species. For example, metapopulation principles are almost certainly relevant to bobwhite biology and management considering the relatively low mobility of the species and the fact that it often inhabits fragmented landscapes (Fies *et al.* 2002); therefore, knowledge of bobwhite ability to disperse and survive in unfamiliar areas is needed. The effect of sex and age on survival would allow us to better understand the causes of observed sex and age ratios. Finally, the cost of reproduction in terms of increased mortality risk to the adult bird is important to the understanding of population processes. The objectives of this study were to estimate bobwhite breeding season survival and to examine the effects of habitat, sex, age, dispersal and reproduction on this parameter.

METHODS

Study Area

I conducted my study on a 133 km^2 area in western Laurens County, Georgia. This area was chosen because land uses and habitats there were typical of the southeastern U.S.A. and because there were relatively large numbers of fields enrolled in the BQI program there. I 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 photos were 10 years old, I correctly classified all habitat types using field reconnaissance and ground-truthing unfamiliar areas with GPS equipment. I produced two maps (one for each year) to reflect any changes in the landscape that occurred during the course of our study. Changes were very slight between years and the following percentages are averages from the two maps.

Habitat types delineated for my study included linear habitats provided by BQI (BQI; 0.27% of the study area), row crop fields (CROP; 13.39%), closed-canopy pine stands (CCPN; 23.36%), hardwoods (HRWD; 32.97%), areas dominated by bermudagrass (TURF; 12.37 %), fallow areas with very little to no woody vegetation (FALL; 5.01%), areas of low woody cover dominated by shrubs and/or young trees including hedgerows and fencerows (LWCO; 4.98%), and a category that included residential areas, buildings, open water and other areas that were generally not of interest and therefore excluded from all analyses (OTHR; 7.64%). Most of the crop fields on my study area were planted in cotton, but there were also peanuts, corn, and soybeans. The mean size of crop fields was 9.55 ha (SE=0.69).

Capture and Telemetry

I 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 were banded, equipped with a 6.4-6.9 g pendant-style (necklace) radiotransmitter, classified by sex and age (adult and juvenile), and released at the trap site. All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on 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).

I located bobwhites on foot using homing techniques (White and Garrott 1990). I moved to within 25-50m at each radio-location to minimize location and habitat classification error. Individual bobwhites were located 4-7 times per week during the breeding season. I assumed that birds were nesting if they were in the same location on 2 consecutive days. Flagging was then placed within 10 m of the potential nest. I confirmed birds to be nesting once they were away from the nest to avoid causing nest desertion. The exact nest location was then recorded. Nests were monitored daily so that the termination date of the nest was known to within one day (Burger *et al.* 1995*b*). If a nest was successful, the resulting brood was located 2-4 times per day until the 14th day post-hatch. All bobwhite locations were plotted onto aerial photos and later entered into a GIS format using ArcView®.

Data Analysis

I examined the effects of several covariates on breeding season survival using an information-theoretic approach. I developed an *a priori* set of 14 candidate models based on literature review, management needs, and my knowledge of bobwhite biology. The model set included the effects of sex (coded F=0, M=1), age (J=0, A=1), within home range habitat variables, brood-rearing (not with a brood $\leq$14 days old = 0, with a brood $\leq$14 days old = 1), nest incubation (not incubating = 0, incubating = 1), and dispersal (non-disperser = 0, disperser = 1). Although other studies have reported differences in bobwhite breeding season survival among years (e.g. Taylor *et al.* 2000), I had no reason to suspect that year would have an effect on survival of birds in my study; therefore, I did not include it in the model set (Burnham and Anderson 2002). I used program MARK to calculate AICc values and parameter estimates for each model. I then calculated AIC_c (AIC corrected for small sample sizes) values, AIC_c weights, model-averaged parameter estimates and unconditional standard errors for each effect and overall survival (Burnham and Anderson 2002).

Habitat variables included the proportions of each habitat within the home range and indices for the interspersion of LWCO and CCPN with open habitats (INLWCO and INCCPN, respectively). I used the animal movements extension (Hooge and Eichenlaub 1997) designed for ArcView® to calculate fixed kernel home ranges (Worton 1989) with a 95% isopleth requiring ≥20 locations to calculate home ranges (DeVos and Mueller 1993). I selected the defaults option which uses *ad hoc* calculation of a smoothing parameter. Although landscape attributes at larger scales likely affect bobwhite demographics (Brady *et al.*1993), I only measured the effect of habitat at the home range level because I believed that habitat at this scale would be most related to the region of bobwhite activity and the ecological process of interest (Addicott *et al.* 1987). Habitat proportions within home ranges were determined by intersecting home ranges with the habitat map. I calculated INLWCO and INCCPN by generating 1000 random points within the open habitats of each home range and calculating the average distance of these points to the two habitat types; therefore, higher values indicated less interspersion. The interspersion of other habitat types were not considered because the interspersion of CCPN and LWCO with open habitat were viewed as the most likely to have an effect on survival and I wished to keep the number of models low, thereby reducing the possibility of spurious results (Anderson and Burnham 2002).

To accommodate the inclusion of the reproductive and dispersal covariates in the model set and because birds were not typically located every day, I measured survival during 34 3-day intervals from 19 May (the last known date that dispersal ended; see chapter 2) to 28 August. Although the breeding season was not completed on 28 August, logistical constraints prevented regular telemetry locations after this date. I incorporated the effects of brood-rearing and incubation as time-varying covariates. Birds were considered to be brood-rearing during an interval if they were with a brood that was ≤14 days old (pre-fledgling period) on ≥1 day of the interval. Birds were classified as incubating in the same manner. If, during an interval, a bird was both incubating and brood-rearing, I assigned whichever reproductive status occupied the most days. I included brood-rearing in every model because I believed it would have the strongest effect on survival.

RESULTS

I used 92 (46 female, 46 male; 28 adult, 64 juvenile) radio-tagged bobwhites in the survival analysis. The model-averaged estimate of survival for bobwhites during 19 May-28 August pooled across years was 0.499 (SE=0.056). Habitat variables were similar among sexes and ages (Table 4.1)

My best approximating model (ω=0.13) showed that survival probability varied among individuals relative to brood-rearing status and INLWCO (Table 4.2). However, the next 3 best models in the set were within 2 ΔAIC_c units of the best models indicating substantial empirical support of these models as well (Burnham and Anderson 2002:70-72). The last three models were >2 but still within 10 ΔAIC_c units of the best model indicating at least a reasonable level of support (Anderson *et al.* 2001).

Brood-rearing had a strong negative effect on survival ($\beta = -1.59$, SE = 0.43), whereas nest incubation had a positive effect ($\beta = 0.74$, SE = 0.56)(Table 4.3). Adults had greater survival probability than juveniles ($\beta = 0.45$, SE = 0.35), and males appeared to be more likely to survive than females ($\beta = 0.33$, SE = 0.32). BQI had a positive, but highly variable, effect on survival ($\beta = 3.41$, SE = 4.64). CROP also had a positive effect, but this effect was much smaller ($\beta = 0.64$, SE = 0.96). Both woodland habitats had a negative effect on survival (CCPN: $\beta = -2.06$, SE = 0.56; HRWD: $\beta = -1.50$, SE = 1.21). High values for INCCPN, and therefore low interspersion of CCPN with open habitat, had a positive effective on survival ($\beta = 0.25$, SE = 0.16). Conversely, high values for INLWCO, and therefore low interspersion of LWCO with open habitat, had a negative effect on survival (β = -0.27, SE = 0.16). However, the proportion of LWCO within home ranges had a very slight negative effect (β = -0.003, SE = 0.01). The effects of all other parameters were slight as well.

DISCUSSION

Most researchers have attributed bobwhite male-biased sex ratios to differential survival between the sexes, but the causes and timing of this differential survival are unclear (Burger 1995*a*). Leopold (1945), Buss *et al.* (1947), and Bennitt (1951) speculated that female mortality was higher during incubation. Conversely, Roseberry and Klimstra (1984:136) suggested that mortality during incubation was low and that differential mortality during the non-breeding season was at least partially responsible for the male-biased sex ratio. Although Stoddard (1931:94-95) speculated that females were captured on the nest more often because they performed the majority of incubation, he also suggested that the flight abilities of females were inferior and that hens were therefore more susceptible to avian predation during winter. Other researchers have reported higher female harvest rate (Pollock *et al.* 1989, Shupe *et al.* 1990, Roseberry and Klimstra 1992). Burger (1995*a*) found that females experienced higher mortality during the non-breeding season, but survival was similar to that of males during the breeding season. Taylor *et al.* (1999) reported higher male breeding season survival on an area dominated by rangeland, but almost identical survival on an area dominated by cropland. Taylor *et al.* (2000) and Smith (2001) actually found higher female survival during the breeding season. In my study, males were somewhat more likely to survive than females during the breeding season, but the effect was not great. I agree with Burger *et al.* (1995*a*) who suggested that although females were more likely to incur mortality costs associated with reproduction, males incurred some of these costs too and were also more susceptible to avian predation while singing (i.e.

advertising for mates); therefore, the survival of the two sexes usually tends not to diverge greatly during the breeding season. However, the physiological costs of reproduction could have effects on non-breeding season survival of females. Females are known to experience a distinct weight loss during late-summer (Roseberry and Klimstra 1971:119). Females could remain in poor condition into the fall months and therefore be less able to evade predators. Kabat and Thompson (1963:72) suggested that the physiological stress of reproduction is the main factor affecting fall mortality.

Adults in this study were more likely to survive than juveniles suggesting that adults may benefit from past experience with habitat and predators. Other studies have reported a somewhat higher rate of survival for juveniles (Burger 1995*a*, Taylor *et al.* 2000, Smith 2001). One explanation for this discrepancy is that age may interact with only certain habitats which differ among study areas. In Chapter 2, my best approximating model demonstrated that dispersal probability varied among individuals relative to interactions between age and proportions of closed canopy pines and early successional habitat within their winter home ranges, such that adults with higher proportions of early successional habitat in their winter home range were less likely to disperse and those with more closed canopy pines were more likely to disperse. In the studies that found higher juvenile survival, closed-canopy pine was either rare or not present. Perhaps, adults are less vulnerable to the negative effects of closed-canopy pine or some other habitat.

Interestingly, I found a somewhat positive effect of incubation, but a negative effect of brood rearing on survival. Bobwhites defend their nests and broods sometimes by attacking perceived aggressors, but more often by performing a broken wing display to lure predators away from the brood or nest (Stokes 1967). However, broods represent more in terms of parental investment and potential reproductive success and therefore parenting adults will assume greater risks to protect chicks than nests (Barash 1977:186). Although Burger (1995) found a negative effect of incubation on survival, the effect of brood-rearing was responsible for 66% of the increased mortality risk during reproduction. The fact that incubation had a positive effect on survival of bobwhites in this study, but a negative effect in Missouri (Burger 1995*a*) suggests some possible study area differences. Of the main predators known to depredate bobwhite nests in the Southeast (see Staller 2001), it is likely that only the raccoon (*Procyon lotor*) kills bobwhites on the nest to any appreciable extent. Predators of bobwhite nests in Missouri have not been identified, but Burger (1995*b*) speculated that mammals were primarily responsible for causing mortality during incubating. Differences between the two studies may be explained by differences in the composition of the nest predator community.

A high rate of parent mortality during brood-rearing may have important consequences for recruitment rates in areas of low bobwhite density. Bobwhites are known to adopt the offspring of other birds (Stoddard 1931:65-66). However, I suspect that adoption of orphaned chicks is rare in low density areas. In a separate study involving brood captures on the same site where this study was conducted, amalgamation (brood-mixing) was suspected in only 1 of 10 broods captured based on large differences in chick weights. Although amalgamated broods may consist of chicks of the same age and weight (Faircloth *et al.*, in press) and there were only a few broods captured, this does suggest that adoption of orphaned chicks may be rare in low density areas. Therefore, death of the parent during the pre-fledgling period will likely result in loss of the entire brood. How certain habitats affect brood-rearing mortality should be investigated. Although I was unable to examine possible habitat effects on brood-rearing mortality, hardwoods had an overall negative effect on survival and I suspect that hardwoods had an especially strong negative effect on survival of brooding adults given that this habitat is preferred by many mammalian predators such as the raccoon (Kaufman 1982). Mammalian predation is known to increase during the breeding season (Curtis *et al.* 1988, Burger *et al.* 1995*a*) and has been attributed to increased susceptibility of nesting and brood-rearing bobwhites to predators with olfactory sense (Burger 1994). However, avian predation risk could also increase during brood rearing.

Although hardwood habitat had a negative effect on survival, bobwhites expressed high selection for it (see Chapter 3). Other researchers have reported disproportionate use of hardwoods as well (Lewis 1999, Parnell 2002). Many of the hardwood stands in my study area contained a dense shrub layer, especially near the edges. Therefore, hardwood likely provided similar structural characteristics and perceived benefits as low woody cover. Taylor *et al.* (1999) also found that habitat selection could not necessarily be used to infer habitat quality. Van Horne (1983) suggested that the best way to understand habitat quality was in terms of the influence of habitat on specific demographic parameters.

The proportion of BQI habitat within individual home ranges had a positive effect on survival. Although the effect of BQI habitat is somewhat confounded with the effect of crop fields which also had a positive effect on survival, the effect of BQI was much greater, providing more evidence that BQI is positively affecting bobwhite populations. These habitats likely provide valuable travel corridors as well as safe feeding areas due to their linear shape, vegetative composition, and interspersion with other habitats. However, the BQI effect was highly variable. This is likely due to the fact that BQI habitats constitute a relatively small proportion of the landscape; therefore, their effect is probably contingent upon the associated crop type and other habitats present. For example, a BQI field border encompassing a cotton field bordered by a closed-canopy pine stand will likely not increase the survival probability of a bobwhite inhabiting that area. Conversely, a field border that encompasses a corn field and is bordered by weedy habitat interspersed with low woody cover will also likely do little to affect survival probability since survival in that area will likely already be relatively high. I suggest that there are intermediate situations in which BQI habitats have the greatest effect on survival and that the effects of other habitats should be considered when determining the eligibility of fields to be enrolled in the BQI program.

Although BQI habitats had a positive effect on survival, other fallow habitats had little impact. Individual bobwhites tended to avoid these areas (see Chapter 3). For some unknown reason, this habitat could have been associated with high predator abundance on my study area. Perhaps there was an abundance of other early successional prey species which attracted predators. Although the habitat appears to be of little value to individuals, broods foraged in the insect-abundant fallow areas extensively. An abundance of fallow habitat probably has a positive effect on chick growth and survival, therefore recruitment.

In my study both the amount and interspersion of closed-canopy pine had a negative effect on survival. Rollins and Carroll (2001) argued that habitat could influence predator search efficiency, therefore the interaction of quail and their predators. The presence of closed-canopy pine probably increases the ability of predators to capture bobwhites. Although avoided by bobwhites (Lewis 1999, Parnell 2002, also see Chapter 3), closed-canopy pine is widely distributed and constitutes a relatively large proportion of the landscape. Therefore, bobwhites almost invariably must incorporate at least some of this habitat within their home ranges. Further, its wide distribution means that it will often be in close proximity to open habitats. The likely explanation for why the interspersion of closed-canopy pine had a negative impact on survival is that bobwhites, when stressed by the attack of a predator, may flush into the nearest woody cover which could be closed-canopy pine. Once inside the stand, the bobwhite is an easy target for avian predators, such as the Cooper's hawk (*Accipiter cooperii*). A high proportion of the southeastern landscape consists of closed-canopy pine and this proportion will likely increase (Burger 2002). Pine stands can be managed to benefit bobwhites through thinning and burning (Lewis 1999, Parnell 2002). The management of pine stands must be a high priority if we are to increase bobwhite populations on a regional level in the Southeast.

High temperatures during the summer months can result in thermal fragmentation of certain habitats (Forrester *et al.* 1998) which could reduce fitness. The shading and evapotranspiration of woody and herbaceous vegetation can mitigate this thermal fragmentation by reducing ground level temperatures (Forrester *et al.* 1998). Conversely, bermudagrass offers little shading due to its growth form. Burkhart (2004) found that patches of bermudagrass could form "heat traps" where temperatures exceed 39 C, the temperature at which Guthery *et al.* (2001*a*) determined to be a critical threshold for heat dissipation. I found only a very slight negative effect of bermudagrass on breeding season survival, suggesting that adults are able to cope with thermal fragmentation. However, the effect of bermudagrass on chick survival may be much more profound. Chicks are much less mobile than adults and Burkhart (2004) found that bermudagrass impeded the mobility of young chicks. Therefore, chicks are likely much more vulnerable to the heat traps produced in bermudagrass, especially in large patches. Information on the effect of bermudagrass on chick survival is needed.

The importance of woody cover to winter survival, when avian predation is highest, has been demonstrated (Williams *et al.* 2000), but its importance to breeding season survival has received less attention. In this study, the configuration of low woody cover was important in determining survival probability but its proportion within home ranges was not. The extremely slight negative effect of woody cover amount suggests that this cover should be very well distributed but not necessarily abundant. It should also be noted that the relationship of survival to the interspersion of woody cover is probably non-linear and increasing interspersion will be beneficial only to a certain point and further increases will be redundant or possibly harmful.

In my study, the survival probability of dispersers was almost identical to that of non-dispersers. Townsend *et al.* (2003) found that the survival of bobwhites that dispersed was nearly 1.5 times that of non-dispersers. However, the mortality that occurs during bobwhite dispersal has yet to be examined. Dispersers may experience increased risks of mortality during dispersal, especially in landscapes where the matrix is particularly inhospitable (Fahrig 2001). It would be difficult to measure this mortality risk, requiring very intensive monitoring during the time when bobwhites are dispersing. Further, determining the effect of habitat on survival during dispersal would also require intensive monitoring so that the exact dispersal path could be determined. However, this knowledge is crucial to both understanding bobwhite ecology and managing bobwhite populations in fragmented landscapes.

Guthery (1997) argued that management practices designed to increase bobwhite populations by increasing survival or productivity are ineffective because density-dependent predation mediates against this approach. He further argued that only way to increase the number of bobwhites on an area was to increase useable space through time. According to this hypothesis, survival would increase if useable space was increased because density would decrease, but this increase in survival would be short-lived because survival would decrease as density returned to its prior level. In a study in Mississippi, Taylor *et al.* (2000) found that survival increased in the first year following the implementation of habitat management, but then declined over the next four years, which could be viewed as support for the useable space hypothesis. However, Roseberry and Klimstra (1984) observed similar fluctuations for unmanaged bobwhite populations in Illinois that typically occurred over four years. Further, Taylor *et al.* (1999) provided evidence that contradicted the useable space hypothesis. In their study, both survival and productivity varied relative to certain habitat variables. Survival varied relative to habitat variables in this study as well, suggesting that demographic parameters may be at least in part determined by habitat quality. Guthery *et al.* (2001*b*) argued that variation in survival among individuals relative to habitat was not in contradiction to the useable space hypothesis. They argued that demographic parameters would converge to a mean that was not affected by habitat quality. However, if the survival probabilities of individuals are, on average, higher or lower due to the presence of a certain habitat, then reason dictates that the average survival of the population would have to change if that habitat is increased or decreased. According to the useable space hypothesis, once density increased to certain level, survival would be reduced by increased density-dependent mortality. However, if a habitat like closed-canopy pine, in which the ability of predators to capture bobwhites is higher than in other habitat types, is converted to a beneficial habitat, then the density-dependent relationship could be altered. Potts (1986) provided evidence that predator reduction alters density-dependent predation of gray partridge (*Perdix perdix*). In addition, he suggested that some aspects of the life history of the gray partridge, e.g. chick survival, were not density-dependent at all. Rollins and Carroll (2001) suggested that predator reduction might also alter density-dependent predation of bobwhites resulting in higher survival and/or productivity at given density than would be expected by the density-dependent reproduction relationship (Roseberry and Klimstra 1984). I suggest that altering habitat composition and configuration could hinder the ability of predators to depredate adults and nests and therefore alter density-dependent predation, resulting in higher survival or productivity than would be expected at a given density.

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Table 4.1. Mean (± SE) proportions of habitats within the home ranges of 92 radio-tagged breeding bobwhites, plus two interspersion indices, classified by sex and age in Laurens County, Georgia during 2002-2003.

	Female (n = 46)	Male (n = 46)	Juvenile (n = 64)	Adult (n = 28)	Pooled (n = 92)
BQI[1]	0.023 ± 0.005	0.025 ± 0.006	0.022 ± 0.005	0.028 ± 0.007	0.024 ± 0.004
CCPN	0.079 ± 0.013	0.085 ± 0.016	0.080 ± 0.012	0.087 ± 0.020	0.082 ± 0.010
CROP	0.191 ± 0.027	0.218 ± 0.022	0.218 ± 0.022	0.173 ± 0.030	0.204 ± 0.018
FALL	0.063 ± 0.016	0.089 ± 0.015	0.083 ± 0.014	0.059 ± 0.013	0.076 ± 0.011
HRWD	0.219 ± 0.020	0.207 ± 0.019	0.207 ± 0.017	0.228 ± 0.021	0.213 ± 0.014
LWCO	0.197 ± 0.024	0.196 ± 0.027	0.167 ± 0.020	0.264 ± 0.035	0.197 ± 0.018
TURF	0.192 ± 0.030	0.130 ± 0.022	0.172 ± 0.022	0.134 ± 0.035	0.161 ± 0.019
INCCPN	267 ± 22	277 ± 19	272 ± 18	271 ± 25	272 ± 14
INLWCO	87 ± 9	76 ± 6	81 ± 6	82 ± 9	81 ± 5

[1] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - agricultural fields. FALL - Fallow area. HRWD – Hardwoods. LWCO – Scrub and scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass .

INCCPN and INLWCO are indices of the interspersion of CCPN and LWCO with open habitat. Higher values for the two indices indicate less interspersion.

Table 4.2. Candidate models used to evaluate breeding season survival of 92 radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003. All models include an intercept term.

Model	**AIC_c**	**Δ AIC_c**	**Model Weight**	**K**[1]
Brood-rearing + INLWCO[2]	415.56	0.00	0.13	3
Brood-rearing + Incubation	415.91	0.35	0.11	3
Brood-rearing	416.01	0.45	0.11	2
Brood-rearing + INCCPN	416.03	0.47	0.11	3
Brood-rearing + INCCPN + TURF	416.20	0.64	0.10	4
Brood-rearing + HRWD + CCPN	417.10	1.54	0.06	4
Brood-rearing + TURF	417.23	1.67	0.06	3
Brood-rearing + Sex + Age	417.32	1.76	0.06	4
Brood-rearing + BQI	417.41	1.85	0.05	3
Brood-rearing + FALL + INLWCO	417.53	1.97	0.05	4
Brood-rearing + CROP	417.56	2.00	0.05	3
Brood-rearing + LWCO	417.96	2.40	0.04	3
Brood-rearing + FALL	418.00	2.45	0.04	3
Brood-rearing + Dispersal	418.01	2.45	0.04	3

[1] Number of parameters included in the model.

[2] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - agricultural fields. FALL - Fallow area. HRWD – Hardwoods. LWCO – Scrub and scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass .
INCCPN and INLWCO are indices of the interspersion of CCPN and LWCO with open habitat. Higher values for the two indices indicate less interspersion.

Table 4.3. Model-averaged estimates, unconditional standard errors, and confidence intervals for effects on breeding season survival of 92 radio-marked bobwhites monitored in Laurens County, Georgia during 2002-2003.

Parameter	**β**	**SE**	**LCI**[1]	**UCI**[2]
Intercept	3.93	0.25	3.43	4.42
Brood-rearing	-1.59	0.43	-2.44	-0.74
Incubation	0.74	0.56	-0.35	1.83
Sex	0.33	0.32	-0.28	0.95
Age	0.45	0.35	-0.24	1.14
Dispersal	-0.01	0.37	-0.73	0.71
BQI[3]	3.41	4.64	-5.69	12.51
CCPN	-2.06	1.46	-4.92	0.80
CROP	0.64	0.96	-1.24	2.52
FALL	0.10	1.45	-2.75	2.94
HRWD	-1.50	1.21	-3.87	0.87
LWCO	-0.003	0.01	-0.03	0.02
TURF	-0.01	0.01	-0.02	0.005
INLWCO	-0.27	0.16	-0.59	0.05
INCCPN	0.25	0.16	-0.08	0.57

[1] Lower 95% C.I. limit.

[2] Upper 95% C.I. limit.

[3] BQI - All linear habitats (field borders, filter strips and weedrows) provided by the Bobwhite Quail Initiative. CCPN - Closed-canopy pine. CROP - agricultural fields. FALL - Fallow area. HRWD – Hardwoods. LWCO – Scrub and scrub/fallow (areas dominated by a mixture of shrubs, young trees, grasses and weeds). TURF - Areas dominated by bermudagrass .

INCCPN and INLWCO are indices of the interspersion of CCPN and LWCO with open habitat. Higher values for the two indices indicate less interspersion.

CHAPTER 5

CONCLUSION

In this study, I provided evidence that the BQI program is beneficial to northern bobwhites in Georgia. During the breeding season, both adults and broods used BQI habitats. Also, the presence of BQI habitats had a positive effect on breeding season survival of adults. However, the use of habitats does not necessarily infer habitat quality (Van Horne 1983) and the positive effect of BQI habitat on survival was highly variable suggesting that the effect is probably contingent upon the associated crop type and other habitats present. Additionally, I was unable to examine the effect of BQI habitat on chick survival or winter survival. Chick survival can strongly influence productivity (Roseberry and Klimstra 1984:80-89). BQI habitats could increase chick survival in agricultural areas; therefore, they may have a much greater impact on populations than this study suggests. They could also provide crucial cover during the winter months when crop fields are typically bare; therefore, they could also have a positive effect on winter survival. Future research should examine the effects of BQI habitats on these and other population parameters and also the possible interactions of BQI habitat with other habitat types.

The effects of other habitat types on bobwhite population parameters must be considered when developing management strategies. For example, I found that the interspersion of woody cover was important in determining survival probability during the breeding season. It also likely has a strong effect on winter survival as well (Williams *et al.* 2000). Additionally areas dominated by bermudagrass were avoided by both adults and broods. Although avoided by broods, I suspect that bermudagrass has a negative impact on chick survival due to decreased mobility and intolerably high temperatures (Burkhart 2004). Invasion of this grass into areas managed for bobwhite will likely hamper BQI program development and its elimination is of great importance. The most important non-BQI habitat that should be considered in any bobwhite management effort in the Southeast is closed-canopy pine. I found that closed-canopy pine was a strongly deleterious habitat. It was avoided by bobwhites, but even small proportions of it and its interspersion with open habitat negatively influenced breeding season survival. I suspect that closed-canopy pine also negatively impacts winter survival. These pine stands will likely constitute an increasing proportion of the southeastern landscape (Burger 2002) and could continue to contribute to the precipitous decline of the bobwhite. However, if properly managed through thinning and burning, pine stands can provide prime habitat and support high densities of bobwhite (Lewis 1999, Parnell 2002). The management of pine stands should be a high priority, possibly the highest priority, of any effort to increase bobwhite densities on regional level in the Southeast. This research also suggests that the Longleaf Pine CPA of the Conservation Research Program, which provides alternative management of agricultural fields converted to woodlands, might be a great benefit to bobwhites in the long-term (Conservation Reserve Program 2001). In order for quail hunting opportunities of the past to return, bobwhites must be reasonably abundant over a relatively large geographic area (Roseberry 2000). I believe that the most viable strategy to accomplish this in the Southeast is through the large-scale management of pine stands.

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