Effects of translocation on population genetics and demographics of a Northern Bobwhite (*Colinus virgnianus*) population among a fragmented landscape in southwestern Georgia

by

Theron M. Terhune

(Under the direction of John P. Carroll)

Abstract

Large scale, contemporary studies of genetic and demographics of a non-migratory, avian species in fragmented landscapes are scarce. Changing land-use and increased urbanization have drastically affected wildlife ecosystems and their inhabitants via fragmentation. The paucity of genetic and demographic information for these species generates a gap in the study of population dynamics within these ecosystems, both among avian species, specifically, and all organisms, generally. Thus, knowledge of the effects changing land-use has on population persistence is precarious at best. The philopatric, non-migratory, and sedentary nature of many of these species potentially limits genetic exchange, contributing to variable demographics, both temporally and spatially, and purported population declines among fragmented, isolated landscapes.

It has been proposed that translocation of individuals between populations may mitigate many of the negative effects of habitat fragmentation and isolation. To date, numerous translocations of multiple species have occurred. However, few have investigated the associated demographic and genetic ramifications. Translocation may serve as an artificial means of dispersal and subsequently introduce novel genes to isolated populations, potentially influencing demographic parameters (e.g., increasing fecundity). Furthermore, it is possible that translocation may operate as a conservation tool for restoring populations of declining and threatened species and, ostensibly, may be of increasing value for biodiversity conservation. However, prior to instituting this technique as a widespread management tool, its efficacy warrants investigation using a native, ubiquitous species not considered Endangered or Threatened.

This dissertation addresses questions germane to translocation by integrating data from molecular lab techniques (microsatellite analysis) with field data collected through radio-location and spatial data present in a geographical information system. I selected the Northern Bobwhite (*Colinus virginianus*), a non-migratory, gallinaceous species of low-mobility, as my model species. Northern Bobwhites are particularly sensitive to habitat fragmentation, have suffered keen population declines during the past several decades, are a socio-economically important game bird, and exhibit a flexible mating regime that have demonstrated a strong propensity to respond rapidly to favorable habitat conditions. Therefore, using Northern Bobwhites logically allows for application of results to numerous species necessitating early-succession ecosystems and exhibit similar life-history characteristics.

My research objectives were to determine: the efficacy of translocation to an isolated population of northern bobwhite, temporal and spatial limitations associated with translocation, and demographic disparities between translocated and resident bobwhites. I also examined genetic effects of translocation in northern bobwhites by: determining genotypic differences among resident and translocated bobwhites prior to initial release; tracking novel allele movement and allele frequency change through space and time; and investigating the magnitude of introgression. This research begins to fill significant gaps with regard to scientific knowledge of translocation effects on fragmented ecological systems, meta-population dynamics, and population genetics.

Index words: *Colinus virginianus*, Northern Bobwhite, Microsatellite DNA, Relocation, Reproduction, Site Fidelity, Survival, Translocation

EFFECTS OF TRANSLOCATION ON POPULATION GENETICS AND DEMOGRAPHICS OF A NORTHERN BOBWHITE (*Colinus virgnianus*) POPULATION AMONG A FRAGMENTED LANDSCAPE IN SOUTHWESTERN GEORGIA

by

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DEDICATION

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Chapter 1

Introduction

1.1 Historical Context

Human kind has shaped the biological and physical world since the early prehistoric introduction of man via both knowledge of and ability to use simple tools and techniques to gain benefit from natural resources and to control the environment ensuring, or simply improving, their livelihood. The advent of agriculture and domestication of animals shifted man's relationship with the environment and wildlife from reliance upon as necessity to one of convenience, leisure, and profitability. As such, the environment, wildlife, and landscape has since dramatically been altered as a result of 4 major changes in land-use practices:

Agriculture. Farming during its infancy was largely a subsistence operation wherein crops were grown for market, cash income, or trade, but majority of the farmland was allocated to produce the necessities a family required and to support farm livestock. Under this system existed a flexible, rotational land-use style with a diversity of crops occupying only a portion of the farm with part of the farm typically set aside as pasture and some fields left fallow. The size of farms was limited to the amount of labor available and therefore usually existed of 1 to only a few families and their workers. In addition to small farms and field size, much of the land was uncultivated; thus numerous hedgerows, fencerows, road edges, streambanks, corners, and woodland patches subsisted. These conditions benefited numerous wildlife species (e.g., bobwhites, rabbits, and later pheasants) and when combined with conservative hunting, if at all, they flourished. More recently though the number of farm owners has decreased while farm sizes have increased substantially.

Sivilculture. The pattern of forested lands has paralleled that of agriculture use. Initial timber harvesting operations were sloppy and often lacked planning for future timber regimes. Often these areas were burned and simply left to natural regeneration. Despite overall negative effects these strategies had on forests and their soil, numerous wildlife species benefited (e.g. white-tailed deer, ruffed grouse). In time, however, the value of trees increased and humans became more interested in growing trees for economic gain. Today, much of the timber lands are controlled by large lumber companies and federal agencies whose primary focus is on timber production and future return. As such, harvested sites are often planted immediately with seedlings (and usually fast growing species, e.g., loblolly pine) and planting regimes are stringent with a devoted effort to utilize every acre for production. Site preparation typically includes chemical application killing brush, weeds, and other vegetation typically used by wildlife. Additionally, intensive monocultures (i.e., single species, high stocking rates) and even-aged stand management have become the norm rather than the exception. Whereas the science of timber production and management continues to be fine-tuned to yield optimal fiber and monetary returns, many wildlife species continue to decline as a result.

Rangeland & Pasture. Rangeland and pastureland trends have also shifted toward intensification. This intensification emphasizes the use of each acre to maximize production for cattle, dairy, or other products. Overgrazing has considerably taxed many rangeland sites (Wuethner and Matteson 2002) leading to planting of exotic grass species able to withstand heavier browsing. Numerous other factors have contributed to the deterioration of native rangelands including drought, fire suppression, highway and interstate development (Brennan and Kuvlesky 2005, Knick et al. 2003). Fescue, Bermuda and other non-native, sod-forming grasses have encroached on native grasslands as well as shrub and thereby reducing habitat quality for numerous wildlife species.

Urbanization. Whereas in early history natural events (e.g., weather) and processes (e.g., succession) was the primary driver of ecosystems and humans had relatively (as compared to subtle impacts on the landscape, ecosystems are now primarily shaped by humans. As such, intensification and changes associated with the previous land-use practices discussed are inextricably linked to human population growth. Recent population growth throughout the world is of a enormous magnitude (Shochat et al. 2006).

Human philosophy regarding natural resources during early settlement ostensibly was one of broad consumption without much thought to future sustainability whereby forest lands were viewed as areas to be conquered, large carnivores were considered threats to livestock or competition for game species, and game species were heavily exploited for food and wholesale trade. As human populations increased, human consumption and the overall inability for some species to coexist began to tax certain wildlife even to extent of extinction for some (e.g., Passenger Pigeon, Ivory-billed Woodpecker). However, coming along with increased human population growth was the desire to assuage the need for recreation where humans at the turn of the 20th century began to realize that natural resources were indeed exhaustible and threatened. This spawned the conservation movement. Increased awareness of human impact on the environment fueled constituent groups to preserve lands giving rise to national parks, national forests, preserves and wilderness areas. Environmental legislation (e.g. Multiple-Use Sustained-Yield Act of 1960, Wilderness Act of 1964, National Forest Management Act of 1974) was passed to promote management among these areas under the tenet of multiple-use and sustained-yield. Such legislation mandated coordinated land management with public participation; National Forests were, for example, required to maintain viable populations of natural plant and animal fauna, encouraging management to benefit threatened and endangered species, and to manage habitat for desired game species (Nelson et al. 1983).

In light of widespread land preservation and attempts to manage this land, human population growth continues to negatively impact natural resources. While numerous opportunistic species have flourished despite human alteration of the landscape (e.g. White-tailed deer [*Odocoileus virginianus*], coyote [*Canis latrans*], non-native invasive plants), it has been to the detriment of many others (e.g. northern bobwhite quail [*Colinus virginianus*], red-cockaded woodpecker [*Picoides borealis*], Bachamn's Sparrow [*Aimophila aestivalis*], LeConte's sparrow [*Ammodramus leconteii*]) and therefore the need for range-wide conservation efforts focussed on identifying remaining habitat, or qualifying its potential, and maximizing management of that habitat to benefit multiple species has become paramount. Consequently, a plethora of research has been undertaken during the past few decades to investigate land-use change and their effects on wildlife as well as experimentation with and investigation of novel management techniques (e.g., translocation).

1.2 Purpose of the Study

The conversion and fragmentation of habitat throughout North America as caused by one or more of the land-uses outlined above has clearly contributed to wide-spread population declines for numerous grassland bird species (Brennan and Kuvlesky 2005, Knopf 1994). Changing land-use practices during the past several decades has caused extreme paradigm shifts in ecological and management decision-making with an emphasis being put on mitigating the effects of habitat fragmentation and urban expansion. These paradigm shifts are consequential to the dynamics of species inhabiting these and similar ecosystems. Metapopulation (i.e., spatially structured populations consisting of distinct units or subpopulations, separated by space or barriers, and connected by dispersal movements) theory and management is becoming a salient rubric for future species preservation and conservation genetics. A suite of problems exist for many species inhabiting these systems (metapopulations) whereby their population status is subject to high vulnerability of extinction and low probability of recolinization (Hanski and Gilpin 1991), particularly among low-mobility species. Researchers have demonstrated that population viability is unlikely among sites with small habitat fragments (Johnson 2001) and others have suggested that several species of grassland birds were intolerant of small patches, preferring to use larger patches

(Herkert 1994). Additionally, species residing in highly fragmented habitats often have lower survival and higher nest predation rates (Burger et al. 1994, Vickery et al. 1992).

Aside from demographic concerns, fragmentation of suitable habitat has reduced gene flow among populations and possibly led to increased inbreeding within isolated populations (Brennan 1991). And, it has recently been demonstrated unequivocally that inbreeding in small populations can suppress population fitness and thereby increase risk of extinction (Keller 1998, Newman and Pilson 1997, Tallmon et al. 2004). Increase in homozygosity may lead to "inbreeding suppression" (i.e. lower viability and fecundity), and may render the population, as a whole, evolutionarily less flexible (Lacy 1987, Selander 1983). Populations lacking genetic diversity are generally less adaptable to changing environments and more susceptible to new predators, diseases, and parasites (Lacy 1987). Increased rates of extinction may be more prevalent among small, isolated habitats. Translocation within these systems may be necessary to maintain "healthy" genetic composition, especially for species with limited dispersal. Given these concerns, a thorough understanding of the basic dynamics operating among meta-population systems, particularly isolated habitat patches, relative to gene flow, genetic diversity, and extinction/recolinization is essential to best guide management and recovery of the species.

Reintroductions and translocations have become a common conservation option to fulfill biodiversity preservation or restoration objectives (Griffith et al. 1989, Seddon et al. 2007). However, many translocation programs have been implemented *ad hoc* with little consideration given to sound science and thereby, in many cases, lack adequate study design and monitoring to gain the knowledge needed to improve their success (Seddon et al. 2007). To date, few studies have comprehensively investigated the efficacy of translocation to restore or augment populations within a fragmented system among Order Galliformes. This dissertation incorporates molecular genetic techniques (microsatelite genotyping) and capture, marking, and radio-telemetry methods to allow objective investigation of the demographic and genetic response to a population located among a highly fragmented landscape following translocation of a non-migratory species, the Northern Bobwhite (*Colinus virginianus*).

1.3 Relevant Research

Despite extensive research on the species, northern bobwhite populations continue to decline throughout much of their endemic range, particularly during the past 3-4 decades. The landscape changes previously described have substantially impacted bobwhites (Brennan 1991, Brennan and Kuvlesky 2005, Church et al. 1993). The plight of the bobwhite, however, is not a novel consequence. Stoddard (1931) reported population declines and ascribed putative causes when stating that: “with the increase of the human population, improvements in farming methods and farming machinery, and the expansion of the livestock industry, came conditions less favorable to the species [bobwhite].” Unfortunately, these concerns are more visible today than ever before; the continuing technological advances of farming machinery and the advent of irrigation systems have exacerbated these declines. As a result, bobwhites are currently seriously threatened with extirpation in significant portions of their range. The Breeding Bird Survey (BBS) indicated a 3.0% / year decline in bobwhite populations during 1966-2007 (Sauer et al. 2008). Although this decline is disconcerting, there is clear indication the rate of decline has increased in recent years. The BBS denoted a declining trend of -0.896%/ year (CI: -0.908, 0.040) during 1966-1979, whereas the rate of decline during 1980-2007 was -3.896%/ year (CI: -3.903, 0.000)(Sauer et al. 2008). The continuation of these trends suggest that bobwhites could be approaching eradication, in some North American states, in the very near future.

The focus of bobwhite restoration efforts has been via direct (i.e., restocking pen-reared and wild bobwhites) and indirect (i.e., research and habitat manipulation) means. As early as the 1930s, state agencies employed techniques such as reduced bag limits, season restrictions or complete closure; predator control; and re-stocking via pen-reared bobwhites (Coggins 1986, Terhune et al. 2006). Others also released pen-reared individuals in attempt to restore local bobwhite populations (Barbour 1950, Phillips 1928, Pierce 1948). The stocking of pen-reared bobwhite has been implemented successfully to augment hunting; however, its utility as a conservation tool to increase native bobwhite populations has proven much less effective (Buechner 1950, Frye 1942, Kozicky 1993, Roseberry et al. 1987). DeVos and Speake (1995) reported that, due to low survival, pen-reared birds were not suitable for re-stocking. Moreover, potentially adverse effects, such as disease transmission (Davidson et al. 1980, Poonacha 1981), spatial displacement of wild bobwhites, increased wild bobwhite mortality (Sisson et al. 2000), and dilution of the native gene pool (Alrich 1946, Landers et al. 1991), warrant caution when releasing pen-reared quail into wild populations. The caveats associated with the release of captive-reared individuals to restore native populations extend beyond bobwhites whereby a myriad of concerns have been highlighted, including: potential loss of natural behaviors; reduced fitness capacities in the form of breeding and nesting, survival, and habitat use; and susceptibility to disease (Cunningham 1996, Rabin 2003, Snyder et al. 1996, Vickery and Mason 2003, Woodford and Rossiter 1994). In general, studies have suggested that projects using captive-born individuals are less likely to be successful compared to those using wild-caught individuals (Beck et al. 1994, Matthews et al. 2005). Re-stocking attempts using captive-reared individuals has proven unsuccessful for population restoration at landscape scales, and research has demonstrated that the most effective way to restore bobwhite populations is to increase the availability of suitable habitat (Brennan 1991, Klimstra 1972).

To date, many habitat management strategies have been proposed to address changing land-use practices and habitat fragmentation to potentially reverse bobwhite population declines. Numerous habitat-based organizations also have emerged, ranging in extent from small, private research groups (e.g., Tall Timbers Research Station [TTRS], Albany Quail Project [AQP]) to moderately sized private organizations (e.g., Quail Forever [QF], Quail Unlimited [QU]) to state and federally organized, monetary-incentive-assisted habitat management programs (e.g., Northern Bobwhite Conservation Initiative [NBCI], Georgia Bobwhite Quail Initiative [GaBQI], Farm Bill, CRP, WHIP, EQUIP, etc). Although these programs have successfully applied the pragmatic knowledge gained from research by increasing and/or improving early-succession habitats at both local and regional scales, bobwhite population response has been variable under these conservation initiative programs (Cook 2004). Notably, attempts to abate declining populations of bobwhite using habitat improvement techniques have produced positive results on a local scale, but not over landscape scales. The lack of response is likely a result of the increasingly fragmented landscape where early-succession habitats are becoming smaller, more isolated, and more ephemeral in duration, thereby limiting natural repopulation. As such, bobwhites found among such habitats may be forced to traverse large areas, often unsuitable habitat, to access other "suitable" patches and thereby potentially reducing their survival (Cook 2004, Folk 2006). That said, bobwhite populations have been reported as stable to even increasing among areas where large-scale, intensive management is present (Palmer and Wellendorf 2007, Sisson et al. 2006, Terhune et al. 2007).

However, even following intensive habitat manipulation, bobwhite populations in some southeastern areas remain low. As such, translocation of wild-caught individuals may provide a means to circumvent caveats associated with the release of captive-reared individuals while increasing the opportunity for successful restoration among sites where habitat has recently been improved. That said, translocations are not novel for upland game birds in North America. Effective translocations of wild turkey (*Meleagris gallapavo*) and ring-necked pheasant (*Phasianus colchicus*) have been implemented (Dickson 1992, Griffith et al. 1989), whereas translocations of ruffed grouse [*Bonasa umbellus*; (Kelly and Kirkpatrick 1979, Kurzejeski and Root 1989, Moran and Palmer 1963, Wentworth et al. 1986, White and Dimmick 1979)] and prairie grouse (Musil et al. 1993, Rodgers 1992, Toepfer et al. 1990) have demonstrated mixed results. Among bobwhites, translocation by state game agencies date as far back as the early 1900s in the U.S. (Griscom 1916, Latham and Studholme 1954, Phillips 1928). These early banding studies revealed variable results from translocations (Latham and Studholme 1954, Stoddard 1931). More recently, similar results have been reported when translocating wild bobwhites in Florida, Tennessee, and Texas (DeVos and Mueller 1989, Jones 1999, Lui et al. 2002, 2000). However, much of this research should be interpreted with caution because the studies suffered from low sample size (Jones 1999) or releases ostensibly occurred in areas with submarginal habitat (Lui et al. 2002, 2000). Still other studies demonstrated the success of translocation when implemented: prior to breeding season, following intense habitat modification, and among a contiguously managed habitat (Terhune et al. 2006, 2005). Taken collectively, translocation is probably not a panacea technique that should be implemented capriciously, but should only be considered when other management actions have been exhausted and when consideration of the species' biology has been incorporated.

1.3.1 Reintroduction Biology: Terminology & Background

The general aim of reintroductions is to establish viable populations for a particular species of interest. The terms introduction, reintroduction, restoration, re-stocking and translocation have mistakenly been used synonymously in recent and past published works. Reintroduction biology as posited by Armstrong and Seddon (2007) is 'research undertaken to improve the outcomes of reintroductions and other translocations' to conserve species. Following the suggestion of Armstrong and Seddon (2007), I adhere to the terminology outlined in the original IUCN position statement on the translcocation of living organisms throughout this dissertation to mitigate confusion (IUCN 2004). This original document defined 'translocation' as any movement of living organisms from one area to another, and recognized three distinct types of translocation:

1. Introduction: movement of an organism outside its historically known native range;
2. Reintroduction: intentional movement of an organism into a part of its native range from which it has disappeared or become extirpated in historic times; and

3. Re-stocking: movement of individuals to build-up an existing population

In this dissertation, I use the term translocation to infer the capture of *wild* individuals for *re-stocking* purposes as defined above.

1.4 OBJECTIVES

Translocation of Northern Bobwhites prior to breeding season is a nascent technique for replenishing native quail stocks where populations are low and/or other management techniques, such as habitat improvement, have been exhausted (Terhune et al. 2006, 2005). Movement of wild-caught individuals to isolated or fragmented habitat provides an opportunity to mitigate the effects of fragmentation by introducing novel alleles into the reproductive population and potentially increasing hybrid vigor. However, scant molecular-based research among bobwhites exists and therefore gene flow has not been adequately excplored (Brennan 1999, Ellsworth et al. 1989). The supplementation of wild bobwhites prior to the breeding season provides an excellent opportunity to bolster fall population on a site by capitalizing on their high reproductive capabilities (Terhune et al. 2006, 2005). Additionally, translocation of wild bobwhites can potentially complement programs designed to expand suitable habitat, and, in some cases, may afford the only means to ensure timely population recovery (Terhune et al. 2005). Furthermore, it is possible that translocation may operate as a conservation tool for restoring populations of declining and threatened species and, ostensibly, is of great significance for biodiversity conservation (Griffith et al. 1989).

Despite long-term exploitation of the technique among upland game birds, the biological implications of translocation remain poorly understood. An important facet of translocation is the ability to determine its efficacy in enhancing local population viability. To do so, thorough investigation of the affect translocation has on individual demographic parameters such as survival and reproduction must occur. Additionally, the amount, if any, of introgression occurring between translocated and resident bobwhites needs to be assessed. Of notable interest is whether translocation can serve as a means to bolstering genetic heterogeneity; thus, potentially instigating a "genetic rescue" (Tallmon et al. 2004, Thrall et al. 1998). The potential effects of reduction in heterogeneity combined with habitat fragmentation and degradation demands rigorous analysis of translocation methodology, results, and strategy. Application of genetic analysis combined with data gained from capture, marking, and radio-telemetry is requisite to advancing the knowledge of translocation and its effect on population demographics and genetics. Whereas this technique has proven successful in certain cases Terhune et al. (2006, 2005), it lacks scientific validation through replication and, when implemented, was instituted on sites located in contiguous, high-quality habitat.

I investigated these issues by integrating individual-specific radio-telemetry, demographic, geographic, and molecular data sets (*see* Table 1.1). I collected extensive field data based on adequate sample sizes, Table 1.2, and I genotyped all translocated individuals and a random sub-sample of all individuals captured on the study site (resident or "hybrid" birds) using 16 polymorphic, microsatellite DNA markers (Faircloth et al. 2008, Schable et al. 2004). To accomplish my objectives, I:

1. Investigated survival, site fidelity, and movement of translocated and resident bobwhites using multi-state models;
2. Examined nest survival, productivity and fecundity for translocated and resident northern bobwhites;
3. Assessed genetic variability and population structure in an isolated population of northern bobwhites compared to non-isolated, panmictic populations; and
4. Examined the rate of genetic introgression, allele frequency, and gene flow following translocation in an isolated fragmented habitat.

1.5 EXPERIMENTAL PLAN

My research methodology comprised two major components: field and lab analysis. During 2003-2005, I collected demographic, geographic and individually-specific radio-telemetry data from resident and translocated northern bobwhites using capture, marking, and radio-location techniques (*see* following chapter Methods; Table 1.1). For compilation of my molecular data set, I chose a subset of previously developed microsatellite DNA markers to conduct genetic analysis for all translocated and a subset of resident bobwhites during each year of the study (Faircloth et al. 2008, Schable et al. 2004).

1.5.1 JUSTIFICATION OF MODEL SPECIES.

Among Order Galliformes, the northern bobwhite is a viable species to investigate the efficacy of translocation. Northern bobwhites represent a prominent game bird with commercial and socio-economic importance (Burger et al. 1999) and are native, habitat generalists that readily respond to favorable habitat conditions with a wide-ranging distribution (Brennan 1999, Burger et al. 1999). Bobwhite are non-migratory, gregarious birds with relatively low natal dispersal, small home ranges, and high reproductive capacity (Brennan 1999). Additionally, bobwhites are relatively numerous among sites employing rigorous habitat management (Palmer and Wellendorf 2007, Terhune et al. 2007) affording opportunity for capture and translocation of individuals as well as collecting adequate sample sizes to render statistically valid inferences (Brennan 1999).

Northern bobwhites have undergone significant declines, and even extirpation of local populations, which have been tightly connected to the changing land uses as previously discussed (Brennan 1991, 1999, Brennan and Kuvlesky 2005, Church et al. 1993, Church and Taylor 1992, Sauer et al. 2008). Research has demonstrated that small populations among fragmented landscapes are at a high risk of extinction (Hanski and Gilpin 1991, Herkert 1994). Bobwhites are particularly sensitive to these types of landscape changes since they typically necessitate large (1200 to 2000 ha), contiguous habitat patches to sustain viable population levels. Local bobwhite populations might be negatively impacted by limited gene flow due to their sedentary nature within these fragmented systems (Brennan 1999). While a few molecular-based studies have been conducted among bobwhites (Ellsworth et al. 1988, 1989, Nedbal et al. 1997), none of these studies extensively investigated genetic differentiation and gene flow in fragmented or isolated habitats following translocation.

1.5.2 Scientific and Management Impacts

This dissertation investigates both demographic and genetic components of translocation in a non-migratory, low-mobility avian species. It addresses questions germane to the utility of translocation and aids in elucidating theory regarding genetic rescue and inbreeding suppression as well as increase our knowledge on meta-populations and the demographics affecting them. Additionally, this research provides pragmatic content needed to successfully implement translocation at a local scale and provides insight to broader application for restoration.

Habitat use, quality, and conservation

Knowledge of demographic parameters and population dynamics following translocation is deficient, impeding its use as a management technique and/or conservation tool. For example, few studies have attempted to assess whether population response following release is a result of the translocation or other factors (habitat modification, favorable weather). The study design for this study was amenable to assessing these effects. As such, I determined whether translocated birds: exhibited high site fidelity following release, utilized habitat similarly to native birds, survived and reproduced at rates comparable to or greater than their resident counterparts, and contributed to overall population growth. In such cases where these criteria are not met, translocation as a means to bolster populations or recolonize areas may not be warranted. In addition, elicitation of a positive population response following translocation within the managed habitat (i.e., study site) and not the unmanaged habitat provides corroborating evidence that the success of translocation is dependent on suitable habitat. Therefore, translocation of avian species to early-successional ecosystems may be more efficacious to regional conservation efforts when habitat management is conducted on larger scales.

Avian communities

Avian species inhabiting early-successional habitats fit nicely within metapopulation ecosystems because early-succession communities are typically ephemeral and often exist in a dynamic, mosaic landscape. Results from this study will augment our current knowledge of meta-population dynamics by providing a better understanding of these processes at a small scale, and will facilitate appropriate management at the landscape level, subsequently benefiting avian species inhabiting early-successional habitats. Additionally, this project will provide insight to population persistence following translocation and associated mechanisms of patch size, alteration of genetic heterogeneity, biogeography and source-sink effects. Application of these techniques may be applied to the conservation and management of this and similar species among avian communities as a whole. Population growth of these species may additionally benefit communities beyond those aided by this research (e.g., avian and mammalian predator communities) by improving resource availability (i.e., food and habitat).

Ecosystem function

The genetic structure of isolated, fragmented systems is poorly understood. Similarly, theories such as genetic rescue and "inbreeding suppression" generally lacks empirical support. This project provides insight to the genetic structure among isolated avian populations and allowed examination of initial allelic states and subsequent allele movement through space and time following introduction of genetically novel individuals. If benefits are conferred, either via hybrid vigor or demographic resiliency, then understanding the rate and pattern of allele movement or the effects of hybrid status could provide valuable information on: (1) the effects of translocation with respect to population genetic "health" and persistence,

(2) the role of dispersal (artificially induced) in increasing genetic diversity in fragmented populations and, (3) the resultant changes in demographic parameters following novel allelic introgression.

BROADER IMPACTS

This research increases our knowledge and awareness of translocation as a conservation tool and provides the framework for future investigations on translocation among bobwhites and similar species. The results reported herein have already provided the impetus for individual state action plans regarding the implementation of northern bobwhite translocation and may therefore continue to provide a foundation for future conservation plans. Finally, these data should facilitate future comparisons of translocation and the underlying ecological mechanisms driving their success.

Literature Cited

Alrich, J. W., 1946. Significance of racial variation in birds to wildlife management. *Journal of Wildlife Management* **10**:86–93.

Armstrong, D. P. and P. J. Seddon, 2007. Directions in reintroduction biology. *Trends in Ecology and Evolution* **23**:20–25.

Barbour, R. W., 1950. A high mortality of pen-raised bob-white quail. *Journal of Wildlife Management* **14**:474.

Beck, B. B., L. G. Rapaport, M. R. S. Price, and A. C. Wilson, 1994. Reintroduction of captive-born animals. In *Creative Conservation: interactive management of wild and captive animals.*

Brennan, L. A., 1991. How can we reverse the the northern bobwhite decline? *Wildlife Society Bulletin* **19**:544–555.

Brennan, L. A., 1999. The Birds of North America. Number 397. A. Poole and F. Gill, eds., Philadelphia, Pennsylvannia, USA.

Brennan, L. A. and W. P. Kuvlesky, Jr., 2005. North american grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* **69**:1–13.

Buechner, H. K., 1950. An evaluation of restocking with pen-reared bobwhite. *Journal of Wildlife Management* **14**:363–377.

Burger, L. D., L. W. Burger, Jr., and J. Faaborg, 1994. Effects of prairie fragmentation and predation on artificial nests. *Journal of Wildlife Management* **58**:249–254.

Burger, L. W., Jr., D. A. Miller, and R. I. Southwick., 1999. Economic impact of northern bobwhite hunting in the southeastern united states. *Wildlife Society Bulletin* **27**:1010–1018.

Church, K. E., J. R. Sauer, and S. Droege, 1993. Population trends on quails in north america. *Proceedings of the National Quail Symposium* **3**:44–54.

Church, K. E. and J. S. Taylor, 1992. Management and research of northern bobwhite (*Colinus virginianus*) in north america: An overview. *Gibier Faune Savage* **9**:787–796.

Coggins, W. A., 1986. The bobwhite quail in alabama. .

Cook, M. P., 2004. Northern Bobwhite Breeding Season Dispersal, Habitat-Use, and Survival in a Southeastern Agricultural Landscape. Master's thesis, University of Georgia.

Cunningham, A. A., 1996. Disease risks of wildlife translocations. *Conservtion Biology* **10**:349–353.

Davidson, W. R., F. E. Kellogg, and G. L. Doster, 1980. An epornitic of avian pox in wild bobwhite quail. *Journal of Wildlife Diseases* **16**:293–296.

DeVos, T., Jr and B. S. Mueller, 1989. Quail relocation - can we fill the void? *Quail Unlimited* **12**:2–4.

DeVos, T., Jr and D. W. Speake, 1995. Effects of releasing pen-raised northern bobwhite on survival rates of wild populations of northern bobwhites. *Wildlife Society Bulletin* **23**:267–273.

Dickson, J. G., 1992. The Wild Turkey: Biology and Management. Stackpole Books, Harrisburg, PA.

Ellsworth, D. L., J. L. Roseberry, and W. D. Klimstra, 1988. Biochemical genetics of wild, semi-wild, and game-farm northern bobwhites. *Journal of Wildlife Management* **52**:138–144.

Ellsworth, D. L., J. L. Roseberry, and W. D. Klimstra, 1989. Genetic structure and gene flow in the northern bobwhite. *Auk* **106**:492–495.

Faircloth, B. C., T. M. Terhune, N. A. Schable, T. C. Glenn, W. E. Palmer, and J. P. Carroll, 2008. Ten microsatellite loci from northern bobwhite (*Colinus virginianus*). *Conservation Genetics* .

Folk, T. H., 2006. Population Ecology of Northern Bobwhites. Ph.D. thesis, Auburn University.

Frye, J. O. E., 1942. The comparative survival of wild and pen-reared bob-whites in the field. *Transactions of North American Wildlife Natural Resources Conference* **7**:169–178.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed., 1989. Translocation as a species conservation tool: Status and strategy. *Science* **245**:477–480.

Griscom, L., 1916. Notes from leon county, florida. *Auk* **33**:329–330.

Hanski, H. and M. Gilpin, 1991. Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**:3–16.

Herkert, J. R., 1994. Breeding bird communities of mid-western prairie fragments: the effects of prescribed burning and habitat-area. *Natural Areas Journal* **14**:128–135.

IUCN, 2004. Position Statement on the Translocation of living organisms: Introductions, Re-introductions, and Re-stocking. Prepared by the Species Survival Commission in collaboration with the Commission on Ecology and the Commission on Environmental Policy, Law, and Administration. IUCN (http://www.iucnsscrsg.org/.

Johnson, D. H., 2001. Habitat fragmentation effects on birds in grasslands and wetlands: a critique of our knowledge. *Great Plains Research* **11**:211–231.

Jones, J. G., 1999. Effects of Relocating Wild Northern Bobwhites Into Managed Quail Habitat in Middle Tennessee. Master's thesis, Tennessee Technological University.

Keller, L. F., 1998. Inbreeding and its fitness effects in an insular population of song sparrows (*Melospiza melodia*). *Evolution* **52**:240–250.

Kelly, S. T. and C. M. Kirkpatrick, 1979. Evaluation of a ruffed grouse reintroduction in northern indiana. *Wildlife Society Bulletin* **7**:288–291.

Klimstra, W. D., 1972. Population dynamics of bobwhite on an intensively managed area in southern illinois. *Proceedings of the National Quail Symposium* **1**:356–360.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. V. Haegen, and C. V. Riper, 2003. Teetering on the edge or too late? conservation and research issues for the avifauna of sagebrush habitats. *Condor* **105**:635–653.

Knopf, F. L., 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* **15**:247–257.

Kozicky, E. L., 1993. The history of quail management with comments on pen-rearing. *Proceedings of the National Quail Symposium* **3**:1–7.

Kurzejeski, E. W. and B. G. Root, 1989. Home range, movements, and habitat use by reintroduced ruffed grouse in northern missouri. *Wildlife Society Bulletin* **17**:106–111.

Lacy, R. C., 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology* **1**:143–158.

Landers, J. L., L. P. Simoneax, and D. C. Sisson, 1991. The effects of released, pen-raised bobwhites on wild bird populations. Technical report, Tall Timbers, Tallahassee, FL.

Latham, R. M. and C. R. Studholme, 1954. The bobwhite quail in Pennsylvania. Technical report, Pennsylvania Game News.

Lui, X., B. S. Mueller, D. S. Parsons, and D. R. Dietz, 2002. Movement patterns of resident and relocated northern bobwhites in East Texas. *Proceedings of the National Quail Symposium* **5**:168–172.

Lui, X., J. R. M. Whiting, B. S. Mueller, D. S. Parsons, and D. R. Dietz, 2000. Survival and causes of mortality of relocated and resident bobwhites in east texas. *Proceedings of the National Quail Symposium* **4**:119–124.

Matthews, F., M. Orros, G. McClaren, M. Gelling, and R. Foster, 2005. Keeping fit on the ark: assessing the suitability of captive-bred animals for release. *Biological Conservation* **121**:569–577.

Moran, R. J. and W. L. Palmer, 1963. Ruffed grouse introductions and population trends on michigan islands. *Journal of Wildlife Management* **27**:606–614.

Musil, D. D., J. W. Connelly, and K. P. Reese, 1993. Movements, survival, and reproduction of sage grouse translocated into central idaho. *Journal of Wildlife Management* **57**:85–91.

Nedbal, M. A., R. L. Honeycutt, S. G. Evans, R. M. Whiting, Jr., and D. R. Dietz, 1997. Northern bobwhite restocking in East Texas: A genetic assessment. *Journal of Wildlife Management* **61**:854–863.

Nelson, R. D., H. Black, Jr., R. E. Radtke, and J. Mumma, 1983. Wildlife and fish management in the forest service: a goal oriented approach. *Transcations of North American Wildlife and Natural Resources Conference* **48**:87–95.

Newman, D. and D. Pilson, 1997. Increased probability of extinction due to decreased genetic effective population size: Experimental populations of (*Clarkia puchella*). *Evolution.* **51**:354–362.

Palmer, W. E. and S. Wellendorf, 2007. Effects of radiotransmitters on northern bobwhite annual survival. *Journal of Wildlife Management* **71**:1281–1287.

Phillips, J. C., 1928. Wild birds introduced or transplanted in north america. Technical report, United States Department of Agriculture, Technical Bulletin.

Pierce, R. A., 1948. The survival of pen raised quail in the wild: a preliminary report. *Proceedings of the Annual Conference of the Southeastern Game and Fish Commission* **2**:1–6.

Poonacha, K. B., 1981. Avian pox in pen-raised bobwhite quail. *Journal of the American Veterinary Medical Association* **179**:8–15.

Rabin, L. A., 2003. Maintaining behavioural diversity in captivity for conservation: natural behaviour management. *Animal Welfare* **12**:85–94.

Rodgers, R. D., 1992. A technique for establishing sharp-tailed grouse in occupied range. *Wildlife Society Bulletin* **29**:101–106.

Roseberry, J. L., D. L. Ellsworth, and W. D. Klimstra, 1987. Comparative post-release behavior and survival of wild, semi-wild, and game farm bobwhites. *Wildlife Society Bulletin* **15**:449–455.

Sauer, J. R., J. E. Hines, and J. Fallon, 2008. The north american breeding bird survey, results and analysis 1966-2007. **Version 5.15.2008**.

Schable, N. A., B. C. Faircloth, W. E. Palmer, J. P. Carroll, L. W. Burger, L. A. Brennan, C. Hagen, and T. C. Glenn., 2004. Tetranucleotide and dinucleotide microsatellite loci from the northern bobwhite (*Colinus Virginianus*). *Molecular Ecology Notes* **4**:415–419.

Seddon, P. J., D. P. Armstrong, and R. F. Maloney, 2007. Developing the science of reintroduction biology. *Conservation Biology* **21**:303–312.

Selander, R. K., 1983. Evolutionary consequences of inbreeding. *Genetics and Conservation* pages 201–215.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope, 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution* **21**:186–191.

Sisson, D. C., H. L. Stribling, and D. W. Speake, 2000. Efficiencey of pointing dogs in locating northern bobwhite coveys. *Proceedings of the National Quail Symposium* **4**:109.

Sisson, D. C., T. M. Terhune, H. L. Stribling, and S. D. M. Jerald Fitch Sholar, 2006. Survival and causes of mortality for northern bobwhites in the southeastern united states. In J. P. C. Brant C. Faircloth, Theron M. Terhune, editor, *Gamebird Proceedings*, volume 6, pages 000–000.

Snyder, N. F., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone, and B. Miller, 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* **10**:338–348.

Stoddard, H. L., 1931. The Bobwhite Quail: Its Habits, Preservation, and Increase. Charles Scribner's Sons, New York, New York.

Tallmon, D. A., G. Luikart, and R. S. Waples, 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution* **19**:489–496.

Terhune, T. M., D. C. Sisson, J. B. Grand, and H. L. Stribling, 2007. Factors influencing survival of radio-tagged and banded bobwhites in georgia. *Journal of Wildlife Management* **71**:1288–1297.

Terhune, T. M., D. C. Sisson, and H. L. Stribling, 2006. The efficacy of relocating wild northern bobwhites prior to breeding season. *Journal of Wildlife Management.* **70**:914–921.

Terhune, T. M., D. C. Sisson, H. L. Stribling, and J. P. Carroll, 2005. Home range, movement, and site fidelity of translocated northern bobwhite (*Colinus virginianus*) in southwest georgia,USA. *European Journal of Wildlife Research* **51**:119–124.

Thrall, P., C. Richards, D. McCauley, and J. Antonovics., 1998. Metapopulation collapse: The consequences of limited gene-flow in spatially structured populations. *Modeling Spatiotemporal Dynamics in Ecology* pages 83–104.

Toepfer, J. E., P. E. Hale, and A. S. Anderson, 1990. Translocating prairie grouse: What have we learned? *Transactions of the North American Wildlife National Resource Conference* **55**:569–579.

Vickery, P. D., M. L. Hunter, and J. Wells, 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* **63**:281–288.

Vickery, S. S. and G. J. Mason, 2003. Stereotypy and perseverative responding in caged bears: further data and analysis. *Applications in Animal Behavior Sciences* **91**:247–260.

Wentworth, E. J., P. E. Hale, and A. S. Johnson, 1986. Experimental relocation of ruffed grouse to the georgia piedmont. *Proceedings Annual Conference Southeast Association Fish and Wildlife Agencies* **40**:373–381.

White, D. and R. W. Dimmick, 1979. Survival and habitat use of northern ruffed grouse introduced into tennessee. *Proceedings Annual Conference Southeast Association Fish and Wildlife Agencies* **32**:1–7.

Woodford, M. H. and P. B. Rossiter, 1994. Disease risks associated with translocation projects. In *Creative Conservation: interactive management of wild and captive animals.*

Wuethner, G. and M. Matteson, 2002. Welfare Ranching: the subsidized destruction of the American West. Island Press, Covelo, California, USA.

Table 1.1: Spatial, molecular and demographic data sources collected during 2003-2005 on Buck Creek Plantation, Marion county, Georgia.

	Telemetry	GIS	Molecular	Demographic
Age, Sex, Weight, Condition at each capture				⊗
Survival	⊗			
Reproduction	⊗		⊗	
Individual Bird Movements and Associations	⊗		⊗	
Social Introgression	⊗		⊗	
Brood Movements	⊗			
Site Fidelity	⊗	⊗	⊗	
Annual Study Site Maps		⊗		

Table 1.2: Summary data from capture and genetic sampling (n) delineated by season, year and sampling period (SP) of northern bobwhite at Buck Creek study site during 2003-2005.

Season-Year	SP	Core	Buffer	Control	Total (n)	Translocated (n)
Spring-2003	1	108	80	155	343 (341)	67 (67)
Fall-2003	2	298	88	169	555 (550)	0
Spring-2004	2	112	106	58	276 (275)	70 (70)
Fall-2004	3	268	81	112	461 (435)	0
Spring-2005	3	0	105	135	240 (240)	0
Fall-2005	4	170	52	0	222 (219)	0

CHAPTER 2

SURVIVAL, MOVEMENT AND SITE FIDELITY FOR TRANSLOCATED AND RESIDENT NORTHERN BOBWHITES FOLLOWING TRANSLOCATION TO A FRAGMENTED LANDSCAPE.[2]

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[2] Terhune, T. M., D. C. Sisson, W. E. Palmer, B.C. Faircloth, H. L. Stribling, J. P. Carroll. To be submitted to *Ecological Applications*

2.1 Abstract

Habitat fragmentation, degradation, and complete loss has taxed early-successional species including both the northern bobwhite and numerous grassland obligate birds. Translocation has been applied in attempt to establish, reestablish and augment wild populations for conservation and biodiversity purposes to counteract the consequences of habitat fragmentation. However, the implementation of such techniques have not been conducted using valid experimental designs and therefore lack robust, empirical data needed to adequately evaluate and advance the science of translocation. Furthermore, a paucity of studies exist assessing site fidelity, movement, and survival of northern bobwhite following translocation among fragmented habitats. We used known-fate and multi-strata models to evaluate hypotheses relative to temporal, biological and group effects on survival and movement of translocated and resident bobwhites. We did not detect differences in either survival or movement between translocated and resident bobwhites suggesting that movement of individuals to a fragmented habitat does not negatively influence these demographic attributes. Additionally, we surmised that two site-specific criteria should be met prior to instituting translocation: habitat management should be conducted to ensure quality habitat exists and the patch size should be a minimum of 607 ha. Translocation should be considered as a conservation option, but should not be a surrogate for habitat restoration (management).

2.2 Introduction

Grassland and early-successional birds remain a source of great conservation concern as this group has been subject to precipitous population declines during the past few decades (Sauer et al. 2008) - more than any other guild of North American bird species (Askins 1993, Brennan and Kuvlesky 2005, Knopf 1994). Numerous individual species within this guild have suffered population declines (Askins 1993, Vickery et al. 1994, 1992), but the decline of the Northern Bobwhite (*Colinus virginianus*; hereafter, bobwhite[s]) is, for many, particularly concerning due to their historical prominence and socioeconomic value (Brennan 1999, Burger et al. 1999, Stoddard 1931). Fragmentation, degradation or complete loss of habitat resulting from changing land-use practices have reduced early-succession habitats (Brennan 1991, 1999, Church et al. 1993, Church and Taylor 1992, Peterson et al. 2002, Roseberry and Sudkamp 1998) and negatively impacted survival of both bobwhites and other grassland obligates (Burger 2002, Guthery and Lusk 2004, Rollins and Carroll 2001, Roseberry 1993). A suite of problems exist for many species inhabiting fragmented systems whereby their population status is subject to high vulnerability of extinction and low probability of recolonization (Bijlsma et al. 2000, Frankham et al. 2004, Hanski and Gilpin 1991, Newman and Pilson 1997, Tallmon et al. 2004), particularly among low-mobility species. Researchers have demonstrated that population viability is unlikely among sites with small habitat fragments (Johnson 2001) and others have suggested that several species of grassland birds were intolerant of small patches and preferred to use larger patches (Herkert 1994). Additionally, species residing in highly fragmented habitats often exhibit lower survival (Burger et al. 1994, Vickery et al. 1992).

Despite bobwhites being one of the most studied gamebirds in North America, their population levels not only continue to decline throughout much of their historic range, but these declines have been exaggerated in recent years (Brennan 1991, Sauer et al. 2008). Low annual survival has plagued bobwhites throughout their range and is considered symptomatic of this landscape-level habitat fragmentation problem (Brennan 1991, Sisson et al. 2006, Terhune et al. 2007). Incidentally, researchers have demonstrated the importance of habitat modification to increase demographic rates such as survival and reproduction, and to long-term population persistence (Klimstra 1972, Landers and Mueller. 1986, Roseberry and Klimstra 1984, Sisson et al. 2006, Stoddard 1931). Escalating habitat alteration and fragmentation has forced bobwhites to utilize poorer quality habitats and small, fugacious patches which may negatively affect dispersal and thereby requiring larger movements to access other suitable habitat patches resulting in purported increased mortality (Cook 2004, Fies et al. 2002, Folk 2006). In spite of regional declines, researchers have documented adequate survival to afford population stability, and even population increases, where long-term, intensive habitat management was conducted (Palmer and Wellendorf 2007, Sisson et al. 2006, Terhune et al. 2007). This research substantiates the necessity for adequate habitat management to abate wide-spread population declines and for long-term population persistence. However, in certain cases where habitat patches are small or isolated and habitat restoration has occurred, the probability of natural re-population remains low. Translocating northern bobwhites prior to breeding season is a nascent technique for replenishing native quail stocks where populations are low and other management techniques, such as habitat improvement, have been exhausted (Terhune et al. 2006, 2005).

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

Among bobwhites, recent studies on wild-quail translocation have incited optimism for the utility of translocation whereby results demonstrated that translocation of individuals to areas following substantial habitat improvements did not negatively impact demographic rates and, even, elicited a positive population response (Terhune et al. 2006, 2005). Despite these successes, which occurred prior to breeding season and was investigated among large, contiguous blocks of managed habitat (Terhune et al. 2006, 2005), the release of wild bobwhites to sites among fragmented landscapes has not been adequately investigated. And, researchers have noted the importance to examining the efficacy of translocation objectively and with an adequate study design to empirically test hypotheses and advance the science of the technique (Brennan 1999, Griffith et al. 1989, Seddon et al. 2007). The efficacy of translocation, however, is predicated on the survival and fidelity of individuals to the designated site following release. As such, it is imperative to assess the effects of translocation on demographic parameters, principally survival and site fidelity, among fragmented landscapes prior to implementing translocation at larger scales. Thus our objective was to compare survival, home range and site fidelity of resident bobwhites to translocated bobwhites following release to an isolated, fragmented habitat in southwest Georgia.

2.3 Study Area

2.3.1 Translocation Site

The study was conducted on a private property (1092 ha; *Figure 2.1*) in Marion County near Tazewell, Georgia (84°24’23.46”W, 32°21’39.07”N). This property is located near the fall line of the Piedmont physiographic region and characterized by gradual rolling hills and sandy-clay to clay type soils. The habitat is: predominantly upland pine forests (59.1%); scattered fallow fields (12.0%); thinned hardwoods, interspersed hardwood hammocks and drains (11%); hardwood-tupelo dominated bottomland (9.5%); wildlife openings (3.5%), roads (2.5%); other (i.e. pasture, food plots, landscape, etc.; 1.3%); and water (1.2%). The upland pine forests contain moderate basal densities (6-9 m^2/ha) consisting of longleaf (*Pinus palustris*), loblolly (*P. taeda*), and slash (*P. ellioti*) pines; upland pines were managed to promote an understory of early-succession vegetation. Typical habitat management included: roller-chopping, mowing, prescribed burning, periodic timber thinning, hardwood management, supplemental feeding, fallow-field management, and cover-patch planting. Mammalian nest predators were managed at an equal rate throughout the study site.

Prior to onset of habitat management in 1996, the property was typical of the region: there was little farming, and the landscape was dominated by pine monocultures (BA >19 m^2/ha) under early enrollment in the Conservation Reserve Program (CRP) and pasture. During 1996-2003, extensive habitat improvements were undertaken on the study site; however, only modest increases in the bobwhite population abundance was observed. This property is considered an "island" of well-managed bobwhite habitat surrounded by a matrix of poor landscapes (e.g. dense pine monocultures [CRP], pasture-land, and late-succession hardwood forests).

2.3.2 Source Site

The source study sites were located on 3 private lands in Baker and Dougherty counties in southwest Georgia, USA. These properties have been under intensive wild quail management for >50 years and are located in the Upper Coastal Plain physiographic region. Additional source-site descriptions have been reported in previous works (see Terhune et al. 2007, 2006, 2005, Yates et al. 1995).

2.4 Methods

2.4.1 Capture and Handling

We captured bobwhites on the study site during Oct-Nov (Fall-trapping period) and Jan-Mar (Spring-trapping period) in 2003-2005 using confusion-style funnel traps (Stoddard 1931, p. 442) baited with milo and cracked corn. We covered traps with brush (e.g., fresh-cut pine limbs) to minimize stress on captured birds and to conceal traps from predators. All bobwhites captured (translocated and resident) were classified by age and sex; and we, additionally, weighed, leg-banded, and collected 10 to 15 feathers from the ventral and humeral feather tracts of all individuals. Half of the collected feathers for each individual were placed in 70% ethanol (ETOH) for preservation prior to genetic analysis. We stored remaining feathers in individually-labeled envelopes to serve as “back-ups” should the feathers in ETOH become lost, unusable, or fail to amplify during PCR.

During the spring-trapping season in 2003 and 2004, we radio-tagged a sub-sample of the “resident” and all translocated bobwhites. We radio-tagged only bobwhites weighing ≥132g (≤5% of body weight) with a 6-g necklace-style radio-transmitter that was equipped with an activity switch (Holohil Systems Ltd., Ontario, Canada). We used necklace-style transmitters because they do not influence body mass dynamics or physiology of captive birds (Corteville 1998, Hernandez et al. 2004), nor do they inhibit survival of bobwhites in the wild (Palmer and Wellendorf 2007, Terhune et al. 2007).

Translocated bobwhites were held overnight in transport boxes and, following feather extraction and data collection, were released in groups of 8-12, not necessarily from the same covey, at random locations within the defined release area (i.e. core area; *see Figure 2.1*). Translocated bobwhites were released within 24-h of capture, and were not fed or provided water, other than feed consumed in traps, prior to release. To avoid re-capturing translocated birds, trapping was not conducted in the release area following their release during spring trapping periods.

Radio-tagged individuals were located ≥3 times weekly during the breeding season (1 Apr - 30 Sep) using the homing method (Kenward 2001, White and Garrott 1990). We approached birds within 25-50 m to minimize location and habitat classification errors, and all ascribed locations were recorded into a Geographical Information System (GIS) using ArcGIS® software (Environmental Systems Research Institute, Inc.). We determined specific causes of mortality when possible, by evidence at the kill site and condition of the radio-transmitter (Curtis et al. 1993). We systematically searched the study area within approximately 5 km of the birds last known location when radio contact was lost.

Bobwhite capture and monitoring procedures outlined in this study for the source sites in Baker and Dougherty Counties were approved by the Georgia Department of Natural Resources (2070 U.S. Hwy. 278, S.E., Social Circle, Georgia 30025) during 2003 and

2004 under permit numbers #29-WMB-03-280 and #29-WSF-04-200. Bobwhite capture and monitoring procedures for the translocation study site in Marion County, Georgia were approved by the Georgia Department of Natural Resources (2070 U.S. Hwy. 278, S.E., Social Circle, Georgia 30025) under permit #29-WMB-00-105, #29-WMB-03-38, and #29-WMB-04-128. All trapping, handling, and sampling techniques were approved by the University of Georgia Institutional Animal Care and Use Committee (2000-2002 IACUC approval numbers: A990028M1, A990028C1; 2003 extension: A200310109-0) and followed guidelines provided by the Ornithological Council's Guidelines for the Use of Wild Birds in Research (American Ornithologists' Union 1999).

2.4.2 Statistical Analysis

Survival

We estimated survival rates of bobwhites in relation to temporal and biological/group effects using the known-fate data type in program MARK (White and Burnham 1999). The known-fate model employs a binomial likelihood and permits incorporation of individual covariates (e.g., gender and age) delineated by groups (e.g. translocated, resident) to evaluate their affect on survival. We constructed models incorporating additive effects and interactions, where biologically relevant, using a logit-link function. Weekly survival was comprised of 3 intervals: 2, 2-day intervals and 1, 3-day interval. To account for this variation and accurately estimate survival we specified the time-interval length in program MARK.

We used an information-theoretic approach (Akaike 1973, Anderson et al. 2000, Burnham and Anderson 2002, Guiasu 1977) to evaluate a set of candidate models developed *a priori* based on biological insight and to test explicit hypotheses. The best approximating model in the candidate set was determined by Akaike's Information Criterion adjusted for small sample bias and overdispersion ($QAIC_c$; Burnham and Anderson 2002, Wedderburn 1974). We used $QAIC_c$ to compare each candidate model, and we considered the model with the lowest $QAIC_c$ value the best approximating model given the data. We assessed the model fit (via evaluation of residual plots and c-hat) of the most general model; for our analysis the most sensible general model was with survival varying weekly for the duration of the study. The relative plausibility of each model in the set of candidate models was assessed by Akaike weights (w_i; Anderson et al. 2000, Burnham and Anderson 2002), where the best approximating model in the candidate set has the greatest Akaike weight. When appropriate, we used model averaging (Akaike 1974, 1978, Burnham and Anderson 2002) to obtain daily survival rates and derived monthly and seasonal survival from the product of weekly survival rates for the respective intervals. To derive additional inference and render direct covariate-specific comparison, we report beta coefficients, their standard errors and 95% confidence intervals for variables of interest (e.g. group); and, for comparison to other studies, we report the derived estimates of DSR (with associated 95% CI).

We conducted two separate analyses with the known-fate data type to delineate: (1) temporal and (2) biological and grouping effects on survival. First we examined a candidate set of temporal models, which included parameterizations for time via week, month, and year effects. We included models with no time-dependence (constant survival), and first- and second-order linear time trends within year, and models with constant or variable survival among years. Additionally, to evaluate potential impact of translocation on survival we included models where survival was constant across week (weeks 1-4) and month (months 1-4) or varied between week and month. We then used the temporal effects model with the lowest $QAIC_c$ value as the basis for formulating a candidate set of models to examine relevant biological, and grouping, effects. We developed, *a priori*, candidate models designed to examine these biologically relevant hypotheses explaining variation in survival. Here, we outline 4 sources of variation used to develop our survival models:

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

2. Age. Age (adult, subadult) cohorts often account for variation in survival (Pollock et al. 1989a) based on the tenet that as individuals age they become more experienced and thus survive better. However, following translocation age has not been investigated. We hypothesized that adult bobwhites would yield higher survival rates than sub-adults, and we hypothesized that a model including an interaction of age and group would yield meaningful results whereby experienced bobwhites (adults) would acclimate more quickly to their new surroundings and as such better select optimal habitats.

3. Gender. A common source of variation in survival is differences between males and females (Pollock et al. 1989a). Male bobwhites, during breeding season, exhibit a higher propensity to disperse and, in general, make larger movements (Cook 2004, Folk 2006). Therefore, we hypothesized that combined with this movement tendency and following translocation that male bobwhites would have lower survival than females.

4. Source. Translocated bobwhites were captured and moved from three different sites (located about 15 km apart) during both 2003 and 2004. However, all three source-sites were adjacent properties and situated in a large block of quality quail habitat and therefore we hypothesized that the source would not explain additional variation in survival.

Home Range, Movement and Site Fidelity

We used multi-strata models in program MARK (White and Burnham 1999) to quantify movement among strata and site fidelity to individual stratum. We delineated 3 strata based on translocation effort and the designated release area: state A was the target area (315 ha) where translocated bobwhites were released; state B was a buffer area immediately surrounding the target area (state A), but still on the study site property, and state C was completely off the study site. Multi-strata models simultaneously estimate apparent survival, re-sighting and movement probabilities among strata (Hestbeck et al. 1991, Kendall and Nichols 2004). Because we estimated survival in the known-fate framework our focus using the multi-strata model was to assess movement, or transition probabilities; however, we modeled survival in the context of strata (states: A, B and C) as mentioned above to gauge the effects of site specific survivability relative to habitat management among strata. We first attempted to reduce the number of parameters by constraining capture probabilities (p=1) equal across time, strata, or both time and strata, while movement probabilities remained both time and stratum specific. Then we modeled movement (Ψ) as constant, or varying by, group, age, or group and age. We estimated movements from strata i to j (i.e., movement from the original state to a different state or movement from a different state back to the original state) separately ($\Psi_{A:B}$, $\Psi_{B:C}$, $\Psi_{A:C}$, $\Psi_{B:A}$, and $\Psi_{C:B}$). We fixed movements from $\Psi_{C:A}$ to zero because there was little or no evidence in the data for this directional movement especially early in the breeding season because no individuals were radio-tagged or released off the study site. We selected models using AIC$_c$, and report model-averaged parameter estimates as described above. To allow comparison of movements to other bobwhite translocation studies (Terhune et al. 2005) we additionally estimated the Arithmetic Center (A$_C$) of breeding season home ranges for each individual and calculated the Euclidean distance from the A$_C$ to the release and trap sites for translocated and resident bobwhites, respectively.

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

2.5 RESULTS

During 2003-2004, we radio-tagged 136 (male=62; female=74) and 127 (male=70; female=57) resident and translocated bobwhites, respectively. We radio-located individuals $\geq$3 times weekly from March to October for a total of 8,869 telemetry locations. We did not exclude from analysis translocated or resident bobwhites that died during the traditional 1-week censor period (Pollock et al. 1989b) immediately following release because we believed those mortalities had relevant implications to the success of translocation.

Survival

The most parsimonious temporal effects model included differences in survival among months for the duration of the season (Table 2.1); this "best" model was 2.6 times more likely than the next best model. However, the next best model containing an additive effect of year also received substantial support (Δ $QAIC_c$=1.1961; Table 2.1). In fact, several temporal models including the null survival model (B_0) received moderate support indicating that the variation in survival is likely more attributable to factors other than or in addition to temporal effects. Our exploratory temporal analysis suggested that the first month following release explained the most variation in survival (Table 2.1), but the effect was positive (B_{Mar}=0.8954 [0.0669,1.7241]). The beta estimates for all other months overlapped zero suggesting that these months did not adequately explain any additional variation in survival.

We used the most plausible temporal effects model ($B_0 + B_1{}^*Mar + B_2{}^*Apr + B_3{}^*May + B_4{}^*Jun + B_5{}^*Jul + B_6{}^*Aug$) as the baseline, general model to evaluate hypotheses relative to biological and group effects on survival. The best approximating model from this analysis included an age effect on survival, but this model did not receive overwhelming support (Table 2.2). Age was included in the top model suggesting that age explained more of the variation in survival than other covariates and explained more variation in survival than the temporal-only (month) model. We did not detect differences in survival among translocated and resident (Model averaged estimate: $B_{translocate}$=0.0017 [-0.4910,0.4867]) or adult ($\hat{S}$=0.4322; 95% CI: [0.0145,0.8478]) and juvenile ($\hat{S}$=0.3118; 95% CI: [0.1274,0.5865]) bobwhites (Model averaged estimate: B_{adult}=0.3296 [-0.1645,0.8236]). The effect of gender on survival was minimal (Model averaged estimate: B_{male}=0.0481 [-0.19845,0.2946]). Variation in monthly survival among translocated and resident bobwhites was also inconsequential (Figure 2.2). Overall survival was 0.4061 (95% CI: 0.2734, 0.5338) and 0.3837 (95% CI: 0.2650, 0.5002) during 2003 and 0.3831 (95% CI: 0.2538, 0.5111) and 0.3699 (95% CI: 0.2465, 0.4937) during 2004 for translocated and resident bobwhites, respectively. The model including source as an explanatory additive effect did not substantially improve the temporal-only model (Table 2.2). Survival among individuals from source site 1 ($\hat{S}$=0.3819; 95% CI: [0.1335,0.6316]), source site 2 ($\hat{S}$=0.3106; 95% CI: [0.0949,0.5600]), and resident individuals ($\hat{S}$=0.3770; 95% CI: [0.2980,0.4628]) was more similar than individuals translocated from source site 3 ($\hat{S}$=0.5012; 95% CI: [0.2215,0.7289]).

Multi-state model analysis of survival indicated that survival among strata A (0.3798 [95% CI: 0.2840, 0.5022]), B (0.3399 [95% CI: 0.0953, 0.5879]) and C (0.2348 [95% CI: 0.006, 0.5578]) was not statistically different, but the model including strata as an explanatory variable received substantial support (W_i=0.4480; Table 2.4).

Home Range, Movement and Site Fidelity

Home range size was similar among translocated and resident bobwhites, but generally larger during 2003 than 2004 (Table 2.3). Multi-strata model analyses indicated that movement was best explained by a location effect (S(.) Ψ_{strata}; Table 2.5) with different transition probabilities occurring between different strata (Table 2.5). The only models receiving substantial support for explaining movement of individuals included strata and no single model lacking this parameter received a model weight (W_i) >0 (Table 2.4). The addition of group, age and gender as additive effects did not improve strata-specified models. The best additive model included the group parameter, but this model received little relative support ($\Delta\ QAIC_c$ = 8.22); in fact, a similar model excluding the group parameter, the strata only model (S(.) Ψ_{strata}) was more than 66 times more plausible (Table 2.4).

Bobwhites that moved off the target release-area (stratum A) tended to stay on the managed property (stratum B; $\Psi_{A:B}$= 0.06) versus off the property (stratum C; $\Psi_{A:C}$=0.003). Site fidelity of translocated individuals ($\Psi_{A:A}$=0.9338) to the target area was lower than resident bobwhites ($\Psi_{A:A}$=0.9540), but remained high. Additionally, some individuals leaving the target area or the study site altogether during one time interval returned to study site strata upon subsequent intervals (Table 2.5).

Distances moved from the trap or release sites to the Arithmetic Center (A_C) of individual home ranges did not vary among translocated and resident bobwhites or among male or females (Figure 2.3) within years; however, mean distance moved from release and trap sites was greater during 2004 then 2003 (Figure 2.3). Most bobwhites (>60%) moved <500 m from their trap or release sites, but >15% of all translocated individuals moved >1000 m from their release site compared to <8% of resident bobwhites moving this same distance (Figure 2.4). Overall, movement (dispersal) did not differ among males and females (Figures 2.3, 2.4, 2.5). Evaluation of Mean Minimum Daily (MMD) movements revealed that greater daily movements occurred early (in March and early April) in the breeding season and immediately following release, but generally stabilized and fluctuated around 50 m for the remainder season (Figure 2.5).

2.6 Discussion

Survival

Evaluation of the hypotheses related to group and gender indicated that their effects on survival was negligible and in accord with our *a priori* predictions. Survival estimates for translocated and resident northern bobwhites were similar both years during this study, and similar to those reported for other translocation studies (DeVos and Mueller 1989, Lui et al. 2000), but higher than those reported by Terhune et al. (2006) whose techniques were congruent to ours. Additionally, breeding season survival of translocated individuals was similar to estimates reported for long-term mark-recapture studies where subsequent population levels were stable to increasing (Palmer and Wellendorf 2007, Terhune et al. 2007). Variation in survival for our data was best explained temporally with an additive effect of age. Whereas translocated adults tended to have higher survival than juveniles suggesting a biological difference (>12%), the statistical effect size did not substantiate this difference. However, small sample size, particularly for adults, and resulting large standard errors may have precluded the detection of a difference in our data. The source of translocated birds did not adequately explain additional variation in survival, despite one site (source site 3) having relatively high survival (>50%) as compared to the other 2 source sites (31 & 38%) and resident (37%) bobwhites. Notably, all three source sites were farm sites under similar management regimes and were located adjacent to intensively managed properties.

Using multi-strata analysis, we were able to assess differences in stratum-specific survival in addition to movement and site fidelity. Although we did not detect statistical differences among strata, models including strata received substantial support. Whereas the difference in survival for strata A and B was only about 6% and strata B and C about 8.5%, the difference in survival between strata A and C was approximately twice as large (>14%). In general, strata-specific survival declined as individuals moved away from the target release area. This declining gradient may be indicative of declining habitat quality. Intensive habitat management on the property occurred on the core (target release; stratum A) area, prior to the onset of the study, for seven years as compared to only a four years on the periphery area (stratum B), and habitat was not managed off the study site (stratum C). Models including stratum-specific group effects did not receive substantial weight suggesting that survival between translocated and resident bobwhites was not different regardless of strata location. In spite of the small number of individuals dispersing completely off the study site, probability of mortality increased substantially for individuals leaving the managed property. These results suggest that quality habitat is important for survival and further corroborates the findings of previous research (Klimstra 1972, Landers and Mueller. 1986, Roseberry and Klimstra 1984, Sisson et al. 2006, Stoddard 1931). Therefore habitat management on recipient sites should be a prerequisite to translocation to ensure adequate vegetative cover and thereby optimizing the probability of survival for individuals released.

Home Range, Movement and Site Fidelity

Differences in home range size between translocated and resident bobwhites was inconsequential; however, home range sizes during 2003 were generally larger than 2004. Urban (1972) posited that habitat largely influences bobwhite mobility during breeding season. As such, the disparity that we observed in home range size may have been a result of either limited food resources or differences in habitat structure between years (Landers and Mueller. 1986, Sisson et al. 2000). Although anecdotal because we did not extensively measure vegetation composition, our direct observation of the quality of fields during 2003 was poor and, consequently, field use (T. Terhune, unpublished data) during 2003 was considerably lower than in 2004. Similarly, food resources were more abundant during 2004 than 2003 due to the application of supplemental feed on a more consistent regimen.

Breeding season dispersal is commonly reported among bobwhites, is generally considered an innate behavior and is an important process from both an ecological and evolutionary perspective (Clobert et al. 2001, Howard 1960). Furthermore, movement probabilities are useful for guiding management and conservation strategies (Spendelow et al. 1995). However, few studies have examined dispersal of bobwhites following translocation (Lui et al. 2002, Terhune et al. 2005). We evaluated dispersal, and its complement - site fidelity, via two metrics: distance moved from the trap or release site to the Arithmetic mean center (A_C) of individual home ranges and estimation of transition probabilities using multi-strata models. Interestingly, distances moved from the release and trap sites to the A_C was lower in 2003 compared to 2004 which is seemingly contradictory to larger home ranges during 2003 than 2004. A_C distances for both groups in our study were considerably larger than other studies (Terhune et al. 2005). This may be attributable to different habitat characteristics among years (Urban 1972) or the presence and abundance of conspecifics whereby individuals located on low-density sites would ostensibly be required to traverse greater distances to search and find suitable mates (Errington 1945, Roseberry and Klimstra 1984, Townsend et al. 2003, Urban 1972). Bobwhite densities reported by Terhune et al. (2005) was ≥ 3.71 birds per ha whereas on our study site density was <1.24 birds per ha. However, more research is warranted to investigate the potential effects, if any, that density dependence has on the efficacy of translocation and movements of individuals translocated to sites of varying population densities.

Ecological advantages of site familiarity may influence site fidelity (Clobert et al. 2001, Lande 1988) and the overall success of translocation because translocated individuals would, in theory, be at a disadvantage as compared to resident bobwhites. Site fidelity of translocated bobwhites to the target release area was moderately lower than resident bobwhites but still high. Majority of the individuals dispersing off the target area remained on the managed property. Less than 2% of all bobwhites (2.4% of translocated) permanently dispersed (i.e., >98% site fidelity) completely off the study site. We did, however, lose radio-contact with a few individuals due to radio-failure or other causes and it is possible that these individuals dispersed off the study site. However, we systematically searched for bobwhites off the study site (up to 10 km) in attempt to radio-locate and identify potential dispersers. The proportion of individuals dispersing off the target area (315 ha) was approximately 16% compared to only 8.5% for resident bobwhites. In order to have ensured 100% site fidelity of translocated bobwhites in this study the property size needed to have been 1256 ha.

Although Mean Minimum Daily (MMD) distances moved were not different among groups or years, bobwhites exhibited larger MMD movements early in the breeding season. In particular, male translocated bobwhites had larger movements during the first 2 weeks post-release compared to their resident counterparts and both male and female resident bobwhites moved greater distances during weeks 4 and 5 post-capture (last week in April and first week in May). The larger movements we observed early in the breeding season may have been a result of male-biased dispersal (Hood 1955, Smith et al. 1982) of translocated bobwhites following release and natural movement behavior associated with covey break-up for resident male and female bobwhites (Church and Taylor 1992, Roseberry 1993, Yoho and Dimmick 1972). Increased mobility during early breeding-season may be best explained by the natural proclivity of individuals searching for mates or suitable nest sites (Townsend et al. 2003). Previous research has suggested that increased movement negatively impacts survival (Cook 2004, Folk 2006), however, the inclusion of movement in survival analyses in our study did not explain additional variation in survival; stratum-specific and temporal effects explained more of the variation in survival for our data. In our study, movements were generally lower than those reported in other studies (Cook 2004, Folk 2006), but it is a well accepted tenet that mobility of bobwhites is typically dictated by the quality of habitat. Generally, researchers have deduced that mobility is lower among intensively managed sites and higher among sites of marginal habitat quality or highly fragmented sites (Cook 2004, Fies et al. 2002, Kabat and Thompson 163, Townsend et al. 2003). That said, intensive habitat management occurred for more then 4 years on our study site prior to translocation and thus an obvious, but important, consideration prior to instituting translocation, at large, is an assessment of habitat quality and subsequent implementation of habitat management where necessary.

Conservation Implications

Conservation and management decisions should be driven by current and sound research. Translocation has become a common management tool in wildlife conservation for establishing, re-establishing, or augmenting existing wild populations (Griffith et al. 1989), but many of the translocations and reintroductions implemented to date have lacked scientific rigor (Seddon et al. 2007). Thus, the knowledge gained from such releases has limited our ability to refine the technique and use empirical data, and subsequent analyses, to guide conservation and management strategies.

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

That said, translocation is not a panacea for preservation or broad-scale restoration of bobwhites and should not, by any means, be viewed as a substitute to habitat management or even be used as a common management practice. Translocation, however, should remain a pragmatic conservation option instituted on a site-by-site basis whereby decisions governing its implementation should take into account knowledge of the species life-history and ecology. This approach would ideally increase the efficacy of translocation and help to guide the role of translocation in conservation planning and management for a particular species. Whereas results from this study are directly applicable to bobwhites, these results may also broadly apply to grassland obligate birds with similar life-history characteristics. This study augments our knowledge of translocation and helps to refine the translocation process as to the appropriate spatio-temporal scale for its successful application.

We believe that four primary mechanisms contributed to the success of translocation: (1) large target release area; (2) quality habitat on the release site; (3) an available source of wild bobwhites; and (4) timing of release. We propose that conservation strategies should primarily focus on habitat restoration and improvement, and employ translocation only as a means to complement this strategy by translocating individuals to establish or augment populations on areas where habitat has been recently restored and that have potential to becoming source populations or connect disjunct and fragmented habitats. Upon adequate habitat management and given a valid source of wild bobwhites, we also recommend translocating individuals 3 to 4 weeks prior (during March) to breeding season to provide ample time to acclimate to their new surroundings, but not longer than 3-4 weeks prior to breeding season to reduce mortality as observed during this study. However, because we did not experimentally investigate the time of release on the success of translocation, we cannot unequivocally relegate the benefit of translocation occurring during other periods (i.e., Fall). Finally, we recommend (based on movement and dispersal data in this study) that release sites be as large as possible, but minimally should be $\geq$607 ha to reduce dispersal from managed habitat.

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Literature Cited

Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. pages 267–281, Akademiai Kiado, Budapest.

Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**:716–723.

Akaike, H., 1978. A bayesian analysis of the minimum AIC procedure. *Annals of the Institute of Statistical Applications of Statistics* **30**:9–14.

American Ornithologists' Union, 1999. Report of committee on use of wild birds in research. *Auk* **116**:1–41.

Anderson, D. R., K. P. Burnham, and W. L. Thompson, 2000. Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**:912–923.

Askins, R. A., 1993. Population trends in grassland, shrubland, and forest birds in eastern north america. *Current Ornithology* **11**:1–34.

Bijlsma, R., J. Bundgard, and A. C. Boerema., 2000. Does inbreeding affect the extinction risk of small populations?: predictions from *Drosophilia*. *Journal of Evolutionary Biology* **13**:502–514.

Brennan, L. A., 1991. How can we reverse the the northern bobwhite decline? *Wildlife Society Bulletin* **19**:544–555.

Brennan, L. A., 1999. The Birds of North America. Number 397. A. Poole and F. Gill, eds., Philadelphia, Pennsylvannia, USA.

Brennan, L. A. and W. P. Kuvlesky, Jr., 2005. North american grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* **69**:1–13.

Burger, L. D., L. W. Burger, Jr., and J. Faaborg, 1994. Effects of prairie fragmentation and predation on artificial nests. *Journal of Wildlife Management* **58**:249–254.

Burger, L. W., Jr., 2002. Quail management: Issues, concerns, and solutions for public and private lands–a southeastern perspective. *Proceedings of the National Quail Symposium* **5**:20–34.

Burger, L. W., Jr., D. A. Miller, and R. I. Southwick., 1999. Economic impact of northern bobwhite hunting in the southeastern united states. *Wildlife Society Bulletin* **27**:1010–1018.

Burger, L. W., Jr., M. R. Ryan, T. V. Dailey, and E. W. Kurzejeski, 1995. Reproductive strategies, success, and mating systems of northern bobwhite in missouri. *Journal of Wildlife Management* **59**:417–426.

Burnham, K. P. and D. R. Anderson, 2002. Model Selection and Multi-Model Inference: A Practical Information Theoretic Approach. Springer-Verlag, New York, New York, USA, second edition.

Calenge, C., 2006. The package adehabitat for the r software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**:516–519.

Church, K. E., J. R. Sauer, and S. Droege, 1993. Population trends on quails in north america. *Proceedings of the National Quail Symposium* **3**:44–54.

Church, K. E. and J. S. Taylor, 1992. Management and research of northern bobwhite (*Colinus virginianus*) in north america: An overview. *Gibier Faune Savage* **9**:787–796.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols, 2001. Dispersal. Oxford University Press, New York, New York.

Cook, M. P., 2004. Northern Bobwhite Breeding Season Dispersal, Habitat-Use, and Survival in a Southeastern Agricultural Landscape. Master's thesis, University of Georgia.

Corteville, L. A., 1998. Effects of Radiotransmitters on Survival, Harvest Rate, and Body Condition of Northern Bobwhite (*Colinus virginianus*). Master's thesis, Mississippi State University.

Curtis, P. D., B. S. Mueller, P. D. Doerr, C. F. Robinette, and T. DeVos., 1993. Potential polygamous breeding behavior in northern bobwhite. *Proceedings of the National Quail Symposium* **3**:55–63.

DeVos, T., Jr and B. S. Mueller, 1989. Quail relocation - can we fill the void? *Quail Unlimited* **12**:2–4.

Errington, P. L., 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomenoa. *Ecological Applications* **15**:1–34.

Fies, M. L., K. M. Puckett, and B. Larson-Brogdon, 2002. Breeding season movements and dispersal of northern bobwhites in fragmented habitats in virginia. In *Proceedings of the National Quail Symposium*, volume 5, pages 173–179.

Folk, T. H., 2006. Population Ecology of Northern Bobwhites. Ph.D. thesis, Auburn University.

Frankham, R., J. D. Ballou, and D. A. Briscoe, 2004. A Primer of Conservation Genetics. Cambridge University Press, Cambridge, United Kingdom.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed., 1989. Translocation as a species conservation tool: Status and strategy. *Science* **245**:477–480.

Guiasu, S., 1977. Information Theory with Applications. McGraw-Hill, New York, New York, USA.

Guthery, F. S. and J. J. Lusk, 2004. Radiotelemetry studies: Are we radio-handicapping northern bobwhites? *Wildlife Society Bulletin* **32**:194–201.

Hanski, H. and M. Gilpin, 1991. Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**:3–16.

Herkert, J. R., 1994. Breeding bird communities of mid-western prairie fragments: the effects of prescribed burning and habitat-area. *Natural Areas Journal* **14**:128–135.

Hernandez, F., J. A. Arredono, F. Hernandez, D. G. Hewitt, and S. J. D. A. R. L. Bingham., 2004. Effects of radiotransmitters on body mass, feed consumption, and energy expenditures of northern bobwhites. *Wildlife Society Bulletin* **32**:394–400.

Hestbeck, P. W., J. D. Nichols, and R. A. Malecki, 1991. Estimates of movement and site fidelity using mark resight data of wintering canada geese. *Ecology* **72**:523–533.

Hood, M. R., 1955. Mississippi quail investigation. *Proceedings of the Southeastern Association of Game and Fish Commissioners* **9**:157–163.

Howard, W. E., 1960. Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* **63**:152–161.

Johnson, D. H., 2001. Habitat fragmentation effects on birds in grasslands and wetlands: a critique of our knowledge. *Great Plains Research* **11**:211–231.

Kabat, C. and D. R. Thompson, 163. Wisconsin quail: 1834-1962, population dynamics and habitat management. *Wisconsin Conservation Department Technical Bulletin* **30**.

Kendall, W. L. and J. D. Nichols, 2004. On the estimation of dispersal and movement of birds. *Condor* **106**:720–731.

Kenward, R. E., 2001. A Manual for Wildlife Radio Tagging. Academic Press, Inc., San Diego, CA.

Klimstra, W. D., 1972. Population dynamics of bobwhite on an intensively managed area in southern illinois. *Proceedings of the National Quail Symposium* **1**:356–360.

Knopf, F. L., 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* **15**:247–257.

Lande, R., 1988. Genetics and demography in biological conservation. *Science* **241**:1455–1460.

Landers, J. L. and B. S. Mueller., 1986. Bobwhite quail management: A habitat approach. Tall Timbers Research Station, Tallahassee, Fl.

Lui, X., B. S. Mueller, D. S. Parsons, and D. R. Dietz, 2002. Movement patterns of resident and relocated northern bobwhites in East Texas. *Proceedings of the National Quail Symposium* **5**:168–172.

Lui, X., J. R. M. Whiting, B. S. Mueller, D. S. Parsons, and D. R. Dietz, 2000. Survival and causes of mortality of relocated and resident bobwhites in east texas. *Proceedings of the National Quail Symposium* **4**:119–124.

Newman, D. and D. Pilson, 1997. Increased probability of extinction due to decreased genetic effective population size: Experimental populations of (*Clarkia puchella*). *Evolution.* **51**:354–362.

Palmer, W. E. and S. Wellendorf, 2007. Effects of radiotransmitters on northern bobwhite annual survival. *Journal of Wildlife Management* **71**:1281–1287.

Peterson, M. J., X. B. Wu, and P. Rho, 2002. Rangewide trends in landuse and northern bobwhite abundance: an exploratory anlaysis. *Proceedings of the National Quail Symposium* **5**:35–44.

Pollock, K. H., C. T. Moore, W. R. Davidson, F. E. Kellog, and G. L. Doster, 1989a. Survival rates of bobwhite quail based on band recovery analysis. *Journal of Wildlife Management* **53**:1–6.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis., 1989b. Survival analysis in telemetry studies: The staggered entry design. *Journal of Wildlife Management* **53**:7–14.

Rollins, D. and J. P. Carroll, 2001. Predation impacts on northern bobwhite and scaled quail. *Wildlife Society Bulletin* **29**:39–51.

Roseberry, J. L., 1993. Bobwhite and the “new” biology. *Proceedings of the National Quail Symposium* **3**:16–20.

Roseberry, J. L. and W. D. Klimstra, 1984. Population ecology of the Bobwhite. Southern Illinois University Press, Carbondale, Illinois, U.S.A., first edition.

Roseberry, J. L. and S. D. Sudkamp, 1998. Assessing the suitability of landscapes for northern bobwhite. *Journal of Wildlife Management* **62**:895–902.

Sauer, J. R., J. E. Hines, and J. Fallon, 2008. The north american breeding bird survey, results and analysis 1966-2007. **Version 5.15.2008**.

Seddon, P. J., D. P. Armstrong, and R. F. Maloney, 2007. Developing the science of reintroduction biology. *Conservation Biology* **21**:303–312.

Sisson, D. C., H. L. Stribling, and D. W. Speake, 2000. Effects of supplemental feeding on home range size and survival of northern bobwhites in south Georgia. In *Proceedings of the National Quail Symposium*, volume 4, pages 128–131.

Sisson, D. C., T. M. Terhune, H. L. Stribling, and S. D. M. Jerald Fitch Sholar, 2006. Survival and causes of mortality for northern bobwhites in the southeastern united states. In J. P. C. Brant C. Faircloth, Theron M. Terhune, editor, *Gamebird Proceedings*, volume 6, pages 000–000.

Smith, G. F., F. E. Kellogg, D. L. Doster, and E. E. Provost, 1982. A 10-year study of bobwhite quail movement patterns. *Proceedings of the National Quail Symposium* **2**:35–44.

Spendelow, J. A., J. D. Nichols, I. C. T. Nisbet, H. Hayes, G. D. Cormons, J. Burger, C. Safina, J. E. Hines, and M. Gochfeld, 1995. Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. *Ecology* **76**:2415–2428.

Stoddard, H. L., 1931. The Bobwhite Quail: Its Habits, Preservation, and Increase. Charles Scribner's Sons, New York, New York.

Tallmon, D. A., G. Luikart, and R. S. Waples, 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution* **19**:489–496.

Terhune, T. M., D. C. Sisson, J. B. Grand, and H. L. Stribling, 2007. Factors influencing survival of radio-tagged and banded bobwhites in georgia. *Journal of Wildlife Management* **71**:1288–1297.

Terhune, T. M., D. C. Sisson, and H. L. Stribling, 2006. The efficacy of relocating wild northern bobwhites prior to breeding season. *Journal of Wildlife Management.* **70**:914–921.

Terhune, T. M., D. C. Sisson, H. L. Stribling, and J. P. Carroll, 2005. Home range, movement, and site fidelity of translocated northern bobwhite (*Colinus virginianus*) in southwest georgia,USA. *European Journal of Wildlife Research* **51**:119–124.

Townsend, D. E., II, J. D. M. Leslie, R. L. Lochmiller, S. J. DeMaso, S. A. Cox, and A. D. Peoples, 2003. Fitness costs and benefits associated with dispersal in northern bobwhites *colinus virginianus*. *American Midland Naturalist* **150**:73–82.

Urban, D., 1972. Aspects of bobwhite quail mobility during spring through fall months. *Proceedings of the National Quail Symposium* **1**:194–199.

Vickery, P. D., M. L. Hunter, and S. M. Melvin, 1994. Effects of habitat area on the distribution of grassland birds in maine. *Conservation Biology* **8**:1087–1097.

Vickery, P. D., M. L. Hunter, and J. Wells, 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* **63**:281–288.

Wedderburn, R. W. M., 1974. Quasi-likelihood functions, generalized linear models, and the gauss-newton method. *Biometrika* **61**:439–447.

White, G. C. and K. P. Burnham, 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study 46 Supplement* pages 120–138.

White, G. C. and R. A. Garrott, 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, Inc., San Diego, CA.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple, 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology* **10**:1142–1154.

Yates, S. W., D. C. Sisson, H. L. Stribling, and D. W. Speake, 1995. Northern bobwhite brood habitat use in south georgia. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **49**:498–504.

Yoho, N. S. and R. W. Dimmick, 1972. Changes in covey affiliation by bobwhite quail in tennessee. *Proceedings of the National Quail Symposium* **1**:28–32.

Table 2.1: Model selection results for examination of temporal factors on survival of resident and translocated northern bobwhites on Buck Creek Plantation, Marion County Georgia, 2003-2004.

Model	QDeviance	K	$QAIC_c$	$\Delta\ QAIC_c$	W_i
$B_0+B_1{}^*Mar+B_2{}^*Apr+B_3{}^*May+B_4{}^*Jun+B_5{}^*Jul+B_6{}^*Aug$	1419.0098	7	1433.0178	0.0000	0.5095
$B_0+B_1{}^*Mar+B_2{}^*Apr+B_3{}^*May+B_4{}^*Jun+B_5{}^*Jul+B_6{}^*Aug+B_7{}^*Yr$	1418.9236	8	1434.9339	1.9161	0.1954
$B_0+B_1{}^*T+B_2{}^*TT$	1430.4377	3	1436.4394	3.4216	0.0921
$B_0+B_1{}^*T$	1433.8818	2	1437.8826	4.8648	0.0447
$B_0+B_1{}^*wk1$	1434.1663	2	1438.1671	5.1493	0.0388
B_0	1436.3101	1	1438.3104	5.2926	0.0361
$B_0+B_1{}^*Yr+B_2{}^*T+B_3{}^*TT$	1430.3319	4	1438.3348	5.3170	0.0357
$B_0+B_1{}^*wk1+B_2{}^*wk2+B_3{}^*wk3+B_4{}^*wk4+...+B_{28}{}^*wk28$	1381.5238	29	1439.6480	6.6302	0.0185
$B_0+B_1{}^*Mar+B_2{}^*Apr+B_3{}^*May+B_4{}^*Jun+B_5{}^*Jul+B_6{}^*Aug+B_7{}^*Yr.Mar$	1411.9855	14	1440.0154	6.9976	0.0154
$B_0+B_1{}^*Yr$	1436.2412	2	1440.2420	7.2242	0.0138
** *Exploratory Analysis*					
$B_0+B_1{}^*Mar$	1422.9358	2	1426.9366	0.0000	0.2878
$B_0+B_1{}^*wk1+B_2{}^*wk2+B_3{}^*wk3$	1419.2986	4	1427.3014	0.3648	0.2398
$B_0+B_1{}^*Mar+B_2{}^*Apr$	1421.5804	3	1427.5822	0.6456	0.2084
$B_0+B_1{}^*wk1+B_2{}^*wk2+B_3{}^*wk3+B_4{}^*wk4$	1418.6413	5	1428.6456	1.7090	0.1225
$B_0+B_1{}^*Mar+B_2{}^*Apr+B_3{}^*May$	1421.5020	4	1429.5049	2.5683	0.0797
$B_0+B_1{}^*Mar+B_2{}^*Apr+B_3{}^*May+B_4{}^*Jun$	1421.3690	5	1431.3733	4.4367	0.0313
$B_0+B_1{}^*wk1+B_2{}^*wk2$	1425.4225	3	1431.4242	4.4876	0.0305

Table 2.2: Model selection results for examination of group and biological factors on survival of northern bobwhites on Buck Creek Plantation, Marion County Georgia, 2003-2004.

Model	QDeviance	K	$QAIC_c$	$\Delta\ QAIC_c$	W_i
$Month + B_7{}^*Age$	1416.0301	8	1432.0403	0.0000	0.2659
$Month$	1419.0098	7	1433.0178	0.9775	0.1631
$Month + B_7{}^*Gender + B_8{}^*Age + B_9{}^*Gender.Age$	1413.0537	10	1433.0694	1.0291	0.15895
$Month + B_7{}^*Group + B_8{}^*Age$	1416.0180	9	1434.0308	1.9905	0.09829
$Month + B_7{}^*Gender$	1418.6498	8	1434.6601	2.6198	0.07175
$Month + B_7{}^*Group$	1418.9484	8	1434.9587	2.9184	0.0618
$Month + B_7{}^*Group + B_8{}^*Age + B_9{}^*Group.Age$	1415.2841	10	1435.2997	3.2594	0.05211
$Month + B_{7-9}{}^*Source$	1416.0793	10	1436.0950	4.0547	0.03502
$Month + B_{7-13}{}^*Month.Group$	1408.5438	14	1436.5737	4.5334	0.02756
$Month + B_7{}^*Group + B_8{}^*Gender$	1418.5930	9	1436.6058	4.5655	0.02712
$Month + B_7{}^*Group + B_8{}^*Gender + B_9{}^*Age + B_{10}{}^*Gender.Age$	1415.1835	11	1437.2024	5.1621	0.02013
$Month + B_7{}^*Group + B_8{}^*Gender + B_9{}^*Grp.Gender$	1417.3817	10	1437.3974	5.3571	0.01826

Table 2.3: Mean home ranges (MCP: 100 & 95% Minimum Convex Polygon; Kernel: 95 & 50% Kernel home ranges) for northern bobwhites on Buck Creek Plantation, Marion County Georgia during 2003-2004.

Year	**Group**	n	**Locs**^{1} ($\bar{x}$)	**95 MCP (SE)**	**100 MCP (SE)**	**50 Kernel (SE)**	**95 Kernel (SE)**
2003	Resident	46	43	22.6349 (4.2036)	33.5029 (4.8608)	5.3384 (0.3464)	23.6611 (1.4503)
	Translocated	42	45	18.8888 (3.9238)	25.3755 (4.2983)	4.1505 (0.3322)	18.6229 (1.2995)
2004	Resident	27	29	9.8123 (1.0980)	13.6229 (1.5602)	4.2434 (0.2808)	17.9132 (1.0496)
	Translocated	30	38	13.1436 (3.4043)	15.7121 (3.7243)	3.7908 (0.2822)	16.5334 (1.0497)
Pooled	Resident	73	37	17.8923 (2.7663)	26.1500 (3.3030)	4.9334 (0.2483)	21.5352 (1.0404)
	Translocated	72	42	16.4950 (2.6966)	21.3491 (2.9839)	4.0006 (0.2262)	17.7523 (0.8782)

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[a] Mean number of telemetry locations per bobwhite.

Table 2.4: Model selection for the estimation of northern bobwhite movement and stratum-specific survival for radio-tagged individuals in Buck Creek Plantation, Marion County Georgia, 2003-2004.

Model	QDeviance	K	$QAIC_c$	$\Delta\ QAIC_c$	W_i
S(.) Ψ_{strata}	2189.1256	7	2203.2440	0.0000	0.5339
S (strata) Ψ_{strata}	2185.4041	9	2203.5948	0.3508	0.4480
S (.) $\Psi_{strata+group}$	2183.0181	14	2211.4654	8.2214	0.0088
S (. + group) $\Psi_{strata+group}$	2185.7668	13	2212.1541	8.9101	0.0062
S (strata + group) $\Psi_{strata+group}$	2181.2676	17	2215.9215	12.6775	0.0009
S(group) $\Psi_{strata+age}$	2181.4795	17	2216.1334	12.8894	0.0009
S(group) $\Psi_{strata+gender}$	2181.5245	17	2216.1783	12.9343	0.0008
S(group) $\Psi_{strata*group+age}$	2175.4799	22	2218.4713	15.2273	0.0003
S(group) $\Psi_{strata*group+gender}$	2173.8195	22	2218.9065	15.6625	0.0002

Table 2.5: Movement rate estimates derived from mulit-strata model in program MARK for translocated and resident northern bobwhites on Buck Creek Plantation, Marion County Georgia, 2003-2004.

Group	Movement Direction[1]	Estimate	SE	95% CI
Translocate	$\Psi_{A:A}$	0.9338	0.0177	0.8894 - 0.9611
	$\Psi_{A:B}$	0.0632	0.0174	0.0364 - 0.1072
	$\Psi_{A:C}$	0.0030	0.0016	0.0054 - 0.0116
	$\Psi_{B:A}$	0.0207	0.0215	0.0026 - 0.1446
	$\Psi_{B:B}$	0.9590	0.0298	0.8411 - 0.9904
	$\Psi_{B:C}$	0.0202	0.0208	0.0025 - 0.1400
	$\Psi_{C:A}$	0.0000		
	$\Psi_{C:B}$	0.0600	0.0352	0.0184 - 0.1783
	$\Psi_{C:C}$	0.9400	0.0426	0.8565 - 1.0000
Resident	$\Psi_{A:A}$	0.9540	0.0001	0.9537 - 0.9542
	$\Psi_{A:B}$	0.0460	0.0001	0.0457 - 0.0462
	$\Psi_{A:C}$	0.0000		
	$\Psi_{B:A}$	0.0228	0.0237	0.0029 - 0.1575
	$\Psi_{B:B}$	0.9546	0.0329	0.8259 - 0.9893
	$\Psi_{B:C}$	0.0226	0.0156	0.0049 - 0.0863
	$\Psi_{C:A}$	0.0000		
	$\Psi_{C:B}$	0.0500	0.0361	0.0117 - 0.1895
	$\Psi_{C:C}$	0.9500	0.0632	0.8261 - 1.0000

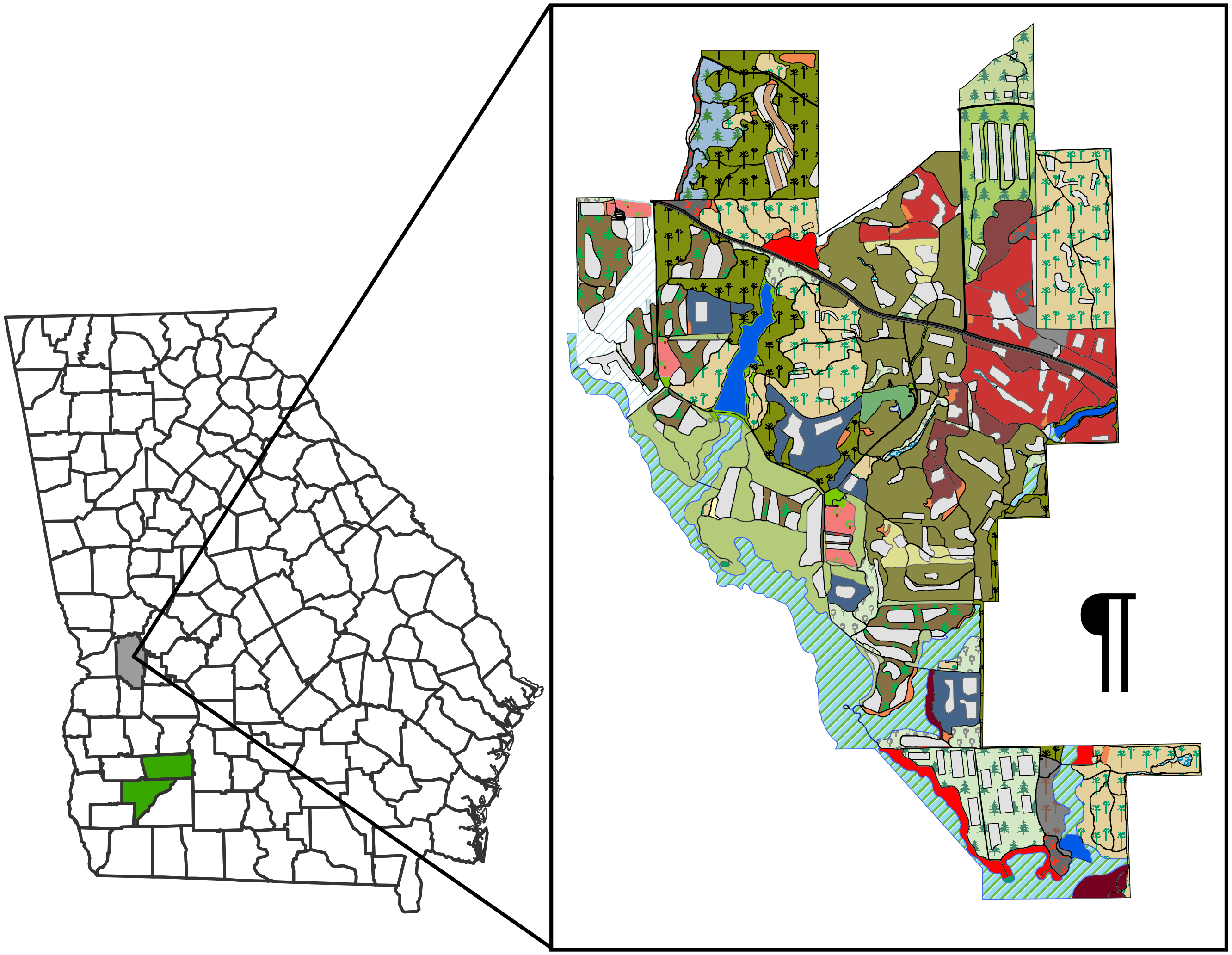

Figure 2.1: Translocation study site in Marion County (grey-shaded), Georgia, USA delineated by sub-divided areas: core (light green), buffer (blue), control (red). The source sites for translocated bobwhites were located in Baker and Dougherty counties, Georgia (green-shaded).

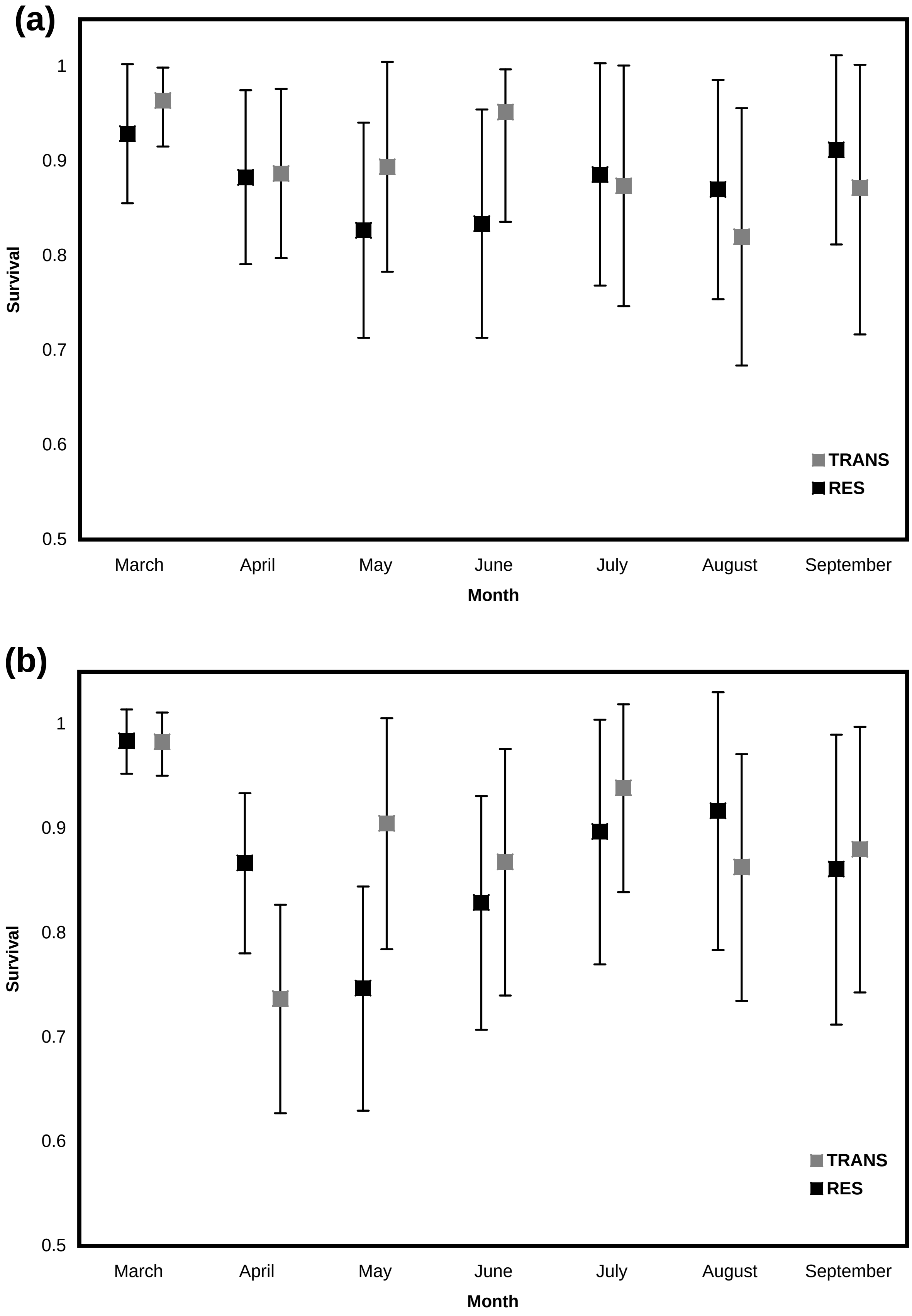

Figure 2.2: Model averaged monthly survival estimates for translocated and resident northern bobwhites located in Baker and Dougherty counties, Georgia during (a) 2003 and (b) 2004.

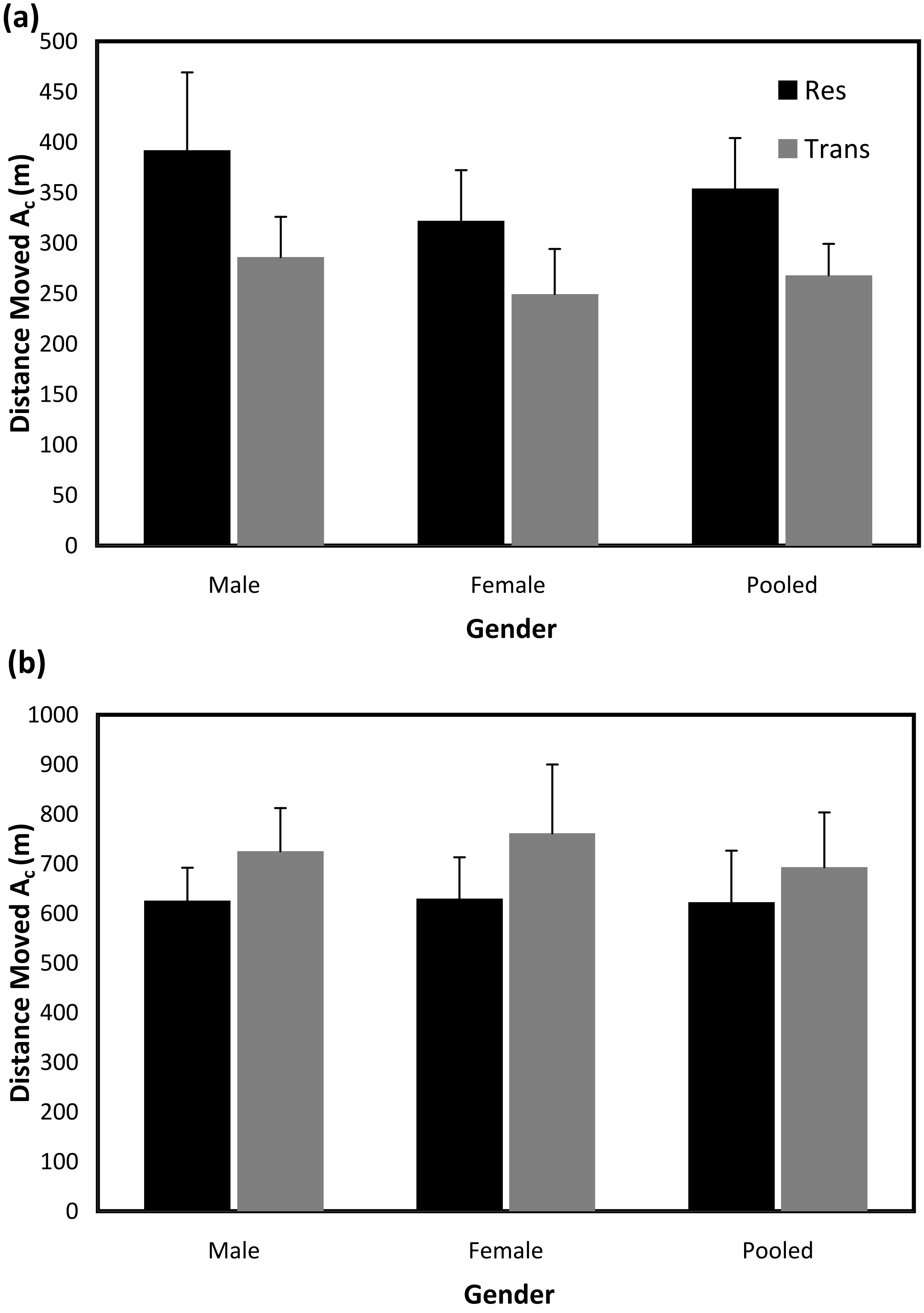

Figure 2.3: Male and female mean distances moved from release or trapsite to the Arithmetic Center (A_C) of breeding season home ranges for translocated and resident northern bobwhites located in Baker and Dougherty counties, Georgia during (a) 2003 and (b) 2004.

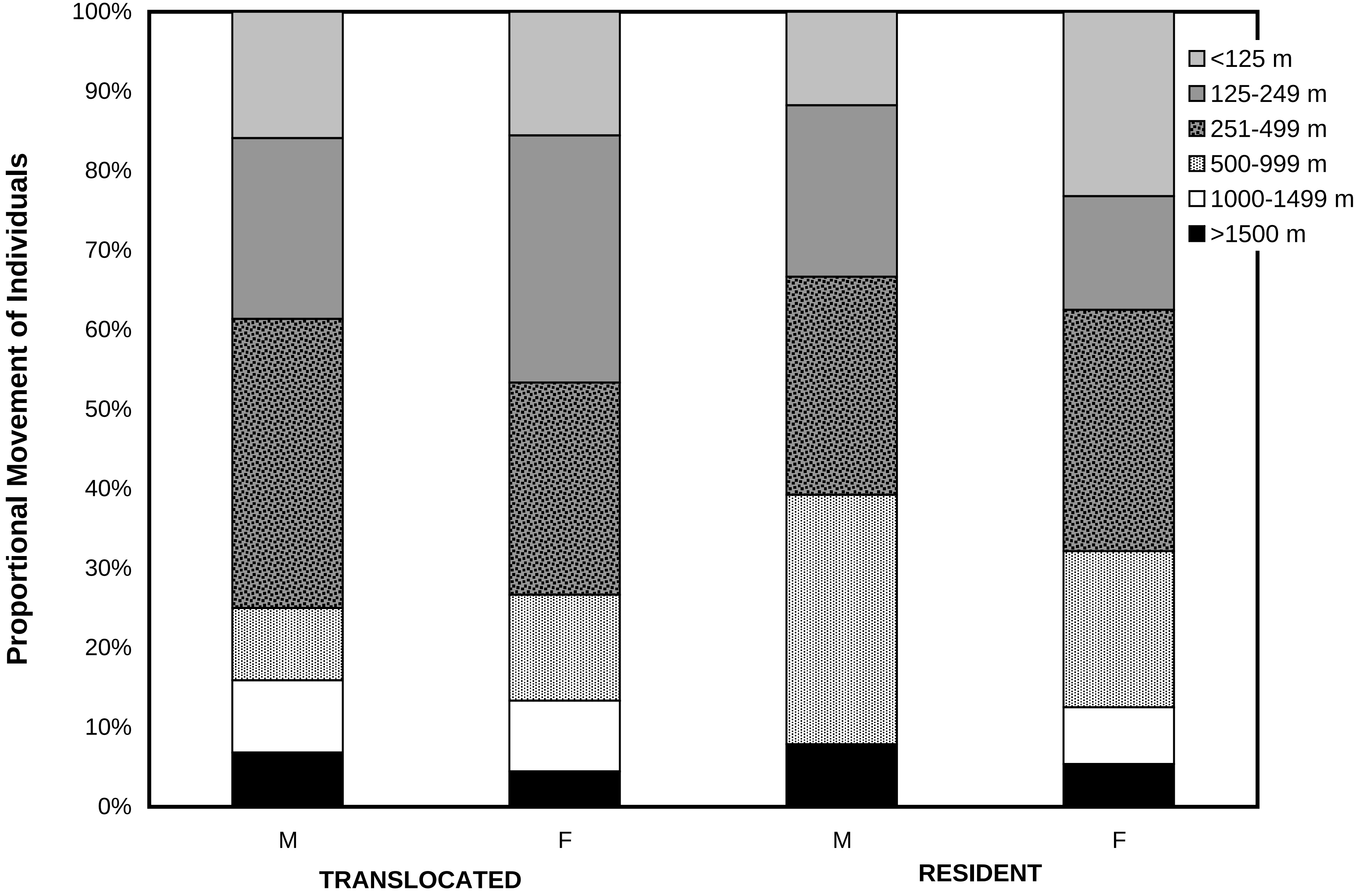

Figure 2.4: Proportion of male and female individual movement for translocated and resident northern bobwhites located in Baker and Dougherty counties, Georgia during 2003-2004. Movement is based on the distance moved (meters) from release or trap sites to the Arithmetic Center (A_C) of their individual home range during the breeding season.

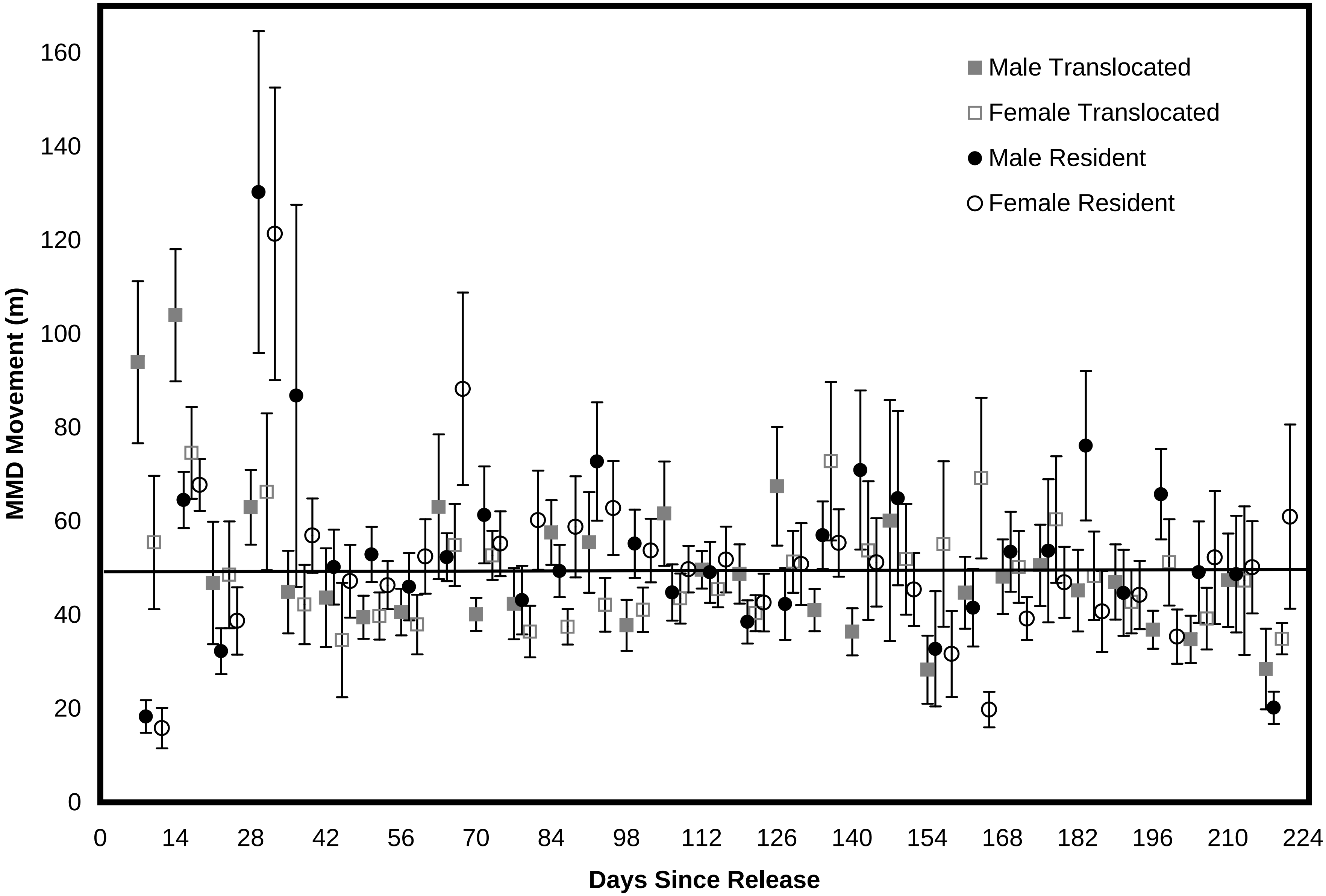

Figure 2.5: Weekly mean minimum daily (MMD) movements delineated by gender for translocated and resident northern bobwhites located in Baker and Dougherty counties, Georgia during 2003-2004.

Chapter 3

Nest survival, productivity and fecundity for translocated and resident northern bobwhites[3]

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[3] Terhune, T. M., D. C. Sisson, W. E. Palmer, B. C. Faircloth, H. L. Stribling, J. P. Carroll. To be submitted to: *Ecological Applications*.

3.1 Abstract

Numerous avian fauna, including Northern Bobwhites (*Colinus virgianus*), inhabiting early-succession ecosystems have experienced significant declines throughout their endemic range and presently exist in disjunct populations, largely attributable to extensive habitat loss and fragmentation. Natural (re)colonization of restored habitat(s) in fragmented landscapes is severely limited, particularly for low-mobility species. Translocation of individuals to these sites may reduce inbreeding and increase suppressed populations. During 2003-2004, we radio-tagged and translocated bobwhites (n = 121) to a fragemented and isolated study site in Marion County, Georgia; a sample of resident bobwhites (n = 123) was also simultaneously radio-tagged and monitored to assess reproductive capacity following release to a fragmented and isolated habitat. Nest survival was similar between groups (translocated, resident), and year, nest type and age did not explain additional variation in our models. We did not detect differences between translocated and resident bobwhites' nesting rate, brood production, clutch size and hatchability. Fecundity and productivity was similar between groups during this study. Translocated individuals initiated incubation of initial nests and renests more rapidly than resident bobwhites. Our results corroborate the use of translocation as a management technique when other management efforts have been exhausted and where conspecifics are present as we did not detect deleterious effects on nest survival, productivity and fecundity of translocated individuals following release as compared to their resident counterparts. This study provides insight to the utility of translocation as a conservation tool for both avian species and, in particular, gamebirds inhabiting early-succession habitats and may also have broader application to species inhabiting other habitat types.

3.2 Introduction

During the past few decades, the southeastern United States and other areas have experienced dramatic land-use change. In particular, intensification of silviculture and agriculture regimes; fire suppression; and urbanization have reduced a once ubiquitous early-succession ecosystem type and, where remaining, these habitats are typically highly fragmented, smaller and more ephemeral in nature. A fundamental concern in conservation biology among fragmented landscapes is the risk of inbreeding, particularly for declining species (Frankham et al. 2004, Soule 1987). Inbreeding may affect important fitness attributes such as survival, fecundity, and development (Frankham et al. 2004, Tallmon et al. 2004); and small populations of species inhabiting fragmented (and isolated) patches may be subject to greater extinction risk (Bijlsma et al. 2000, Frankham et al. 2004, Hanski and Gilpin 1991, Newman and Pilson 1997, Tallmon et al. 2004).

Regional declines in Northern Bobwhite (*Colinus virgianus*; hereafter, bobwhite[s]) populations are evident from analyses of Breeding Bird Survey data (Sauer et al. 2008) and review of the scientific literature (Brennan 1991, Guthery and Lusk 2004, Palmer and Wellendorf 2007, Terhune et al. 2007). Despite northern bobwhites being one of the most studied gamebirds in North America, their population levels continue to decline range-wide and these declines have been more precipitous in recent years (Brennan 1991, Sauer et al. 2008). Bobwhites have become subject to widespread land-use change and when combined with pejorative effects of the general influence of non-native vegetation, sod-forming grasses and changing predator abundance (Rollins and Carroll 2001), among others, their future population status remains bleak. They are sensitive to these landscape changes since they typically necessitate large (1200 to 2000 ha), contiguous habitat patches to sustain viable population levels (Brennan 1991, Roseberry and Klimstra 1984). Therefore, bobwhites may serve as an "indicator species" to the effects of habitat fragmentation and management thereof on avian communities, generally, and upland gamebirds (i.e., Galliformes), specifically.

Low annual survival (Guthery and Lusk 2004) has plagued bobwhites throughout their distribution and is indicative of a landscape-level habitat problem (Sisson et al. 2006, Terhune et al. 2007). This problem is not, however, unique to bobwhites, but rather has affected an entire ecosystem comprised of early–succession vegetation and associated fauna (Burger

2002, Church et al. 1993). Researchers have documented adequate survival and concomitant reproduction efforts affording population stability, and even population increases, where effective habitat management was in place (Palmer and Wellendorf 2007, Terhune et al. 2007). This research substantiates the necessity for adequate habitat management to abate population declines and for long-term population persistence. However, in certain cases where habitat patches are small or isolated and habitat restoration has occurred, the probability of natural re-population is low. Further complicating population persistence and re-population among fragmented habitats is the inability to reproduce panmictically, especially among low-mobility species. Individuals are therefore constrained to breeding in these smaller, more isolated patches, thereby increasing the likelihood of inbreeding and susceptibility to stochastic-related (e.g. adverse weather) events (Keller 1998, Lacy 1987, Newman and Pilson 1997, Selander 1983, Tallmon et al. 2004).

Translocation is a nascent management technique for purposes of introduction, reintroduction, and re-stocking (i.e., augmentation). It may additionally serve as an artificial means of dispersal (Terhune et al. 2006, 2005) to infuse novel alleles into an isolated or fragmented population with high inbreeding potential to reduce genetic homozygosity rendering the population, as a whole, more evolutionarily flexible (Lacy 1987, Selander 1983). Beyond genetic influences and inbreeding, demographic data such as survival, fecundity, movement and dispersal patterns, population response, and reproductive effort are equally as important. A critical demographic attribute among "r-selected" species is reproductive output; as such, high reproduction offsets their high annual mortality rendering long-term population persistence possible when other factors are not detrimental (e.g. weather, predator communities). Taken collectively, population persistence of r-selected species, with low dispersal potential, in fragmented systems is precarious at best. A key component to the efficacy of translocation is to capitalize on the flexible, extensive reproductive strategy and individual tenacity of "r-selected" species. The northern bobwhite is a good model species to investigate the effects of translocation on reproductive output because they are a non-migratory species, habitat generalists, and exhibit high reproductive output. They are also viewed as a species with high economic and social value (Burger et al. 1999) and readily respond to habitat alteration due in large part to their flexible mating strategy (Faircloth 2008).

When restoring or augmenting populations via translocation it is imperative to understand the implications associated with the technique to best guide management and decisions germane to the timing and implementation of translocation. Previous research has demonstrated that the most opportunistic time to implement this technique is prior to breeding season (Terhune et al. 2006, 2005), and thereby capitalizing on their reproductive capacities. However, they did not adequately explore the affect translocation has on reproductive effort beyond basic nesting parameters (e.g. nest survival) and their research was limited to sites situated in contiguous, high-quality habitat. Our objective was to assess the reproductive capacities of bobwhites following translocation to site located among a fragmented landscape. In particular, we compared nest survival; fecundity, measured via progeny produced per breeding female; and productivity (overall reproductive output) of translocated and resident bobwhites. In addition, we evaluated the effects of various explanatory variables (e.g. group, year) to explain the variation in sub-level reproduction parameters including clutch size, incubation date, and egg "hatchability" to gain insight to the effects of translocation on natality.

3.3 Study Area

3.3.1 Translocation Site

The study was conducted on a private property (1092 ha; *Figure 2.1*) in Marion County near Tazewell, Georgia (84°24'23.46"W, 32°21'39.07"N). This property is located near the fall line of the Piedmont physiographic region and characterized by gradual rolling hills and sandy-clay to clay type soils. The habitat is: predominantly upland pine forests (59.1%); scattered fallow fields (12.0%); thinned hardwoods, interspersed hardwood hammocks and drains (11%); hardwood-tupelo dominated bottomland (9.5%); wildlife openings (3.5%), roads (2.5%); other (i.e. pasture, food plots, landscape, etc.; 1.3%); and water (1.2%). The upland pine forests contain moderate basal densities (6-9 m^2/ha) consisting of longleaf (*Pinus palustris*), loblolly (*P. taeda*), and slash (*P. ellioti*) pines; upland pines were managed to promote an understory of early-succession vegetation. Typical habitat management included: roller-chopping, mowing, prescribed burning, periodic timber thinning, hardwood management, supplemental feeding, fallow-field management, and cover-patch planting. Mammalian nest predators were managed at an equal rate throughout the study site.

Prior to onset of habitat management in 1996, the property was typical of the region: there was little farming, and the landscape was dominated by pine monocultures (BA >19 m^2/ha) under early enrollment in the Conservation Reserve Program (CRP) and pasture. During 1996-2003, extensive habitat improvements were undertaken on the study site; however, only modest increases in the bobwhite population abundance was observed. This property is considered an "island" of well-managed bobwhite habitat surrounded by a matrix of poor landscapes (e.g. dense pine monocultures [CRP], pasture-land, and late-succession hardwood forests).

3.3.2 Source Site

The source study sites were located on 3 private lands in Baker and Dougherty counties in southwest Georgia, USA. These properties have been under intensive wild quail management for >50 years and are located in the Upper Coastal Plain physiographic region. Additional source-site descriptions have been reported in previous works (see Terhune et al. 2007, 2006, 2005, Yates et al. 1995).

3.4 Methods

3.4.1 Capture and Handling

We captured bobwhites on the study site during Oct-Nov (Fall-trapping period) and Jan-Mar (Spring-trapping period) in 2003-2005 using confusion-style funnel traps (Stoddard 1931, p.

442) baited with milo and cracked corn. We covered traps with brush (e.g., fresh-cut pine limbs) to minimize stress on captured birds and to conceal traps from predators. All bobwhites captured (translocated and resident) were classified by age and sex; and we, additionally, weighed, leg-banded, and collected 10 to 15 feathers from the ventral and humeral feather tracts. Half of the collected feathers for each individual were placed in 70% ethanol (ETOH) for preservation prior to genetic analysis. We stored remaining feathers in individually-labeled envelopes to serve as "back-ups" should the feathers in ETOH become lost, unusable, or fail to amplify during PCR.

During the spring-trapping season in 2003 and 2004, we radio-tagged a sub-sample ($n = 60$) of "resident" and translocated bobwhites. We radio-tagged only bobwhites weighing $\geq$132g ($\leq$5% of body weight) with a 6-g necklace-style radio-transmitter that was equipped with an activity switch (Holohil Systems Ltd., Ontario, Canada). We used necklace-style transmitters because they do not influence body mass dynamics or physiology of captive birds (Corteville 1998, Hernandez et al. 2004) and their affect on survival of bobwhites is negligible (Palmer and Wellendorf 2007, Terhune et al. 2007).

Translocated bobwhites were captured during late-February to early-March 2003 and 2004. They were held overnight in transport boxes and, following feather extraction and data collection, were released in groups of 8-12, not necessarily from the same covey, at random locations within the defined release area (i.e. core area; *see Figure 2.1*). Translocated bobwhites were released within 24 h of capture, and were not fed or provided water, other than feed consumed in traps, prior to release. To avoid re-capturing and concentration translocated birds to 'bait' sites, no trapping in the release area occurred following their release.

Bobwhite capture and monitoring procedures outlined in this study for the source sites in Baker and Dougherty Counties were approved by the Georgia Department of Natural Resources (2070 U.S. Hwy. 278, S.E., Social Circle, Georgia 30025) during 2003 and 2004 under permit numbers #29-WMB-03-280 and #29-WSF-04-200. Bobwhite capture and monitoring procedures for the translocation study site in Marion County, Georgia were approved by the Georgia Department of Natural Resources (2070 U.S. Hwy. 278, S.E., Social Circle, Georgia 30025) under permit #29-WMB-00-105, #29-WMB-03-38, and #29-WMB-04-128. All trapping, handling, and sampling techniques were approved by the University of Georgia Institutional Animal Care and Use Committee (2000-2002 IACUC approval numbers: A990028M1, A990028C1; 2003 extension: A200310109-0) and followed guidelines provided by the Ornithological Council's Guidelines for the Use of Wild Birds in Research (American Ornithologists' Union 1999).

3.4.2 Bobwhite and Nest Monitoring

Radio-tagged individuals were located ≥ 3 times weekly during the breeding season (1 Apr - 30 Sep) using the homing method (Kenward 2001, White and Garrott 1990). We approached birds within 25-50 m to minimize location and habitat classification errors, and all ascribed locations were archived into a Geographical Information System (GIS) using ArcView® software (Environmental Systems Research Institute, Inc.). We determined specific causes of mortality when possible, by evidence at the kill site and condition of the radio-transmitter (Curtis et al. 1993). We systematically searched the study area within approximately 5 km of the birds last known location when radio contact was lost.

Additionally, we assumed inactive birds, determined via an activity switch, observed in the same location on 2 consecutive days to be nesting. We approached inactive hens and marked their location with flagging tape at a distance of 5-10 m and recorded the location on an aerial photograph. We determined exact nest location, archived its location using a Global Positioning System (GPS; Garmin V Plus) and determined the number of eggs when the incubating hen was off the nest. We monitored nests daily and we determined fate of the nest as abandoned, successful, or unsuccessful. An unsuccessful nest was any nest in which ≥ 1 egg was destroyed and the adult bird did not return to incubate the remaining clutch.

An abandoned nest was a nest in which the hen did not complete incubation and all eggs were still intact. A successful nest included those in which ≥ 1 egg hatched.

3.4.3 Data Analysis

Nest Survival

A priori hypotheses and predictions

We developed, *a priori*, candidate models designed to examine biologically relevant hypotheses explaining variation in nest survival of northern bobwhites. Here, we outline 5 sources of variation used to develop our nest survival models:

1. Time. Temporal variation in nest survival among northern bobwhites is expected because the duration of the nesting season is long (Apr-Oct). Additionally, it has been reported that nest survival is higher at the tails, early (Apr) and late (Sep & Oct), than the middle of nesting season. Nest predators may develop a "search image" as the season progresses thereby improving their nest foraging skills and subsequent success; however, during late nesting season, as "buffer" foods (e.g. blackberries, persimmons) become more readily available to nest predators, pressure on nests is potentially alleviated. To assess temporal variation, we developed 5 time-related models: a naive constant survival model(B_0); a linear time-trend model ($B_0 + B_1{}^*T$); two curvilinear models: quadratic time-trend ($B_0 + B_1{}^*T + B_2{}^*TT$) and cubic time-trend ($B_0 + B_1{}^*T + B_2{}^*TT + B_3{}^*TTT$); and a discrete-time model delineated by month ($B_0 + B_1{}^*Jun + B_2{}^*Jul + B_3{}^*Aug + B_4{}^*Sep$).

2. Year. Annual variation in nest survival may be influenced by both biotic and abiotic factors such as variable weather patterns, fluctuations in predator abundance, food availability, and wild (or prescribed) fires. We anticipated that by modeling year effects we would account for annual variation not specifically addressed in any other sources of variation.

3. Group. In this study, we compared two groups: translocated and resident. We hypothesized that resident bobwhites would have higher nest survival than translocated birds, simply because resident bobwhites were more familiar with the study site and therefore would ostensibly select more optimal nesting sites.

4. Nest Type. We delineated nest type into 3 categories: initial nest attempt, renest, and double brood attempt. Despite previous research indicating similar nest survival between nest types (Burger et al. 1995), we hypothesized that renesting attempts would have higher nest survival because as bobwhites gained nesting experience and translocated individuals gained familiarity with the study site, nest-site selection would improve with the progression of nesting season.

5. Age. Age cohorts often account for variation in survival (Pollock et al. 1989, Terhune et al. 2007) and nest survival based on the tenet that as individuals age they become more experienced and thus survive better. We hypothesized that adult bobwhites would yield higher nest survival than sub-adults, and we hypothesized that a model including an interaction of age and group would yield meaningful results whereby experienced nesters would select more optimal nesting sites and, furthermore, adult, translocated individuals would, having adapted better than sub-adults, also have higher survival.

Modeling daily nest survival rate

We estimated daily survival rate (DSR) for bobwhite nests and evaluated competing models explaining variation in nest survival using the nest survival model in program MARK (White and Burnham 1999). We modeled our binomially distributed data (nest fate = 1 if failed and 0 if successful) with the user-defined, logit-link function while simultaneously considering the effects of: time (linear and quadratic time trends, and month using indicator variables); year (2003, 2004); treatment (resident, translocated); nest type (initial nest, renest, double-brood attempt); and age (adult, sub-adult). For our data, we standardized 1 May as day 1 and numbered nest observations sequentially thereafter until day 150 (20 Sep), the final day of nesting activity during our study (see Dinsmore et al. 2002, Rotella et al. 2004). Each nest was coded with the following 5 pieces of required information to input into program MARK (see Dinsmore et al. 2002, White and Burnham 1999): (1) the day the nest was found (k); (2) the last day the nest was checked and known alive (l); (3) the last day the nest was checked (m); (4) the nest fate (f); and (5) the frequency (count) of individuals with similar encounter history (always one in our data). Additionally, we used indicator variables to assign individual nest encounters to group-specific covariates as outlined above (i.e. year, group, age and nest type).

We used an information-theoretic approach (Akaike 1973, Anderson et al. 2000, Burnham and Anderson 2002, Guiasu 1977) to evaluate the set of candidate models. The best approximating model in the set of candidate models was determined by Akaike's Information Criterion adjusted for small sample bias and overdispersion ($QAIC_c$; Burnham and Anderson 2002, Wedderburn 1974)). We used $QAIC_c$ to compare each candidate model, and we considered the model with the lowest $QAIC_c$ value the best approximating model given the data. The relative plausibility of each model in the set of candidate models was assessed by Akaike weights (w_i; Anderson et al. 2000, Burnham and Anderson 2002), where the best approximating model in the candidate set has the greatest Akaike weight. When appropriate, we used model averaging (Akaike 1974, 1978, Burnham and Anderson 2002) to obtain daily survival and estimated nest survival as the product of DSR across the 23-d incubation period. To derive additional inference and render direct covariate-specific comparison, we report beta coefficients, their standard errors and 95% confidence intervals, odds ratios, and effect size for variables of interest (e.g. group); and, for comparison to other studies, we report the derived estimates of DSR (with associated 95% CI).

Assessment of Reproductive Effort

We used fecundity and productivity as broad-level metrics to compare reproductive effort between translocated and resident bobwhites both among and between years. These estimates require the inclusion of several sub-level variables (e.g. clutch size, nesting rate). Thus, we evaluated sub-level variables using a combination of general means (PROC MEANS; SAS Institute. 2004) and weighted means; log-linear models (PROC GENMOD; SAS Institute. 2004); and the maximum likelihood estimator (MLE) with associated intuitive estimator of variance (Williams et al. 2002).

Productivity and Fecundity Measures

Fecundity is measured as the number of live births a female produces during a defined interval, generally one year (Caughley 1978); and, specifically, fecundity is the number of juvenile females hatched per breeding female (Caughley 1978, Cowardin and Johnson 1979, Skalski et al. 2005). We derived an estimate of overall fecundity, F, calculated as the probability that a breeding female successfully hatches a clutch (π) multiplied by mean brood size (γ) and mean number of nests produced per year (ψ). Thus, the estimator for F is:

$$\hat{F} = (\pi) * \left(\frac{\gamma}{2}\right) * (\psi) \tag{3.1}$$

where $\hat{F}$ is the number of juvenile females hatched; π is the estimated probability that a breeding female successfully hatches a clutch (i.e. nest success rate); γ is the estimated mean brood size (see equation 3.6); and ψ is the mean number of nests built. The above estimator assumes a 1:1 sex ratio (Skalski et al. 2005), which is a legitimate assumption for bobwhites (Faircloth 2008). We calculated variance using the delta method (Hilborn and Mangel 1997, Snedecor and Cochran 1989, Williams et al. 2002):

$$v\hat{a}r = \left(var\left(\hat{\pi}\right) * \left(\hat{\gamma}\hat{\psi}\right)^2\right) + \left(var\left(\hat{\gamma}\right) * \left(\hat{\pi}\hat{\psi}\right)^2\right) + \left(var\left(\hat{\psi}\right) * \left(\hat{\pi}\hat{\gamma}\right)^2\right) \tag{3.2}$$

Additionally, for comparison to other studies, we also estimated productivity (P) – the total number of juveniles, males and females, produced per breeding female. A common estimator for P is:

$$\hat{P} = \hat{H} * \bar{x} \tag{3.3}$$

where $\hat{H}$ is the probability that a breeding female produces a successful clutch and $\bar{x}$ is the mean clutch size. Because equation 3.3 does not account for multiple nesting attempts we used an adjusted productivity estimate using a conditional, joint binomial probability function. Thus, we estimated our total net productivity by using a weighted mean of the average brood size and separate hatching success rate relative to nest attempt:

$$\hat{P} = \hat{h}_1\hat{b}_1 + \hat{h}_2\hat{b}_2 + \hat{h}_3\hat{b}_3 \tag{3.4}$$

where $\hat{h}_i$ is the probability a female incubates and successfully hatches an i^{th} nest and $\hat{b}_i$ is the mean brood size for the i^{th} nesting attempt (Skalski et al. 2005). Following Skalski et al. (2005), the weighted mean brood size was calculated as:

$$\hat{b} = \frac{1}{y_i}\sum_{j=1}^{y_i} b_{ij} \tag{3.5}$$

where b_{ij} is the mean brood size for the i^{th} nesting attempt (i = 1, 2,..., n) for the j^{th} breeding female (i = 1, 2,..., y_i). We derived individual estimates of b as:

$$b = \hat{CS} * \hat{HR} \tag{3.6}$$

where $\hat{CS}$ is the clutch size and $\hat{HR}$ is hatch rate, and we estimated the variance using the delta method (Hilborn and Mangel 1997, Snedecor and Cochran 1989, Williams et al. 2002).

Evaluation of Sub-level Reproductive Factors

We used several measures to evaluate these factors and compare productivity between groups: initial nests and renesting attempts; clutch size; egg "hatchability;" incubation date; and renesting interval. We defined egg "hatchability" as the proportion of fully incubated (23 d) eggs that hatched. Additionally, we defined the renesting interval as the number of days elapsed since termination or successful hatch of the previous nesting attempt to the subsequent renesting attempt (as determined by the onset of incubation). We estimated nesting rate, renesting rate, double brood rate, and hatching rate using MLE and the intuitive estimator of variance (Williams et al. 2002, p. 45). We also calculated mean brood size and chicks and broods produced per hen delineated by group and year (PROC MEANS; SAS Institute. 2004).

To derive explicit inference about factors related to reproduction we developed, *a priori*, a set of candidate models designed to examine biologically relevant hypotheses explaining variation in clutch size (CS), incubation date (IncDate), and hatch rate (HR) of northern bobwhites. We selected the following explanatory variables, based on a literature review, previous knowledge and experience of northern bobwhite reproductive ecology: temporal variation, year, group (translocated, resident), nest type, age, and body condition (i.e., capture weight). Because of small sample size among di- and polychotomous groups (e.g. nest type) and to prevent "over-fitting" the data we did not model multi-way interactions or higher order terms. We used log-linear regression models in GENMOD (SAS 9.1; SAS Institute. 2004) to examine the effects of explanatory variables of interest on individual sub-level factors (i.e., CS, IncDate, HR). We evaluated model adequacy (goodness-of-fit) of the global models (i.e., model containing all effects in the respective *a priori* candidate-model sets) and models in the candidate set using a combination of visual examination of the residual plots, global fit (e.g., deviance) and log-likelihood statistics, and evaluation of overdispersion (Allison 1991, McCullagh and Nedler 1989). We invoked the scale option (DSCALE SAS Institute. 2004) to estimate the magnitude of overdispersion (the ratio of deviance to degrees of freedom [dev/df]) (Allison 1991, McCullagh and Nedler 1989) and to correct for biased standard error and chi-square statistics when data were overdispersed. We ranked and selected models using AIC_c (Sugiura 1978), and we model-averaged all parameters in the candidate model set ($w_i > 0.0$; Akaike 1974, 1978, Burnham and Anderson 2002) when reporting beta coefficients and calculating effect size.

3.5 RESULTS

During 2003-2004, female resident (n=69) and translocated (n=57) northern bobwhites incubated 53 and 58 nests, respectively. Additionally, resident (n=64) and translocated (n=64) male bobwhites incubated 6 and 4 nests, respectively; however, we did not include male-incubated nests in productivity and fecundity measures because we were unable to assign these nests with confidence to the group (translocated, resident) responsible for egg-laying.

Nest Survival

Preliminary analysis of the global model indicated that our data was slightly overdispersed ($\hat{c} > 1$); therefore we adjusted the variance inflation estimate ($\hat{c} = 1.5$) to account for this overdispersion in our data. Numerous models received support in explaining the variation in nest survival, but no single model was overwhelmingly better than the others (Table 3.1). The most parsimonious model was the naive constant (time) survival model (Table 3.1); however, the support for this model was not overwhelming (the evidence ratio for this best model compared to the second-best model, including a quadratic time effect, is 1.49). Moderate support was evident for annual differences in nest survival ($w_i = 0.0632$; Table 3.1) where nests during 2004 exhibited a weak tendency to survive better than those in 2003, but the confidence intervals included zero ($B_{2003} = -0.1171$; 95% CI: -0.9000, 0.6658). In contrast to our hypothesis, resident bobwhites did not have higher nest survival than translocated birds ($B_{resident} = -0.0189$; 95% CI: -0.7862, 0.7843) because no differences between groups was detected and the effect size between groups on nest survival was negligible (-0.0004; 95% CI: -0.0217, 0.0210). Similarly, in contrast to our hypothesis, differences in nest type (attempt) was not evident in our data ($B_{renest} = -0.0788$; 95% CI: -0.8834, 0.7258) and the effect size among nest type was trivial (-0.0016; 95% CI: -0.0246, -0.0213). Age of bobwhites did not adequately explain variation in nest survival (Table 3.1); adult-incubated nests did not demonstrate higher survival than juvenile-incubated nests ($B_{adult} = 0.1672$; 95% CI: -0.6914, 1.0258). Further, the model including an interaction of treatment (group) and age had a $QAIC_c > 5$, lending little support for adult, translocated individuals exhibiting better nest survival than juvenile, translocated bobwhites.

Daily nest survival (DSR) was high both years for translocated and resident bobwhites (Table 3.2). Nest success was high for both translocated and resident bobwhites during 2003 (Res: 59.81% [±16.43]; Trans: 60.66% [±17.65]) and 2004 (Res: 64.03% [±20.73]; Trans: 63.43% [±18.64]). Overall mean nest success (pooled across years and groups) was 61.68% (±11.25).

Reproductive Effort

Nesting rate, renesting rate, broods produced per hen, and double broods produced per hen was similar between groups (Table 3.2). Translocated bobwhites produced more nests per hen during 2004, but there was not a significant difference during 2003 (Table 3.2). After removing nests for which clutch data was incomplete, 115 nests remained for analysis of clutch size and time of season. The most parsimonious log-linear model explaining the variation in clutch size included time of season (Julian Date: JDate), year and group parameters (Table 3.3). Clutch size declined linearly ($B_{JDate} = -0.0048$; 95% CI: -0.0061, -0.0036) with time (Figure 3.1), but the effect of year ($B_{2003} = 0.0320$; 95% CI: -0.0790, 0.1429), group ($B_{resident} = -0.1668$; 95% CI: -0.5787, 0.2452), and nest type ($B_{initial} = 0.0020$; 95% CI: -0.0235, 0.0276) was negligible. Hatchability was similar between groups for both initial ($F_{1,50} = 0.1200; P = 0.7330$; *see* Figure 3.2) and renesting (second and third) attempts ($F_{1,26} = 2.260; P = 0.1451$; *see* Figure 3.2).

Initiation of nest incubation was best explained by nest type and group (Table 3.4) effects whereby the top three ranking models all included these parameters. Whereas model weights demonstrated that moderate support was evident for annual variation in nest incubation (Table 3.4), examination of model averaged estimates indicated that variation due to other explanatory variables was inconsequential for our data (Figure 3.3). Mean incubation date for initial nest attempts was 150.94 (± 6.54) and 161.54 (± 7.96) and resnesting attempts was 205.18 (± 8.71) and 218.94 (± 9.60) for tranlocated and resident bobwhites, respectively

(Figure 3.4). Interestingly, translocated individuals more quickly incubated second and third nests than their resident counterparts whether the initial attempt was successful ($F_{1,29} = 2.310; P = 0.139$; *see* Figure 3.5) or unsuccessful ($F_{1,11} = 5.571; P = 0.038$; *see* Figure 3.5). Overall, fecundity (*see* Figure 3.6) and productivity (*see* Figure 3.7) was slightly higher for translocated bobwhites as compared to resident bobwhites, but the difference was not significant as all confidence intervals overlapped except for fecundity during 2004.

3.6 Discussion

Cost of reproduction is a central dogma in evolutionary ecology whereby it has been suggested that increased investment in immediate reproduction has predicted consequences in future reproduction efforts (Charnow and Krebs 1974, Williams 1966). These purported consequences may be direct, via reduced viability of offspring (i.e., hatchability), or delayed, via reduced survival of progeny and/or a reduction in their quality of future reproductive efforts. One factor mediating reproductive cost is stress and resulting reduced immune functionality (Sheldon and Verhulst 1996) rendering increased vulnerability to disease. Translocation may incur additive stress on individuals thereby relegating their potential reproductive contribution. Additionally, researchers have suggested that egg quality diminishes with increased production (Nager et al. 2000) and individuals with higher fitness are capable of producing more eggs that are larger and of superior quality (Lack 1968, Monaghan and Nager 1997, Williams 1966).

Among bobwhites, previous research has demonstrated that clutch size declines linearly with the progression of nesting season (Burger et al. 1995, Cox et al. 2005). Our results followed a similar trend; however, differences between groups was negligible suggesting that translocation does not negatively affect egg-production. Egg-hatchability was also similar between groups suggesting that translocation does not induce additive energy demands affecting immediate reproductive viability, at least beyond the costs normally incurred during reproduction, as compared to resident individuals. However, it has been demonstrated that resource quality and availability also influences demographic (i.e. survival and reproduction) attributes (Sisson et al. 2000). In this study, intensive habitat management preceded translocation and thus habitat quality was considered good for this species; therefore quality habitat rendering ample food resources may have defrayed stress-related effects of translocated individuals. As such, these results advocate that prior habitat management to ensure resource availability may prove instrumental to the overall success of translocation. Future research designed with multiple releases at multiple sites is warranted to directly compare the affect of habitat quality on the success of translocation and to determine the lower and upper bounds within this habitat gradient and their associated probabilities of success.

Variation in nest survival was best explained by time covariates rather than group-specific covariates indicating that variation in nest survival was more attributable to variation between and among years. Therefore, variation in nest survival may be better explained by unmeasured parameters (e.g. predator abundance, weather) which may fluctuate both between and within breeding seasons. The lack of variation in nest survival was not unexpected because nest survival is largely driven by predation (Rollins and Carroll 2001) and groups modeled for were affected by the same predator community. As compared to other studies, nest survival estimates during both years was high. High nest survival may be a result of mammalian nest-predator management, density-dependence or a combination thereof. Additionally, our results corroborate previous research whereby translocating individuals to new sites does not inhibit their ability to successfully produce nests and subsequent offspring (Terhune et al. 2006) and this additionally suggests that bobwhites do not require long acclimation periods following release to initiate reproduction.

Reproductive effort was ostensibly greater for translocated individuals during both years and pooled across years, but metrics used to measure fecundity and productivity did not yield significant results. The lack of significant difference is likely an artifact of large variance in both estimates and may, in part, be due to small sample sizes and the cumulative measures of variance associated with each sub-level reproductive parameter. Few bobwhite studies, however, have published reliable, statistically robust (i.e., inclusion of variance estimates) estimates of fecundity and productivity, thus limiting the comparison of our data to other studies. Notably, fecundity during 2004 was higher for translocated bobwhites; this disparity may have been influenced by poor survival of resident birds early in the nest season (Terhune et al., in preparation) and therefore resulting in higher nests produced per hen (*see* Figure 3.2). By definition, fecundity and productivity refer to an explicit time during a species' annual life-cycle (Skalski et al. 2005) thereby requiring a discrete time of reference to render these estimates meaningful. For bobwhites, many researchers confer that this time-period is recruitment to the fall population. When field observations on clutch size are acquired prior to this time of reference, as is often the case, productivity and fecundity estimates should be adjusted to account for mortality of juveniles from the date of hatch to the time of reference [i.e., fall; (Skalski et al. 2005)] to ensure tenable recruitment estimation - particularly for inclusion into population modeling and sensitivity analyses [e.g. Leslie Matrices; (Caswell 2001)]. However, juvenile survival of northern bobwhites is difficult to assess and has not been adequately investigated; and habitat quality, weather, and predation among others may significantly impact juvenile survival. In this study, we were unable to determine juvenile survival. Therefore, our estimates more appropriately represent the reproductive effort of individuals and groups rather than actual recruitment to the fall population. Additionally, northern bobwhites exhibit a flexible mating regime (Faircloth 2008) whereby both males and females incubate nests and multiple nesting attempts is common during a single breeding season. We did not include male incubation in our production index because we were not able to determine whether a male-incubated nest was produced via a translocated or resident hen; therefore, our reproductive index is likely a conservative estimate of the actual reproductive effort. These metrics, however, yield robust estimates for comparison between groups and years to assess the potential effects germane to reproductive effort following translocation as the data collection and methods used were identical among groups and years. Future studies investigating brood (juvenile) survival produced by translocated as compared to resident broods would be beneficial.

Overall translocated individuals' proclivity to produce progeny was seemingly higher than resident bobwhites during this study and is in accord with previous research (Terhune et al. 2006). They initiated incubation of first nests earlier than resident birds and more readily initiated second and third attempts regardless of whether or not the previous attempt was successful. Furthermore, nest production by translocated birds during 2003 was the highest reported nest production rate in the region including those investigated among documented long-term, on-going research studies (D.C. Sisson, personal communication). Although fecundity and productivity for translocated bobwhites was not significantly higher than resident bobwhites, the question of why individuals exhibit such a high propensity to reproduce following translocation is eminent.

It has been corroborated in several animal taxa, including birds (Beason et al. 1995, Cochran et al. 2004, Wilschko et al. 2003, Wilschko and Wilschko 1972), that the earth's magnetic field plays an important role in a species' ability to orient and navigate. The mechanisms by which avian species detect geomagnetic fields remain debatable. However, two primary, independent hypotheses have been proposed: a photo-period dependent mechanism (Cochran et al. 2004, Leask 1977, Wiltschko and Wiltschko 1995) and one based on the presence of biogenic ferromagnetic mineral magnetite (Kirschvink and Gould 2001, Wilschko et al. 2003). Often these hypotheses are viewed as competing (Kirschvink et al. 2001); although, more recently, researchers have advocated that individual species are influenced via both mechanisms (Wiltschko and Wiltschko 2006). Among gamebirds, the influence of photo-period on reproduction has been reported (Kirkpatrick and Leopold 1952), but the influence of magnetite on reproduction and other demographic parameters is uncertain. If bobwhites are capable of detecting changes in geomagnetic influences, then perhaps, translocation serving as an artificial means of dispersal, triggers reproductive drive. In an evolutionary context, artificial dispersal (translocation) of individuals might elicit a higher propensity to reproduce and thereby increasing their fitness (Darwin 1859, Dobzhansky 1936, Muller 1942). Translocated individuals incubated initial nests earlier than resident bobwhites and exhibited shorter renesting intervals during this study lending support to the notion of increased reproductive effort. Other possible causes might be related to the physiology of stress; however, this study was not designed to assess specific mechanisms (e.g. magnetite) affecting initiation of breeding in bobwhites and therefore warrants further research.

3.7 Conservation Implications

The reproductive capacity of northern bobwhites is high and variation in sub-level parameters governs the magnitude of population levels and, in many respects, long-term population persistence. The variation in these parameters may be exaggerated among fragmented and isolated habitats wherein population stochasticity is common. Aside from reproductive potential, numerous factors may affect the population status of species among small, ephemeral habitat patches. That said, the efficacy of translocation to eliciting a population response and introducing novel alleles for purported beneficial genetic effects (e.g. increased genetic diversity and fitness) is contingent on the success of translocated individuals' capacity to reproduce. Translocated individuals in this study demonstrated that productivity and fecundity was not suppressed following release. We did not detect differences in nest survival, nest production, brood production, clutch size, and etc. between resident and translocated bobwhites. Interestingly, translocated individuals nested and renested earlier than their resident counterparts, but the contribution to the overall productivity was not significant.

The lack of disparity between reproductive output between groups may have been masked by quality habitat management implemented prior to release whereby abundant resource availability afforded translocated individuals optimal opportunity to survive and reproduce. To understand how tranlocated individuals fare in different [lower] quality habitat(s) one would have to design a study where releases occur in differing habitat types; however, wild individuals are difficult to obtain and thus may limit this type of study design and, importantly, is not a pragmatic option for a declining species. As such, we do not recommend release of individuals, particularly species classified as threatened or endangered, to areas considered to be of sub-marginal habitat quality. And, importantly, resource quality and availability potentially affects altricial species' reproduction and survival of offspring differently than precocial species. This study demonstrates that translocation prior to breeding season, and to sites with high-quality habitat, does not negatively alter the reproductive capacities of bobwhites and thus potentiates the utility of translocation as a conservation tool, particularly among r-selected species. Translocation as a conservation tool for rare, threatened and endangered species should, however, be approached with caution and adequate knowledge of the species' ecology is imperative to its success. Furthermore, deficient source-stocks of wild individuals may severely limit the efficacy and practicality of translocation at regional and landscape levels. Future research should investigate the long-term ramifications on reproductive output of hybrids (progeny resulting from cross-breeding of translocated and resident birds) as compared to group-specific progeny (translocated vs. resident) and investigate the impact of such translocations on other species (e.g. predators) and ecosystem-level dynamics. Finally, translocation in this study was implemented where conspecifics were present, therefore translocation of individuals to areas with few to no conspecifics might yield different results. As such, future research designed to examine translocation to varying densities would be beneficial.

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Literature Cited

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. pages 267–281 . Akademiai Kiado, Budapest.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control **19**:716–723.

Akaike, H. 1978. A bayesian analysis of the minimum AIC procedure. Annals of the Institute of Statistical Applications of Statistics **30**:9–14.

Allison, P. D. 1991. Logistic regression: Using the SAS system, theory and application. SAS Institute, Inc. & John Wiley & Sons, Inc., Cary, North Carolina.

American Ornithologists' Union. 1999. Report of committee on use of wild birds in research. Auk **116**:1–41.

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. Journal of Wildlife Management **64**:912–923.

Beason, R. C., N. Dussourd, and M. E. Deutschlander. 1995. Behavioral evidence for the use of magnetic material in magnetoreception by a migratory bird. Journal of Experimental Biology **198**:141–146.

Bijlsma, R., J. Bundgard, and A. C. Boerema. 2000. Does inbreeding affect the extinction risk of small populations?: predictions from *Drosophilia.* Journal of Evolutionary Biology **13**:502–514.

Brennan, L. A. 1991. How can we reverse the the northern bobwhite decline? Wildlife Society Bulletin **19**:544–555.

Burger, L. W., Jr. 2002. Quail management: Issues, concerns, and solutions for public and private lands–a southeastern perspective. Proceedings of the National Quail Symposium **5**:20–34.

Burger, L. W., Jr., D. A. Miller, and R. I. Southwick. 1999. Economic impact of northern bobwhite hunting in the southeastern united states. Wildlife Society Bulletin **27**:1010–1018.

Burger, L. W., Jr., M. R. Ryan, T. V. Dailey, and E. W. Kurzejeski. 1995. Reproductive strategies, success, and mating systems of northern bobwhite in missouri. Journal of Wildlife Management **59**:417–426.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: A practical information theoretic approach. 2nd edition edition. Springer-Verlag, New York, New York, USA.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Massachussetts.

Caughley, G. 1978. Analysis of vertebrate populations. John Wiley & Sons Ltd., New York, New York.

Charnow, E. L., and J. R. Krebs. 1974. On clutch size and fitness. *Ibis* **116**:217–219.

Church, K. E., J. R. Sauer, and S. Droege. 1993. Population trends on quails in north america. Proceedings of the National Quail Symposium **3**:44–54.

Cochran, W. W., H. Mouritsen, and M. Wikelshki. 2004. Migrating songbirds recalibrate their magnetic compass from twighlight cues. Science **304**:405–408.

Corteville, L. A. 1998. Effects of radiotransmitters on survival, harvest rate, and body condition of northern bobwhite (*Colinus virginianus*). Master's thesis, Mississippi State University.

Cowardin, L. M., and D. H. Johnson. 1979. Mathematics and mallard management. Journal of Wildlife Management **43**:18–35.

Cox, S. A., F. S. Guthery, J. J. Lusk, A. D. Peoples, S. J. DeMaso, and M. Sams. 2005. Reproduction by northern bobwhites in western oklahoma. Journal of Wildlife Management **69**:133–139.

Curtis, P. D., B. S. Mueller, P. D. Doerr, C. F. Robinette, and T. DeVos. 1993. Potential polygamous breeding behavior in northern bobwhite. Proceedings of the National Quail Symposium **3**:55–63.

Darwin, D. 1859. On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life. 1st edition. John Murray, London, United Kingdom.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology **83**:3476–3488.

Dobzhansky, T. 1936. Studies on hybrid sterility. ii. localization of sterility factors in *Drosphilia pseudoobscura* hybrids. Genetics **21**:113–135.

Faircloth, B. C. 2008. An integrative study of social and reproductive systems in northern bobwhite (*colinus virginianus*): A non-migratory, avian species bearing precocial young. Ph.D. thesis, University of Georgia.

Frankham, R., J. D. Ballou, and D. A. Briscoe. 2004. A primer of conservation genetics. Cambridge University Press, Cambridge, United Kingdom.

Guiasu, S. 1977. Information theory with applications. McGraw-Hill, New York, New York, USA.

Guthery, F. S., and J. J. Lusk. 2004. Radiotelemetry studies: Are we radio-handicapping northern bobwhites? Wildlife Society Bulletin **32**:194–201.

Hanski, H., and M. Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biological Journal of the Linnean Society **42**:3–16.

Hernandez, F., J. A. Arredono, F. Hernandez, D. G. Hewitt, and S. J. D. A. R. L. Bingham. 2004. Effects of radiotransmitters on body mass, feed consumption, and energy expenditures of northern bobwhites. Wildlife Society Bulletin **32**:394–400.

Hilborn, R., and M. Mangel. 1997. The ecological detective: Confronting models with data. Princeton University Press, Princeton, New Jersey.

Keller, L. F. 1998. Inbreeding and its fitness effects in an insular population of song sparrows (*Melospiza melodia*). Evolution **52**:240–250.

Kenward, R. E. 2001. A manual for wildlife radio tagging. Academic Press, Inc., San Diego, CA.

Kirkpatrick, C. M., and A. C. Leopold. 1952. The role of darkness in sexual activity of the quail. Science **116**:280–281.

Kirschvink, J. L., and J. L. B. Gould. 2001. Biogenic magnetite as a basis for magnetic field sensitivity in animals. Biosystems **13**:181–201.

Kirschvink, J. L., M. M. Walker, and C. E. Diebl. 2001. Magnetite based magentirecption. Current opinion in Neurobiology **11**:462–467.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection, and population subdivision. Conservation Biology **1**.

Leask, M. J. M. 1977. A physiochemical mechanism for magnetic field detection by migratory birds and homing pigeons. Nature **267**:144.

McCullagh, P., and J. A. Nedler. 1989. Generalized linear models. Chapman and Hall, London.

Monaghan, P., and R. Nager. 1997. Why don't birds lay more eggs? Trends in Ecology and Evolution **12**:270–274.

Muller, H. J. 1942. Isolating mechanisms, evolution, and temperature. Biology Symposium **6**:71–125.

Nager, R. G., P. Monaghan, and D. C. Houston. 2000. Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. Ecology **81**:1339–1350.

Newman, D., and D. Pilson. 1997. Increased probability of extinction due to decreased genetic effective population size: Experimental populations of (*Clarkia puchella*). Evolution. **51**:354–362.

Palmer, W. E., and S. Wellendorf. 2007. Effects of radiotransmitters on northern bobwhite annual survival. Journal of Wildlife Management **71**:1281–1287.

Pollock, K. H., C. T. Moore, W. R. Davidson, F. E. Kellog, and G. L. Doster. 1989. Survival rates of bobwhite quail based on band recovery analysis. Journal of Wildlife Management **53**:1–6.

Rollins, D., and J. P. Carroll. 2001. Predation impacts on northern bobwhite and scaled quail. Wildlife Society Bulletin **29**:39–51.

Roseberry, J. L., and W. D. Klimstra. 1984. Population ecology of the bobwhite. 1st edition. Southern Illinois University Press, Carbondale, Illinois, U.S.A.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation **27**:187–205.

SAS Institute. 2004. Version 9.1 of the SAS system for windows. Cary, NC, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The north american breeding bird survey, results and analysis 1966-2007. **Version 5.15.2008**.

Selander, R. K. 1983. Evolutionary consequences of inbreeding. Genetics and Conservation pages 201–215 .

Sheldon, B. C., and S. Verhulst. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends in Ecology and Evolution **11**:317–321.

Sisson, D. C., H. L. Stribling, and D. W. Speake. 2000. Effects of supplemental feeding on home range size and survival of northern bobwhites in south Georgia. in Proceedings of the national quail symposium, volume 4, pages 128–131 .

Sisson, D. C., T. M. Terhune, H. L. Stribling, and S. D. M. Jerald Fitch Sholar. 2006. Survival and causes of mortality for northern bobwhites in the southeastern united states. in J. P. C. Brant C. Faircloth, Theron M. Terhune, editor. Gamebird proceedings, volume 6, pages 000–000 .

Skalski, J. R., K. E. Ryding, and J. J. Millspaugh. 2005. Wildlife demography: Analysis of sex, age, and count data. Elservier Academic Press, Burlington, MA, USA.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods. Iowa State University Press, Ames, Iowa.

Soule, M. E. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, United Kingdom.

Stoddard, H. L. 1931. The bobwhite quail: Its habits, preservation, and increase. Charles Scribner's Sons, New York, New York.

Sugiura, N. 1978. Further analysis of the data by akaike's information criterion of model fitting and the finite corrections. Communications in Statistics, Theory and Methods **A7**:13–26.

Tallmon, D. A., G. Luikart, and R. S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. Trends in Ecology and Evolution **19**:489–496.

Terhune, T. M., D. C. Sisson, J. B. Grand, and H. L. Stribling. 2007. Factors influencing survival of radio-tagged and banded bobwhites in georgia. Journal of Wildlife Management **71**:1288–1297.

Terhune, T. M., D. C. Sisson, and H. L. Stribling. 2006. The efficacy of relocating wild northern bobwhites prior to breeding season. Journal of Wildlife Management. **70**:914–921.

Terhune, T. M., D. C. Sisson, H. L. Stribling, and J. P. Carroll. 2005. Home range, movement, and site fidelity of translocated northern bobwhite (*Colinus virginianus*) in southwest georgia,USA. European Journal of Wildlife Research **51**:119–124.

Wedderburn, R. W. M. 1974. Quasi-likelihood functions, generalized linear models, and the gauss-newton method. Biometrika **61**:439–447.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement pages 120–138 .

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., San Diego, CA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.

Williams, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of lack's principle. American Naturalist **100**:687–690.

Wilschko, W., U. Munro, H. Ford, and R. Wilschko. 2003. Magnetic orientation in birds: non-compass responses under monochromatic light of increased intensity. Proceedings of the Royal Society **270**:2133–2140.

Wilschko, W., and R. Wilschko. 1972. Magnetic compass of european robins. Science **176**:62–64.

Wiltschko, R., and W. Wiltschko. 2006. Magnetoreception. Bioessays **28**:157–168.

Wiltschko, W., and R. Wiltschko. 1995. Migratory orientation of european robins is affected by the wavelength of light as well as by a magnetic pulse. Journal of Compartive Physiology **177**:363–369.

Yates, S. W., D. C. Sisson, H. L. Stribling, and D. W. Speake. 1995. Northern bobwhite brood habitat use in south georgia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies **49**:498–504.

Table 3.1: Summary of model selection results for nest survival of northern bobwhites on Buck Creek Plantation, Marion County Georgia, 2003-2004.

Model	QDeviance	K	$QAIC_c$	$\Delta\ QAIC_c$	W_i
B_0	224.9383	1	226.9404	0.0000	0.1648
$B_0 + B_1^*T + B_2^*TT$	221.7216	3	227.7341	0.7937	0.1108
$B_0 + B_1^*T$	223.7617	2	227.7681	0.8277	0.1090
$B_0 + B_1^*age$	224.7892	2	228.7956	1.8552	0.0652
$B_0 + B_1^*yr$	224.8518	2	228.8582	1.9178	0.0632
$B_0 + B_1^*renest$	224.9018	2	228.9080	1.9676	0.0616
$B_0 + B_1^*trt$	224.9360	2	228.9423	2.0019	0.0606
$B_0 + B_1^*T + B_2^*TT + B_3^*TTT$	221.6313	4	229.6526	2.7122	0.0425
$B_0 + B_1^*T + B_2^*TT + B_3^*trt$	221.7205	4	229.7417	2.8013	0.0406
$B_0 + B_1^*T + B_2^*trt$	223.7597	3	229.7722	2.8318	0.0400
$B_0 + B_1^*Jun + B_2^*Ju1 + B_3^*Aug + B_4^*Sep$	220.1498	5	230.1817	3.2413	0.0326
$B_0 + B_1^*renest + B_2^*double$	224.4504	3	230.4632	3.5228	0.0283
$B_0 + B_1^*yr + B_2^*age$	224.6048	3	230.6175	3.6771	0.0262
$B_0 + B_1^*T + B_2^*yr + B_3^*T.yr$	222.7614	4	230.7825	3.8421	0.0241
$B_0 + B_1^*trt + B_2^*age$	224.7870	3	230.7998	3.8594	0.0239
$B_0 + B_1^*yr + B_2^*trt$	224.8513	3	230.8639	3.9235	0.0232
$B_0 + B_1^*T + B_2^*TT + B_3^*yr + B_4^*T.yr + B_5^*TT.yr$	219.2567	6	231.3010	4.3606	0.0186
$B_0 + B_1^*T + B_2^*TT + B_3^*TTT + B_4^*trt$	221.6307	5	231.6624	4.7220	0.0156
$B_0 + B_1^*yr + B_2^*age + B_3^*yr.age$	224.0496	4	232.0709	5.1305	0.0127
$B_0 + B_1^*yr + B_2^*trt + B_3^*age$	224.6048	4	232.6261	5.6857	0.0096
$B_0 + B_1^*trt + B_2^*age + B_3^*trt.age$	224.7143	4	232.7355	5.7951	0.0091
$B_0 + B_1^*yr + B_2^*trt + B_3^*yr.trt$	224.8474	4	232.8686	5.9282	0.0085
$B_0 + B_1^*T + B_2^*TT + B_3^*yr + B_4^*T.yr + B_5^*TT.yr + B_6^*trt$	219.2499	7	233.3094	6.3690	0.0068
$B_0 + B_1^*T + B_2^*TT + B_3^*yr + B_4^*T.yr + B_5^*TT.yr + B_6^*trt + B_7^*yr.trt$	219.2480	8	235.3243	8.3839	0.0025

Table 3.2: Reproduction parameters for resident and translocated northern bobwhites on Buck Creek Plantation, Marion County Georgia, 2003-2004.

	Resident				Translocated			
Parameter	n	$\bar{x}$	SE	95% CI	n	$\bar{X}$	SE	95% CI
Nesting Rate[a]								
2003	20	0.5405	0.0819	(0.3800, 0.7011)	17	0.6296	0.0929	(0.4475, 0.8118)
2004	15	0.4688	0.0882	(0.2958, 0.6417)	17	0.5667	0.0905	(0.3893, 0.7440)
Pooled	35	0.5072	0.0602	(0.3893, 0.6252)	34	0.5965	0.0650	(0.4691, 0.7239)
Renesting Rate[b]								
2003	5	0.1351	0.0562	(0.0250, 0.2453)	3	0.1111	0.0605	(0.0074, 0.2297)
2004	1	0.0313	0.0308	(0.0290, 0.0915)	3	0.1000	0.0548	(0.0074, 0.2074)
Pooled	6	0.0870	0.0339	(0.0205, 0.1534)	6	0.1053	0.0406	(0.0256, 0.1849)
Broods per hen[c]								
2003	20	0.5405	0.0819	(0.3800, 0.7011)	20	0.7407	0.0980	(0.5487, 0.9328)
2004	14	0.4375	0.0877	(0.2656, 0.6094)	19	0.6333	0.1244	(0.3895, 0.8772)
Pooled	34	0.4928	0.0602	(0.3748, 0.6107)	39	0.6842	0.0786	(0.5302, 0.8382)
DBL per hen[d]								
2003	6	0.1622	0.0606	(0.0434, 0.2809)	5	0.1852	0.0748	(0.0387, 0.3317)
2004	2	0.0625	0.0428	(0.0214, 0.1464)	5	0.1667	0.0680	(0.0333, 0.3000)
Pooled	8	0.0870	0.0339	(0.0205, 0.1534)	10	0.1754	0.0504	(0.0767, 0.2742)
Nests per hen[e]								
2003	33	0.8919	0.0510	(0.7918, 0.9919)	30	1.1111	0.0676	(0.9786, 1.2436)
2004	20	0.6250	0.0856	(0.4573, 0.7927)	28	0.9333	0.0455	(0.8441, 1.0226)
Pooled	53	0.7681	0.0508	(0.6685, 0.8677)	58	1.0175	0.0177	(0.9829, 1.0522)

Table 3.2 – Continued

	Resident				Translocated			
Parameter	n	$\bar{X}$	SE	95% CI	n	$\bar{X}$	SE	95% CI
Nest Survival[f]								
2003	33	0.9779	0.0061	(0.9623, 0.9871)	30	0.9785	0.0064	(0.9616, 0.9881)
2004	20	0.9808	0.0072	(0.9603, 0.9908)	28	0.9804	0.0065	(0.9627, 0.9898)
Pooled	54	0.9790	0.0057	(0.9644, 0.9877)	58	0.9794	0.0056	(0.9651, 0.9879)

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[a] Proportion of females attempting ≥1 nest.

[b] Proportion of females with a failed initial nest attempt that attempt second nest.

[c] Proportional number of broods produced per female alive 1 April.

[d] Proportion of females that successfully hatch ≥2 nests.

[e] Proportional number of nests produced per radio-tagged female alive 1 April.

[f] Daily survival rates (DSR) derived from program MARK.

Table 3.3: Log-linear models used to describe variation in clutch size for nests produced translocated and resident bobwhites on Buck Creek Plantation, Marion County Georgia, 2003-2004.

Model	*Ł*	K	AIC_c	$\Delta\ AIC_c$	W_i
$B_0{}^{*}Jdate + B_1{}^{*}YR + B_2{}^{*}GRP + B_3{}^{*}(YR * GRP)$	3729.5361	5	-7448.5166	0.0000	0.9687
$B_0{}^{*}Jdate + B_1{}^{*}NTYPE + B_2{}^{*}YR + B_3{}^{*}GRP + B_4{}^{*}(YR * GRP)$	3727.1045	6	-7441.4240	6.8631	0.0313
$GlobalModel$	3687.7397	9	-7355.7487	91.5927	0.0000

Table 3.4: Log-linear models used to describe variation in incubation date of nests for translocated and resident bobwhites on Buck Creek Plantation, Marion County Georgia, 2003-2004.

Model	Ł	K	AIC_c	$\Delta\ AIC_c$	W_i
$B_0{}^*NTYPE + B_1{}^*GRP + B_2{}^*(NTYPE^*GRP)$	1813.1435	4	-3617.9479	0.0000	0.4031
$B_0{}^*NTYPE + B_1{}^*GRP$	1811.9208	3	-3617.6399	0.4453	0.3226
$B_0{}^*NTYPE + B_1{}^*GRP + B_2{}^*YR$	1812.4267	4	-3616.5143	1.4336	0.1968
$B_0{}^*NTYPE + B_1{}^*GRP + B_2{}^*YR + B_3{}^*(NTYPE^*GRP)$	1812.4952	5	-3614.4776	3.2965	0.0775
$B_0{}^*NTYPE + B_1{}^*GRP + B_2{}^*A1$	1797.2089	4	-3586.0788	31.8692	0.0000

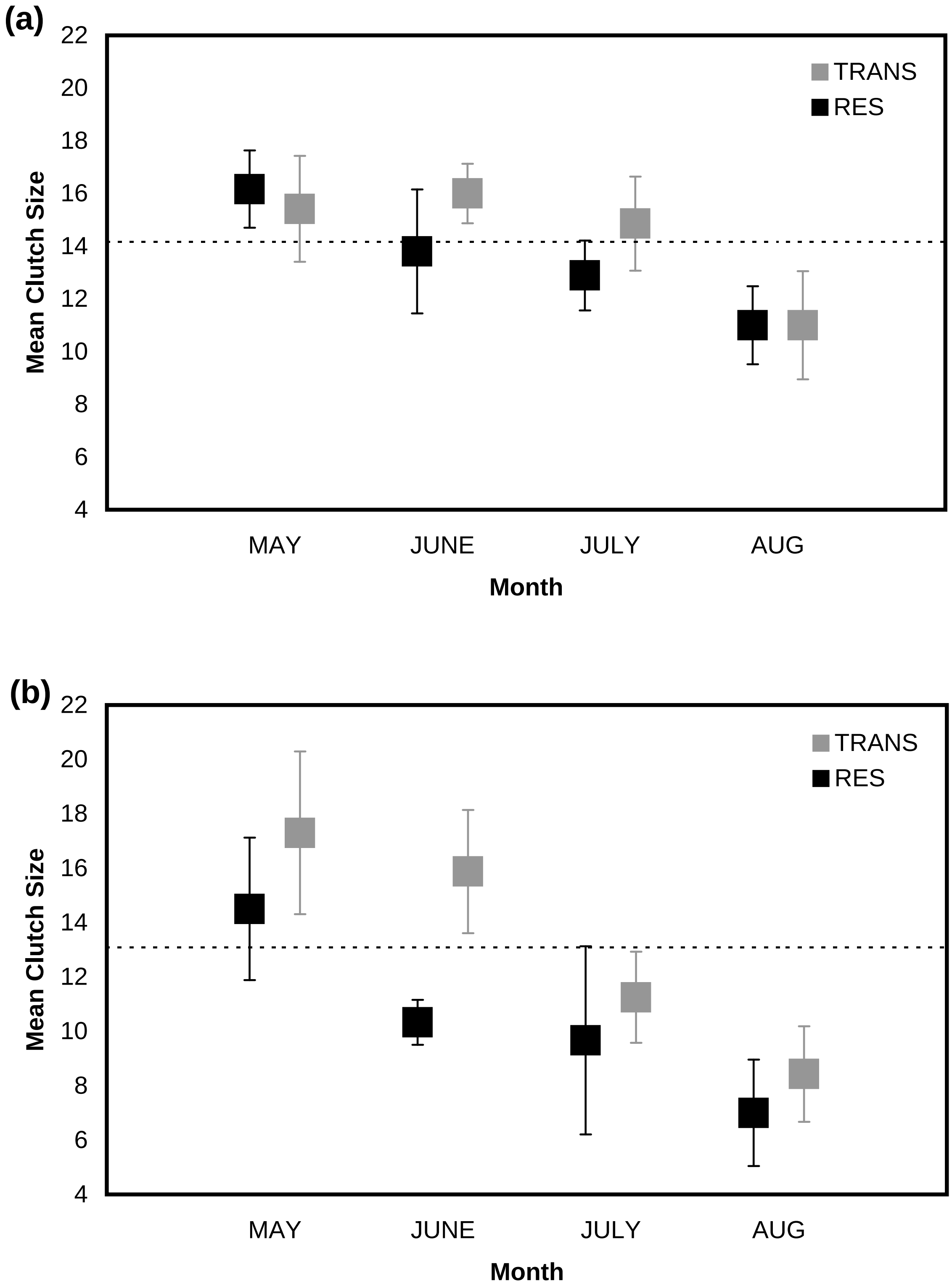

Figure 3.1: Mean clutch sizes for translocated and resident northern bobwhites on Buck Creek Plantation during (a) 2003 and (b) 2004 delineated by month. Note: dotted line indicates the mean clutch size for translocated and resident bobwhites combined for the entire breeding season.

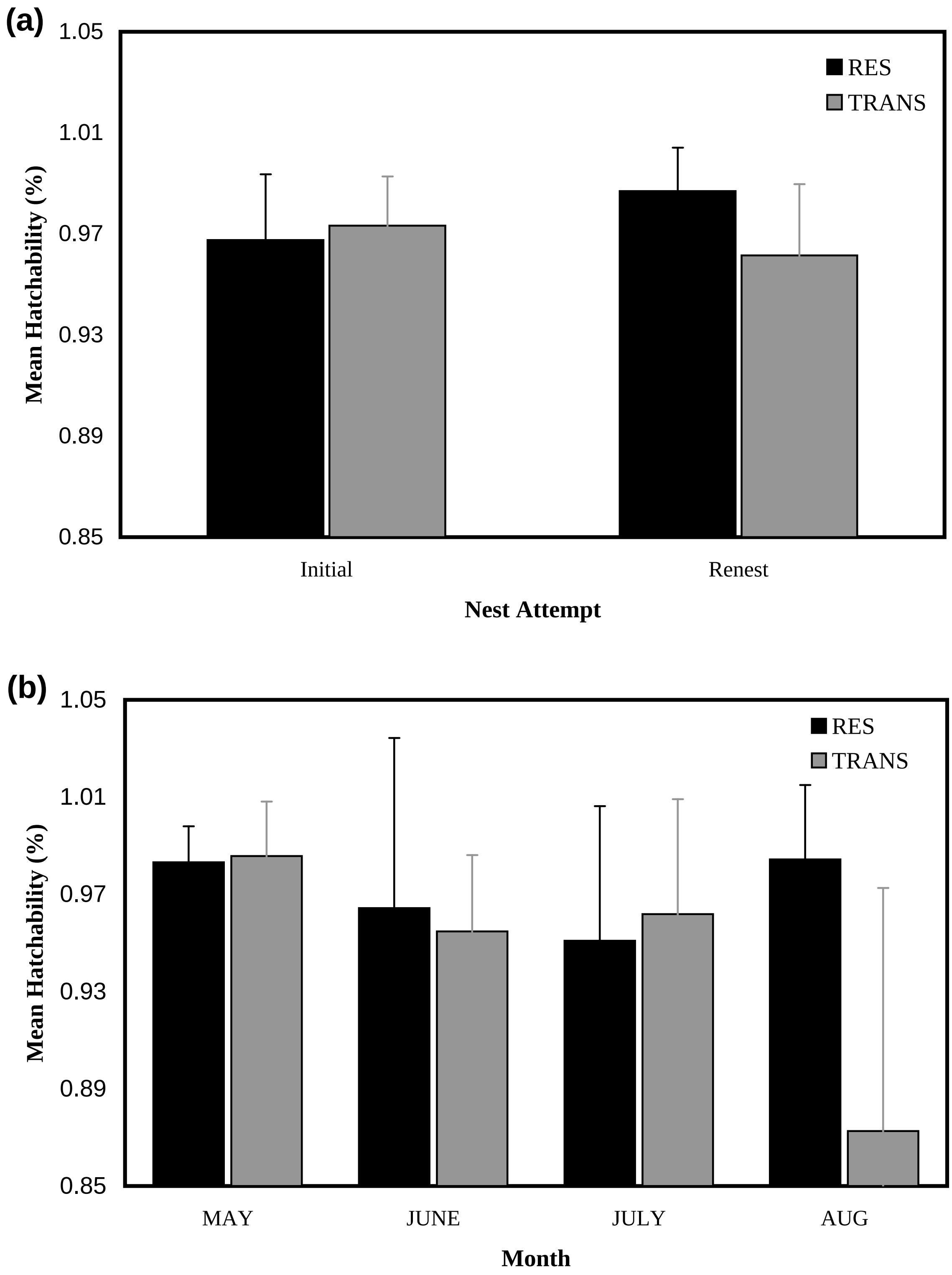

Figure 3.2: Mean hatchability (%) for translocated and resident northern bobwhites on Buck Creek Plantation during 2003 and 2004 combined and delineated by: (a) nest attempt (initial [first-found] nest attempt, Renest [second nesting attempt and/or double brood attempt]) and (b) month.

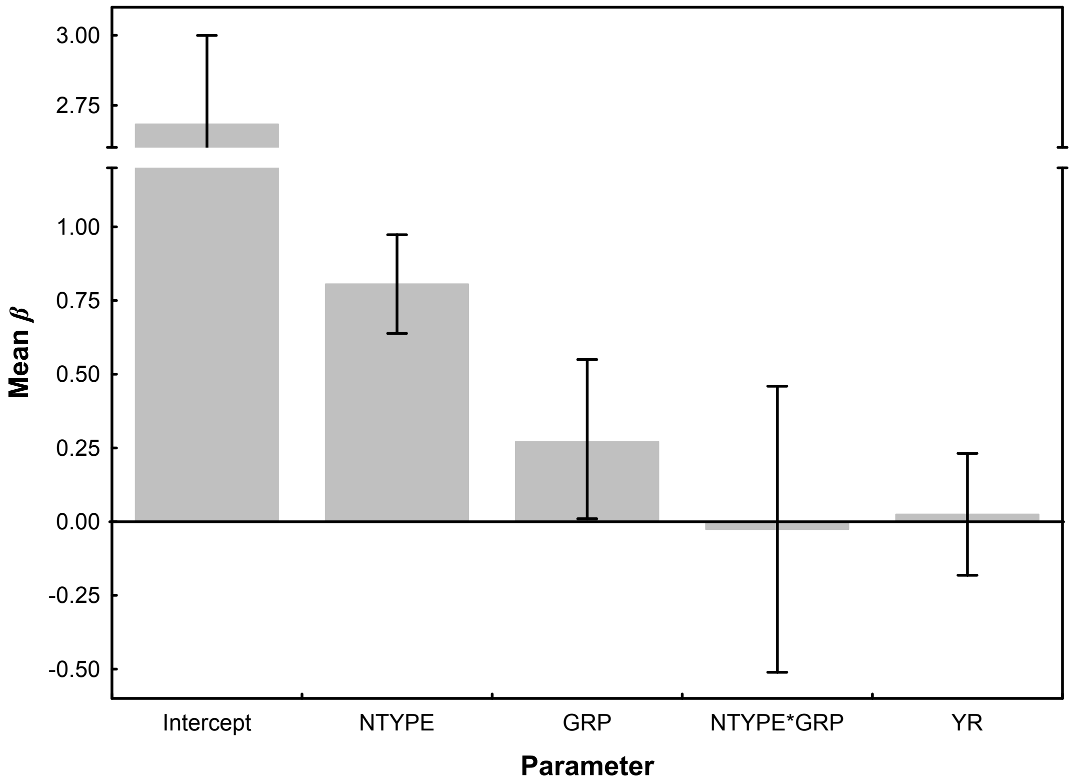

Figure 3.3: Model averaged parameter estimates (± 95% CI) for models explaining variation in incubation date on Buck Creek Plantation, Marion county, Georgia during 2003 and 2004.

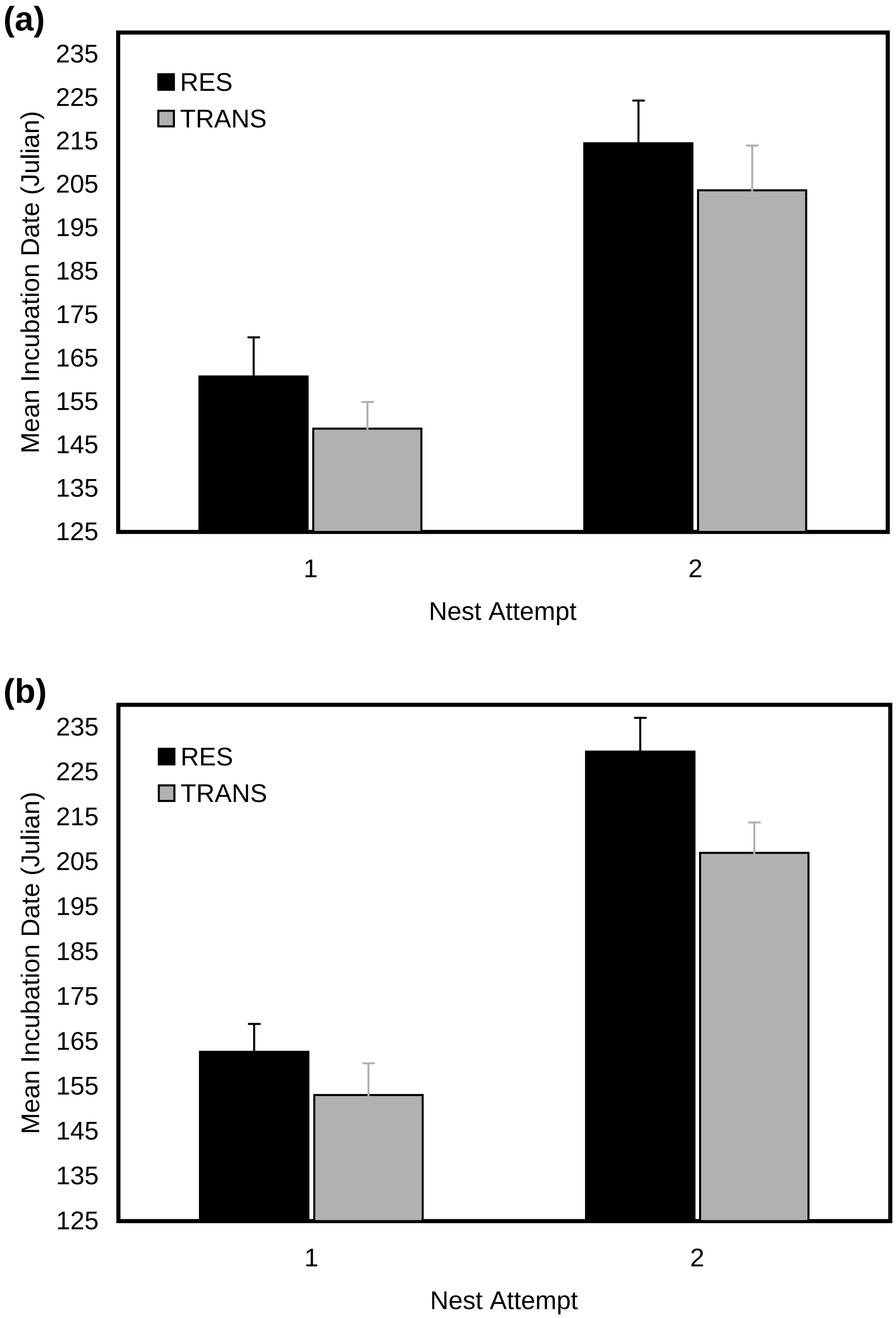

Figure 3.4: Mean incubation date for translocated and resident northern bobwhites on Buck Creek Plantation during 2003 (a) and 2004 (b)delineated by nest attempt (1 = initial [first-found] nest attempt, 2 = Renest [second nesting attempt and/or double brood attempt]).

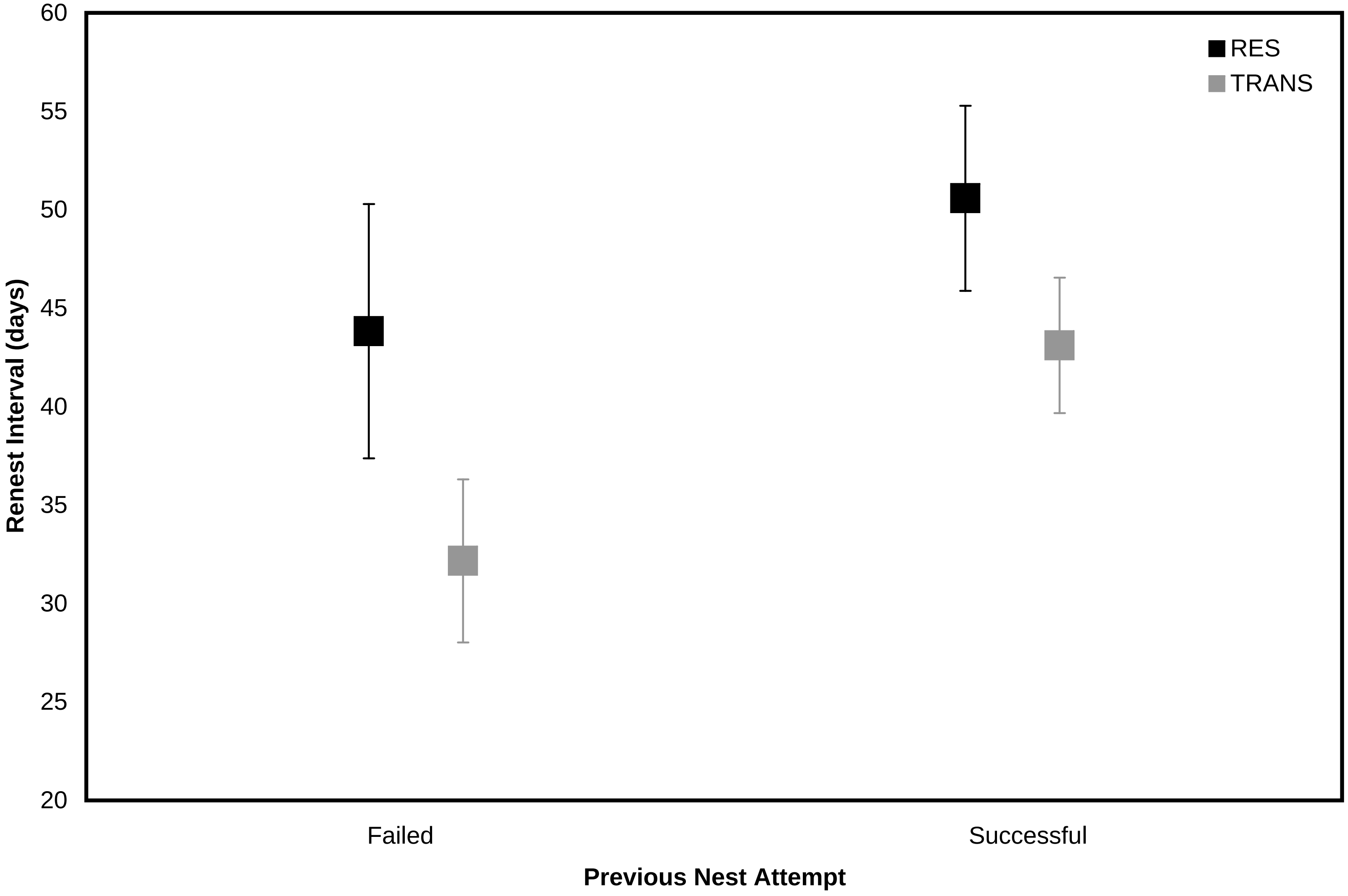

Figure 3.5: Mean renesting interval (measured in days) for translocated and resident northern bobwhites on Buck Creek Plantation during 2003 and 2004 pooled across years and delineated by the success or failure of the previous nesting attempt.

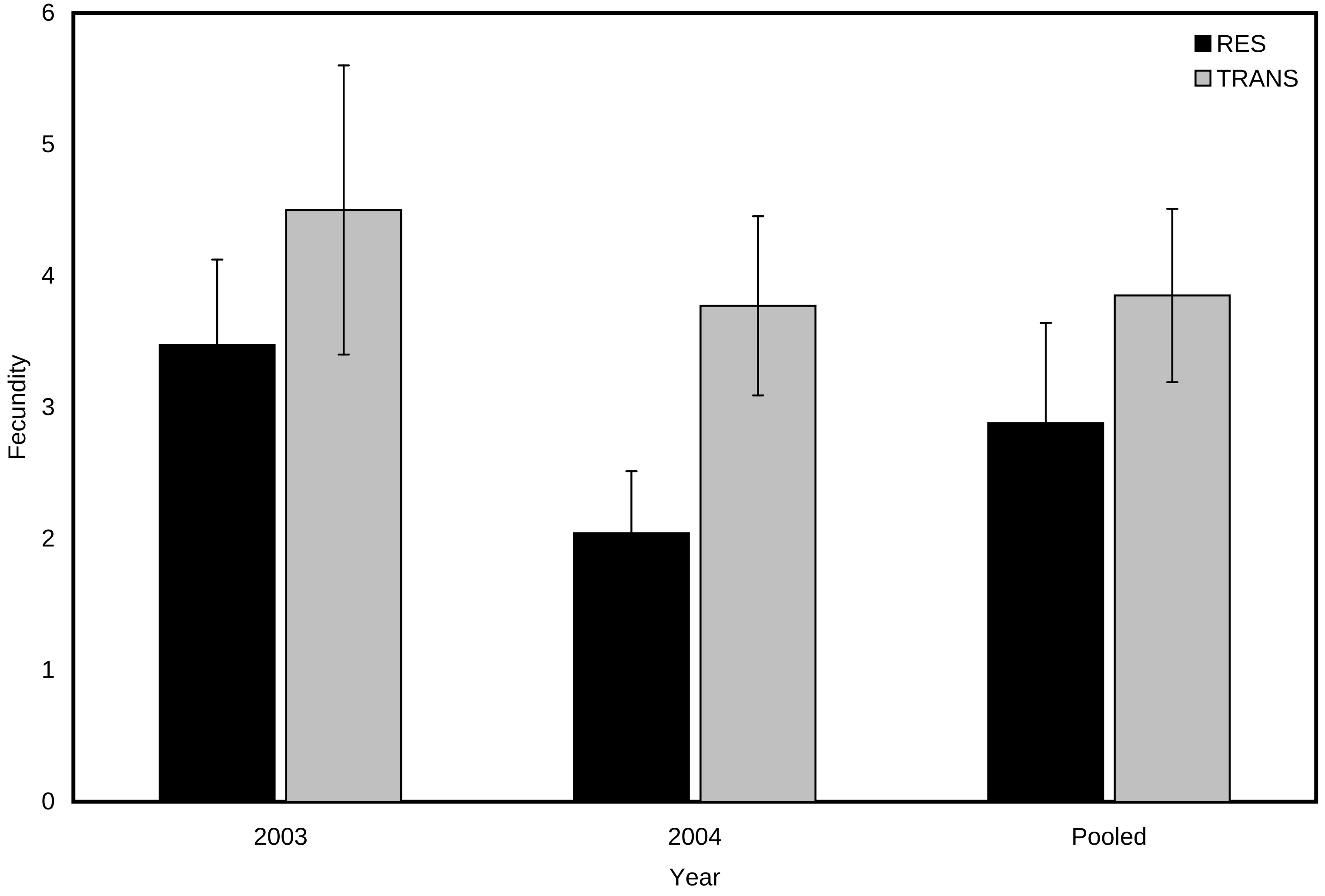

Figure 3.6: Fecundity for translocated and resident northern bobwhites on Buck Creek Plantation, Marion county, Georgia during 2003 and 2004.

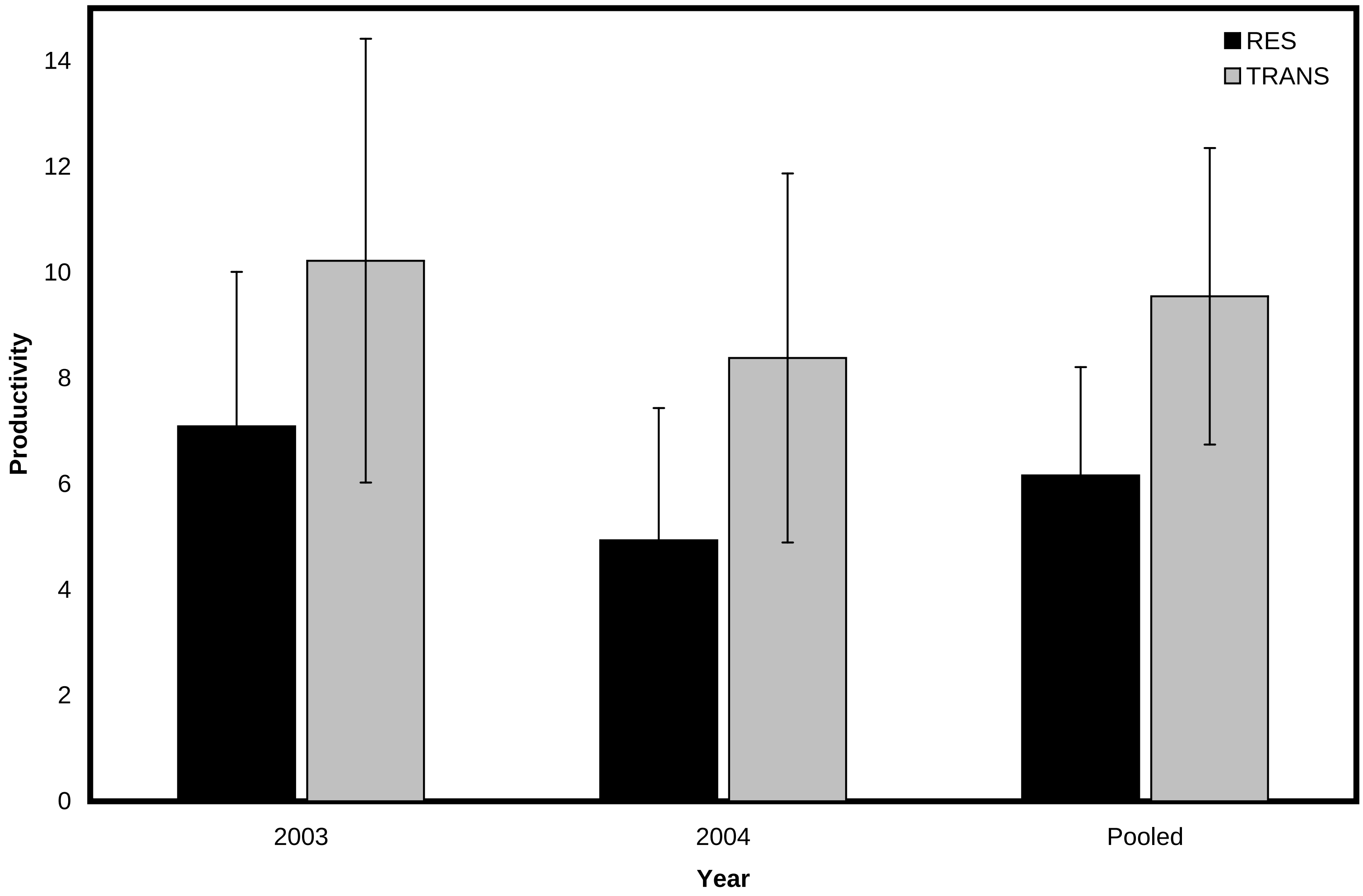

Figure 3.7: Productivity (the number of chicks hatched per hen) for translocated and resident northern bobwhites on Buck Creek Plantation, Marion county, Georgia during 2003 and 2004.

CHAPTER 4

GENETIC VARIABILITY AND POPULATION STRUCTURE IN A FRAGMENTED POPULATION OF NORTHERN BOBWHITES COMPARED TO NON-ISOLATED, PANMICTIC POPULATIONS[4]

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[4] Terhune, T. M., B. C. Faircloth, D. C. Sisson, W. E. Palmer, S. H. Eo, H. L. Stribling, J. P. Carroll. To be submitted to *Journal of Avian Biology*.

4.1 ABSTRACT

Habitat fragmentation has dramatically altered the landscape and, as a result, negatively affected numerous fauna and flora by reducing important demographic attributes and genetic variation. The Northern Bobwhite (*Colinus virginianus*) is a prominent gamebird in North America with social and economic value that has consequently suffered precipitous population declines as a result of widespread changing land-use and loss of early-succession habitats. Demographic information has been extensively documented for bobwhites both among contiguous and fragmented habitats, but genetic assessment of bobwhite populations among the latter has not been extensively investigated. Thus, deficient knowledge of the effects, if any, that habitat fragmentation and isolation has on genetic composition among bobwhite populations exists. Our objective was to investigate the assumed hypothesis of panmixia among geographically proximate and distant populations of bobwhites. We used a panel of 16 microsatellite loci to genotype individuals (n = 430) located on seven sites exhibiting varying degrees of fragmentation in Georgia and Florida. We assessed the genetic condition for each sampled site using frequency (e.g. allele frequency, $F_{ST,IS}$, R_{ST}) and Bayesian-clustering methods to assess inter- and intra-population genetic structure. We did not find differences in heterozygosity, number of alleles, F_{IS} values, or allelic richness) between populations; however, significant genetic differentiation between a physically isolated site and all other sites was observed using an unbiased estimator of R_{ST}. Bayesian cluster analysis identified 5 distinct clusters contravening the hypothesis of assumed panmixia across all sampled populations, but the prevalence of high ancestry to multiple clusters suggests admixture among populations. A noticeable geographical gradient of admixture between regional groups of populations was evident for our data whereby populations located proximately were more closely related than more distant populations. We suggest, based on estimated high levels of heterozygosity and retention of high genetic diversity in spite of habitat fragmentation, that small, fragmented and even isolated habitat patches should not be discounted as future conservation potential.

4.2 INTRODUCTION

Habitat fragmentation, degradation or loss in its entirety is a salient problem facing conservation of biodiversity worldwide (Sala et al. 2000). Human population growth resulting in urbanization and habitat fragmentation has important ecological and genetic consequences for endemic fauna and flora. In general, species in fragmented systems may experience reduced habitat and population size, increased spatial isolation and reduced dispersal opportunity, thereby contributing to erosion of genetic variation and increased inter-population genetic divergence due to increased random genetic drift, elevated inbreeding, and disrupted gene flow (Couvet 2002, Ernst et al. 2003, Frankham 1996, Lacy and Lindenmayer 1995). Loss of genetic integrity of a species is inextricably linked to population viability and demographic attributes and may potentially inhibit the ability of individuals to adapt to random environmental (e.g. adverse weather events) and ecological (e.g. disease outbreaks, predator dynamics) fluctuations. Consequently, this may yield possible inbreeding depression, poor survival and reproduction (Litvaitis 1993, Robinson et al. 1995), and an increase in extinction probability (Reed and Frankham 2003, Westemeier et al. 1998).

The relationship between levels of genetic variation and fitness has been well documented where low genetic variation generates purported short-term decreases in fitness and long-term loss of adaptive flexibility (Cassinello et al. 2001, Coltman et al. 1999, Frankham et al. 2004, Lande 1988, Reed and Frankham 2003). However, the magnitude of these effects on the genetic diversity within and divergence among populations likely varies with the degree of fragmentation. Inversely, gene flow as contribution from one to only a few individuals may neutralize both differentiation and loss of genetic diversity (Mills and Allendorf 1996, Wright 1931). As such, translocations have been used as a means to simulate natural gene flow to mitigate potential loss in genetic variation which has been termed a genetic rescue (Tallmon et al. 2004).

Populations occurring within contiguous or sufficiently connected (via corridors or a stepping-stone habitat-patch matrix) habitats are expected to adhere to an isolation-by-distance paradigm, whereby temporal (i.e. time since isolation) and spatial (geographic distance) factors are the primary mechanisms contributing to genetic differentiation and population divergence (Frankham et al. 2002, Slatkin 1993). When geographic distances or when time since isolation between habitat fragments increases, genetic diversity decreases and population divergence likely ensues (Frankham et al. 2002). Numerous avian species (e.g. Cerulean Warbler) have been negatively impacted by habitat fragmentation and isolation. The Red-cockaded Woodpecker (*Picoides borealis*) is an example where habitat loss and fragmentation has caused demographic (rapid population declines) and genetic (reduced genetic variation among small patches) consequences to the extent of being listed as endangered (Stangel et al. 1992). These dramatic consequences occurred in spite of their ability to disperse relatively large distances (Walters et al. 1988). Therefore, low-mobility species may be particularly susceptible to habitat fragmentation because limited dispersal of individuals and immigrants would presumably reduce gene flow and potentially cause inbreeding depression (Sisk et al. 1997).

Many species within the Order Galliformes (Madge and McGowan 2002) are sedentary, but arguably one of the most sedentary species within this Order is the prominent gamebird, the Northern Bobwhite Quail (*Colinus virginianus*; hereafter bobwhite[s]). Bobwhites have commercial and socio-economic importance (Burger et al. 1999) and are native, habitat generalists that readily respond to favorable habitat conditions with a wide-ranging distribution (Brennan 1999, Burger et al. 1999). They are non-migratory, gregarious birds with relatively low natal dispersal, small home ranges, and high reproductive capacity (Brennan 1999). Additionally, northern bobwhites have undergone significant population declines, and even extirpation of local populations, which have been tightly connected to changing land use and associated habitat fragmentation (Brennan 1991, 1999, Brennan and Kuvlesky 2005, Church et al. 1993, Church and Taylor 1992, Sauer et al. 2008). Bobwhites are particularly sensitive to fragmentation since they typically require large (1200 to 2000 ha), contiguous habitat patches to sustain viable population levels (Brennan 1991, Roseberry and Klimstra 1984).

Despite the northern bobwhite being the most studied gamebird in North America, few empirical, detailed studies have been conducted on inter- and intra-population genetic structure specific for *C. virginianus*. While a few molecular-based studies have been instituted among bobwhites (Ellsworth et al. 1988, 1989, Eo 2008, Nedbal et al. 1997, Valentine 2007), none of these studies extensively investigated genetic differentiation and gene flow in fragmented or isolated habitats in comparison to adjacent populations. Recent studies have investigated genetic structure among Order Galliformes (Eo 2008) using a combination of mtDNA and nuclear DNA (microsatellites) and specifically within *Colinus* species to delineate conservation and management units with respect to sub-species. However, Eo (2008) obtained samples primarily from harvested birds and the main objective in this study was to determine taxonomic differentiation within *Colinus* sp. with respect to the regional distribution and was not designed to extensively sample populations that were isolated or fragmented in their analyses. In general, Eo (2008) found that putative clusters and subsequent population divergence existed within Midwestern and Eastern bobwhites, but moderate sub-structuring did not warrant taxonomic or explicit geographical designation within the eastern region. In light of the apparent low mobility of northern bobwhites coupled with their disbanded and, at best, hint of spatial structure, more detailed genetic information is needed to better understand the impacts of habitat fragmentation and isolation on genetic variation and to best guide conservation strategies in the future.

In this study, we used a panel of 16 microsatellite markers (Faircloth et al. 2008, Schable et al. 2004) to address inter- and intra-population genetic structure of northern bobwhites on seven separately owned and managed properties in northern Florida and southwestern Georgia in terms of genetic diversity, population differentiation and physical isolation from other bobwhite populations and habitat. Specifically, we tested the hypothesis of assumed panmixia among geographically proximate and distant populations to describe potential effects of habitat fragmentation on a non-migratory, low-mobility avian species.

4.3 METHODS

This study was a part of a larger study investigating the demographic and genetic effects of translocation. During 2002 - 2003, we collected samples from seven sites located in Georgia and north Florida. Three of the seven sites (Farm Sites 1 - 3 [FS 1 - 3]) were located in Baker and Dougherty counties near Albany, Georgia. These three sites were located among intensive, center-pivot irrigated, farm systems where habitats existed in a low-to-moderately fragmented landscape, but they were not isolated from other bobwhite populations [see (Hughes et al. 2005) for detailed farm site descriptions]. The isolated site, Buck Creek Plantation (1092 ha) is located in Marion County near Tazewell, Georgia (located 96 km northwest of the northernmost non-isolated sampled population site). Prior to onset of habitat management in 1996, the property was typical of the region: there was little farming, and the landscape was dominated by pine monocultures (BA >19 m^2/ha) under early enrollment in the Conservation Reserve Program (CRP) and pastureland. During 1996-2003, extensive habitat improvements were undertaken on the study site; however, only modest increases in the bobwhite population abundance was observed. This property is considered an “island” of well-managed bobwhite habitat surrounded by a matrix of poor landscapes (e.g. dense pine monocultures [CRP], pasture-land, and late-succession hardwood forests). The remaining three sites (Foshale [FO], Pebble Hill [PH], and Tall Timbers [TT]) were located in the Red Hills region between Tallahassee, Florida and Thomasville, Georgia [for detailed site descriptions see (Faircloth 2008, Palmer and Wellendorf 2007)].

4.3.1 SAMPLE COLLECTION

We collected samples via two methods: trapping and hunter-harvest. Trapping was conducted during Oct-Nov (Fall-trapping period) and Jan-Mar (Spring-trapping period) in 2002-2003 using confusion-style funnel traps (Stoddard 1931, p. 442) baited with milo or cracked corn. We covered traps with brush (e.g., fresh-cut pine limbs) to minimize stress on captured birds and to conceal traps from predators. All bobwhites captured (translocated and resident) were classified by age and sex; and we, additionally, weighed, leg-banded, and collected 10 to 15 feathers from the ventral and humeral feather tracts. Half of the collected feathers for each individual were placed in 70% ethanol (ETOH) for preservation prior to genetic analysis. We stored remaining feathers in individually-labeled envelopes to serve as "back-ups" should the feathers in ETOH become lost, unusable, or fail to amplify during PCR. For hunter-harvested bobwhites, hunters placed a single wing from one bobwhite per covey in an envelope with tab closures and pre-printed sample number codes.

Bobwhite capture and monitoring procedures outlined in this study for the source sites in Baker and Dougherty Counties were approved by the Georgia Department of Natural Resources (2070 U.S. Hwy. 278, S.E., Social Circle, Georgia 30025) during 2003 and 2004 under permit numbers #29-WMB-03-280 and #29-WSF-04-200. Bobwhite capture and monitoring procedures for the study site in Marion County, Georgia were approved by the Georgia Department of Natural Resources (2070 U.S. Hwy. 278, S.E., Social Circle, Georgia 30025) under permit #29-WMB-00-105, #29-WMB-03-38, and #29-WMB-04-128. All trapping, handling, and sampling techniques were approved by the University of Georgia Institutional Animal Care and Use Committee (2000-2002 IACUC approval numbers: A990028M1, A990028C1; 2003 extension: A200310109-0) and followed guidelines provided by the Ornithological Council's Guidelines for the Use of Wild Birds in Research (American Ornithologists' Union 1999).

4.3.2 Microsatellite Genotyping

We extracted DNA from feathers using DNeasy kits (Qiagen, Inc) with a modification to the digestion step, adding 25 μL of 100 mg/mL DTT (Dithiothreitol) along with proteinase K. We eluted DNA with either: 2 washes of 60 μL Buffer AE or 1 wash 120 μL Buffer AE. Prior to amplification, we treated all samples 1:3 with 10% Chelex resin (BioRad Laboratories) to remove PCR inhibitors. We performed 96-well PCR amplifications of 16 microsatellite loci (Faircloth et al. 2008, Schable et al. 2004) in 10 μL volumes using CAG- or M13R-tagged primers (Glenn and Schable 2005). Reaction concentrations were 0.5 U AmpliTaq Gold (Applied Biosystems), 1X Gold Buffer, 1X BSA (New England Biolabs), 1.5 mM MgCl, 1.25 mM dNTPs, 0.5 μM untagged primer; 0.05 μM CAG or M13-reverse tagged primer, 0.45 μM dye-labelled tag (HEX, FAM, NED + CAG or M13-reverse), 3.3 μL ddH2O, and 2 μL DNA template (5-10 ng). We included multiple negative controls in each plate of PCR reactions.

We used one of two locus-dependent touchdown thermal cycling profiles (Don et al. 1991), each encompassing a 10 C span of annealing temperatures (ranges: 60 - 50 C; 65 - 55 C). Cycling parameters included a Taq activation step at 95 C for 5 m followed by 20 cycles at 95 C for 20 s; 60 or 65 C for 30 s minus 0.5 C per annealing cycle; and 72 C for 90 s followed by 25 cycles at 95 C for 20 s; 50 or 55 C, respectively, for 30 s; 72 C for 90 s. We used a final extension period of 10 min at 72 C.

We scored fragments using an ABI 3730xl sequencer (Applied Biosystems) with ROX500 fluorescent size standard. We sized fragments using GENEMAPPER version 4.0 software (Applied Biosystems) and the Global Southern method. Initial tests indicated that the Global Southern method resulted in reduced intra-run variation in microsatellite fragment length relative to other sizing methods. We binned all fragments using the same binset to ensure that binned fragments were consistent across years, and we discarded ambiguous genotypes from the data set and re-genotyped plates with failing negative controls.

To assess the rate of genotyping error, we randomly selected a 15% sample from the entire data set, assigned each individual a random identification string, and blindly genotyped, scored, and binned these samples (Hoffman and Amos 2005). We exported all samples from the GENEMAPPER database, converted each to a useful format using GMCONVERT (Faircloth 2006). We then re-assigned error samples their true identification and compared each to the corresponding non-error sample to compute the genotyping error rate on a per-locus and overall basis ($\bar{x} \pm 95\%$ CI).

4.3.3 Genetic diversity and differentiation among sample sites

We characterized genetic variation within sampling sites by calculating the mean number of alleles, observed heterozygosity and expected heterozygosity using Cervus (Kalinowski et al. 2007, Marshall et al. 1998). Additionally, because the number of alleles is correlated with sample size, we calculated allelic richness, an unbiased estimator of the number of alleles, using the rarefaction procedure as implemented in FSTAT (Goudet 1995). We estimated F_{IS} and pairwise F_{ST} using FSTAT (Goudet 1995). We also used GENEPOP (Raymond and Rousset 1995a,b, v. 3.4) and SPAGEDI (Hardy and Vekemans 2002, v. 1.2) to assess global and pairwise population differentiation of microsatellite allele frequencies. We assessed departures from Hardy-Weinberg equilibrium by population and pooled using Cervus. Using procedures outlined in Faircloth (2008), we tested for linkage using two-point analysis in CRIMAP (Lander and Green. 1987) for all pairwise combinations of loci assuming that loci were linked when the log-odds for the pairwise-comparison was > 3.0. To account for multiple comparisons among loci, when relevant, we interpreted significance following a sequential Bonferroni correction of alpha (Rice. 1989).

Additional patterns of genetic differentiation was conducted and graphed using Factorial Correspondence Analysis (FCA) using individual genotypic scores and delineated by sampling population using GENETIX (Belkhir et al. 2001). Factor analysis implemented in GENETIX is a methodology considered a special case of principal components analysis in which the correspondence analysis is applied to contingency tables rendering correspondence matrix. Groups of individuals are represented as multidimensional positions in hypersapce having as many dimensions as alleles for each loci. The algorithm determines the independent directions in hyperspace where the size of the vector is proportional to the number of individuals in a point of hyperspace multiplied by the square of the distance to the center of the coordinates (Guinand 1996). The primary objective of this method is to decompose the overall multidimensional data (multi-locus geneotyped individuals) to a small number of dimensions where the deviations from expected values can be represented.

4.3.4 Bayesian STRUCTURE analysis

To differentiate inter-population genetic structure present in northern bobwhites, we analyzed samples with no *a priori* designation of sampling location (site) using a model-based Bayesian clustering approach. We used program STRUCTURE (Pritchard et al. 2000) to infer population substructure and assign individuals to one or more of these inferred clusters based on their individual multilocus genotype. Structure estimates the likelihood of K (the number of clusters) with the assumptions of Hardy-Weinberg and linkage equilibrium (Falush et al. 2003). We conducted 10 independent runs of K=1-10 with a 50,000-iteration burn-in period and 100,000 Monte Carlo Markov Chain (MCMC) iterations using the F model (correlated allele frequencies/admixture). Previous analyses (Eo 2008) has demonstrated that widely distributed populations of northern bobwhite in the southeastern U.S. are closely related, and Falush et al. (2003) suggests that the F model is more plausible for delineating sub-structure among populations that are closely related. Following Evanno et al. (2005), we calculated Δ K, an *ad hoc* quantity related to the second order rate of change of the log likelihood of the data P(X|K) with respect to the number of population clusters (K), to determine the optimal cluster size given the data.

In order to further test the hypothesis that groups of sampling sites (populations) exhibit panmixia or not, we conducted additional STRUCTURE analyses to investigate genetic structure based on geographical region and amount of fragmentation. We defined 2 distinct groups (delineated by region): Region 1 was the sampling areas located in north Florida (FO, TT) and south Georgia (PH); Region 2 consisted of the farm sites (FS1, FS2, FS3) near Albany, Georgia; and Region 3 consisted of only the isolated site (BC)in Macon County, Georgia.

4.4 Results

4.4.1 Microsatellite Genotypes

All samples (n = 430; Table 4.1) were analyzed using 16 microsatellite markers (loci); however, we removed individuals with less than 50% complete multi-locus genotypes for all loci and thus our overall sample size following removal was 419. Of these 419 genotyped individuals, >80% had missing data for 2 or less loci. Two loci (CV-PA12A and CV-PA1F) were linked and another (CV-P1F2) demonstrated Mendelian problems associated with the presence of null alleles (Faircloth 2008); therefore we removed CV-PA12A and CV-P1F2 prior to inter-population genetic analysis. Additionally, 2 loci (CV-PA3G and CV-PBA4) departed significantly from Hardy-Weinberg equilibrium (HWE) following Bonferroni correction (Rice. 1989) for multiple populations.

4.4.2 Genetic diversity and differentiation among sample sites

Microsatellite genotypes at all loci excluding those removed due to linkage disequilibrium or HWE were assessed for allelic diversity and expected heterozygosity (Table 4.2; Appendix B). These loci exhibited 100% polymorhpism. The number of alleles ranged from 2-19 with an overall mean of 9.142 (± 0.531) and F_{IS} estimates were similar among all sample locations (Table 4.2). Global differentiation across all populations was corroborated with allele frequencies ($F_{ST} = 0.0141$, $R_{ST} = 0.0991$); the global R_{ST} was significantly higher than pR_{ST}, suggesting that R_{ST} is a superior metric for assessing genetic variation in our study (Balloux and Goudet 2002, Balloux and Lugon-Moulin 2002, Slatkin 1995). Low R_{ST} values were observed among sampled populations. However, significant differentiation was identified between FO and all three farm sites (FS1-3); and the isolated site (BC) was significantly different than all other sites except FO (Table 4.3).

Factor Correspondence Analysis (FCA) suggested moderate population structure among sampled sites (Figure 4.1). However, there was substantial overlap between individuals among sampled populations: FCA-I, FCA-II and FCA-III explained 33.7%, 17.0% and 15.53% of the variation, respectively, for our data. FCA revealed moderate sub-structuring of FS3, PH, and BC (the isolated site), but with several individuals within these populations overlapping those in other populations and thereby exhibiting genetic similarities to other populations (Figure 4.1).

4.4.3 Bayesian STRUCTURE analysis

Posterior probabilities derived from the Bayesian-based STRUCTURE analysis suggested that our data are best explained by the distribution of individuals into five clusters (K=5; Figure 4.2). However, the proportional membership among individuals within each sampled population to the inferred five clusters suggested admixture among populations (Figure 4.3). At K=5, the F_{ST} values calculated by STRUCTURE for the inferred clusters ranged from 0.04 to 0.18 aligning with those estimated among current (sampled) populations. We extracted individuals exhibiting high ancestry assignment, when K=5, to depict regions of concentration of high-ancestry for each cluster delineated by sampling location (Figure 4.4) to visually represent genetic variation within regions and among sites within regions. Visual assessment of high-ancestry plots suggests that a moderate gradient of genetic sub-structuring is evident from North to South with some within-region variation (BC compared to Farm Sites compared to PH, TT, and FO). However, all sampled populations exhibit cluster-overlap with several other sampled populations suggesting some extent of admixture. In particular, genetic differentiation was evident among BC and FS3 sites (Figure 4.4). Individuals with higher ancestry to cluster E (red; Figure 4.4) tended to be concentrated in the isolated site (BC), whereas those with higher ancestry to cluster C (purple; Figure 4.4) were most prevalent in FS3. Notably, the Farm Sites all have a small proportion of individuals assigned to the red cluster (cluster E), whereas the 3 southern-most sites (FO, PH, and TT) lack genetic representation of this cluster. The PH site contained individuals exhibiting high ancestry to only 3 distinct clusters, but small sample size (n=19) may limit the interpretation of the actual genetic representation within this site. Separate STRUCTURE analyses run by region (North-Region (NR): BC; Central-Region (CR): FS1, 2, 3 and BC; and South-Region (SR): FO, PH, TT) indicated that 2 clusters was the optimal cluster size for the CR whereas 1 cluster was the optimal cluster size for both NR and SR.

4.5 Discussion

The current scientific literature is plagued with the notion that habitat fragmentation and isolation is considered a bane to population persistence and the cause for widespread population declines for many species - especially those exhibiting low dispersal (Ambuel and Temple 1983, Fisher 1930, Litvaitis 1993, Robinson et al. 1995, Roth and Johnson 1993, Temple and Cary 1998, Westemeier et al. 1998). Smith and Hellman (2002), however, imputed that populations in small habitat fragments often perform equally as well as those found among larger patches and research has corroborated this paradigm (Tewksberry et al. 1998, Zanette 2001). In the context of maintaining genetic variation, our results further substantiate this assertion.

Despite being physically distanced from other known bobwhite populations, genetic diversity on BC, the study site located in the most fragmented landscape, was high. It is perhaps unexpected that the purported isolation and fragmentation of this site did not cause a reduction in heterozygosity and did not, as a result, inflate inbreeding depression. Nevertheless, this bodes well for the genetic integrity of bobwhites as our results imply that BC exhibited similar genetic diversity (e.g. allelic richness, F_{IS}, H_O and H_E) compared to other non-isolated sites. Furthermore, examination of farm sites exhibiting moderate fragmentation also demonstrated high genetic diversity and thereby these populations are not seemingly limited by depauperate genetic variation. In retrospect, these results are positive for the species whereby habitat fragmentation is apparently not as deleterious on the genetic state of bobwhites as previously thought. There are several plausible explanations for the apparent "healthy" (i.e. high genetic diversity) genetic state observed among both BC and moderately fragmented sites. Here we consider two of the most likely: the first explanation suggests that heterozygosity may be maintained by gene flow among populations and the second relates to lack of extensive temporal isolation.

The primary mechanism of gene flow is movement of individuals. Our results suggest that sufficient levels of gene flow occurred among sampled populations to inhibit complete genetic differentiation of individual sampling units, thereby implying adequate movement of individuals between these sites. This is reflected in the low pair-wise R_{ST} values among sampled populations and F_{ST} values among STRUCTURE-derived clusters. It has been proposed that only a few to as little as one migrant per generation is needed to abate deleterious inbreeding effects and to maintain allelic diversity (Mills and Allendorf 1996, Wright 1931). The farm sites, while undoubtedly fragmented as a result of intensive farming practices, are not isolated and are located adjacent, or in close proximity, to large intensively-managed bobwhite populations. As such, the probability of immigration to these sites while potentially lower than larger, contiguous habitats is probably high. In fact, long-term capture-recapture studies indicate a few individual dispersal movements to adjacent sites among these and surrounding areas (D. C. Sisson, unpublished data). Additionally, and contrary to the widespread, traditional recognition of bobwhites being a low-mobility species with limited dispersal, more recent studies have suggested that bobwhite movements and dispersal is greater than previously thought (Cook 2004, Fies et al. 2002, Folk 2006). Folk (2006) reported dispersal distances as high as 17 km for bobwhites in a fragmented landscape. In our study, the mean distance between farms sites was 13 km and <1 km to other bobwhite populations. Thus, immigration is a plausible and even probable explanation for low genetic differentiation observed among these sites. Regarding the most isolated site (BC), however, the probability of gene flow from immigration is much less likely because no known bobwhite populations are located within 20 km and the distance to the nearest sampled population was approximately 96 km. As such, the possible number of immigrants to BC is severely limited and thus adequate gene flow as an explanation for low genetic differentiation among this site lacks merit.

A more plausible explanation for the lack of complete genetic divergence of the BC site as compared to other sites is the relatively recent isolation of this population. Habitat loss and fragmentation of early-succession habitats in the southeastern United States has occurred in stages during the last several decades related to numerous land-use changes (e.g. intensification of agriculture, fire suppression, urbanization) and has been particularly precipitous and most detrimental to bobwhites during the past 2-3 decades (Brennan 1991, Burger 2002, Church et al. 1993, Kuvlesky et al. 1993). However, in an evolutionary sense this time period is relatively recent (Frankham et al. 2004). Whereas some heterozygosity might initially be lost, significant erosion of genetic variation requires the population to remain small for several generations or forced to near extirpation (Allendorf 1986, Nei et al. 1975). This combined with the complex, but flexible, mating strategy (Faircloth 2008) of bobwhites may contribute to higher retention of allelic states through time.

Mapping of inferred high-ancestry individuals delineated by sampling regions (North Region = NR; Central Region = CR; and South Region SR) suggest areas of concentration that demonstrate differential admixture among and between regions. The occurrence of high-ancestry individuals outside the predominant cluster-type(s) within each sampling site suggests either retention of long-term ancestral allele frequencies similar to that of other sites or movement of individuals to and from other sites (i.e. immigration). As such, visual assessment of mapped clusters suggest that movement of individuals is more common among sites within regions than between regions and occur along a gradient from North to South. For example, cluster E (red; Figure 4.3) is represented in all sampled sites (farm sites) of the CR and NR, but not represented within any of the sites of the SR. Similarly, FS1 and FS2 within the CR as well as TT and FO within the SR (Figure 4.3) exhibit very similar proportionately high-ancestry assignment as compared to other sites and these movements are corroborated via mark-recapture studies in these areas (D.C. Sisson and W.E. Palmer, unpublished data).

Interestingly, cluster D appears in all sites except FS1 and FS2. Additionally, evaluation of Bayesian clusters, high-ancestry maps, and FCA suggest that BC and FS3 are quite disparate from other sampled sites and FS3 and PH are clear anomalies within their respective regions. Although anecdotal, a possible explanation here is that both BC and FS3 sites have historically released pen-reared birds (prior to 1996; D.C. Sisson, personal comm.). Sites within the South Region at one time received widespread translocations of Mexican Quail (likely *Colinus virginianus texanus*) during the early 1900s (Stoddard 1931) and current releases of pen-reared individuals is common on areas nearby these sites, but the influx and genetic contribution of these individuals is likely small due to high mortality rates often associated with pen-reared individuals (Buechner 1950, DeVos and Speake 1995, Frye 1942). However, both FS1 and FS2 have been extensively managed for wild bobwhites for more than 65 years and no historical records suggest release of pen-reared birds.

A final phenomenon potentially explaining the cryptic genetic structure observed in our data is that BC (1996), FS3 (1994-1996), and PH (1992) all experienced relatively recent population bottlenecks whereas the other sites have maintained relatively high (>1.24 birds per ha) densities for several decades. Both the duration and size of the bottleneck may affect the extent of a reduction in genetic variation and both theory (Nei et al. 1975) and experimental studies (Spencer et al. 2000) demonstrated a reduction in the number of alleles. However, even following short-term bottlenecks (such as that experienced on PH) substantial loss in heterozygosity does not necessarily result (Leberg 1992, Spencer et al. 2000). Therefore, the missing cluster (cluster B; Figure 4.3) observed for PH combined with the apparent “normal” heterozygosity level might be explained by the relative short-term bottleneck occuring less than 20 years ago or may simply be an artifact of low sample size. Regarding both BC and FS3, the cryptic genetic structuring observed may be attributable to this recent population bottleneck, but is more likely a result of the combination of the recent population bottleneck, habitat fragmentation, and historical releases of pen-reared bobwhites.

Despite our observation of overall low sampling unit differentiation, both Bayesian and frequency methods demonstrated genetic structuring. The identification of five Bayesian clusters suggests that among the regions sampled, northern bobwhites do not constitute a single panmictic population and thus rendering support for the hypothesis that there is some degree of population structure and thereby rejecting the hypothesis of panmixia. However, substantial overlap of clustering among populations (Figures 4.3 & 4.4) combined with low R_{ST} values and seemingly low-ancestral assignment for some individuals within sampled populations obfuscates our interpretation of both inter- and intra-population genetic structure as this is evidence of admixture (supporting the null hypothesis of panmixia). Taken collectively, we are unable to assert with high confidence that there are five, or even more than one, discrete population(s) with unequivocal assignment of all individuals to Bayesian-derived clusters. That said, the apparent cryptic genetic structure observed in our analysis may suggest future implications relative to patch connectivity and purported genetic directionality or merely highlight the convoluted historical management strategies and conservation actions implemented over the past 100 years in attempt to propagate bobwhites within this region. For example, a salient difference between the isolated site (BC) and the other sampled locations suggest that habitat isolation contributes to population divergence, but the representation of clusters occurring in other sites suggest either immigration (gene flow) or lack of temporal isolation to render explicit genetic population divergence. If the latter is the case, however, future population divergence might be inevitable given no gene flow occurs either naturally or artificially (e.g., translocation) which might result in speciation.

4.6 CONSERVATION IMPLICATIONS

Northern Bobwhites are ostensibly more permeable to the landscape and less sensitive to the deleterious genetic consequences of habitat fragmentation than previously thought. These results are good news for the genetic integrity and evolutionary outlook of bobwhites amidst an increasing fragmented landscape. Large populations inevitably tend to lose genetic variability more slowly than small populations, and long-term effects of random drift would be defrayed by selection, mutation, or the occasional movement of bobwhites among populations; and thus, maintenance and protection of large, contiguous habitats is important to the conservation of a species, especially those with limited dispersal. However, our results demonstrate that despite moderate fragmentation or even apparent isolation, these smaller, fragmented or geographically distanced sites retained relatively high genetic variation and therefore they should not be regarded as “lost causes.” Rather these populations may provide unique genetic combinations for future use or serve as “stepping stones” (Kimura and Weiss 1964) for gene flow and provide valuable genetic contribution to newly restored populations of nearby sites. That said, we do not suggest the creation of small populations for conservation biodiversity purposes, but rather suggest managing these naturally occurring small habitat fragments particularly those proximately located to other populations.

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Literature Cited

Allendorf, F. W., 1986. Genetic drift and loss of alleles versus heterozygosity. *Zoo Biology* **5**:181–190.

Ambuel, B. and S. A. Temple, 1983. Area-dependent changes in the bird communities and vegetation of southern wisconsin forests. *Ecology* **64**:1057–1068.

American Ornithologists' Union, 1999. Report of committee on use of wild birds in research. *Auk* **116**:1–41.

Balloux, F. and J. Goudet, 2002. Statistical properties of population differentiation estimators under stepwise mutation in a finite island model. *Molecular Ecology* **11**:771–783.

Balloux, F. and N. Lugon-Moulin, 2002. The estimation of population differentiation with microsatellite markers. *Molecular Ecology* **11**:155–165.

Belkhir, K. P., P. Borsa, L. Chikhi, N. Raufaste, and F. Bonhomme, 2001. GENETIX, software under Windows TM for the genetics of populations. Labroratory Genome, Populations, Interactions CNRS UMR 5000, Univeristy of Montpellier II.

Brennan, L. A., 1991. How can we reverse the the northern bobwhite decline? *Wildlife Society Bulletin* **19**:544–555.

Brennan, L. A., 1999. The Birds of North America. Number 397. A. Poole and F. Gill, eds., Philadelphia, Pennsylvannia, USA.

Brennan, L. A. and W. P. Kuvlesky, Jr., 2005. North american grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* **69**:1–13.

Buechner, H. K., 1950. An evaluation of restocking with pen-reared bobwhite. *Journal of Wildlife Management* **14**:363–377.

Burger, L. W., Jr., 2002. Quail management: Issues, concerns, and solutions for public and private lands–a southeastern perspective. *Proceedings of the National Quail Symposium* **5**:20–34.

Burger, L. W., Jr., D. A. Miller, and R. I. Southwick., 1999. Economic impact of northern bobwhite hunting in the southeastern united states. *Wildlife Society Bulletin* **27**:1010–1018.

Cassinello, J., M. Gomendio, and E. R. S. Roldan, 2001. Relationship between coefficient of inbreeding and parasite burden in endangered gazelles. *Conservation Biology* **15**:1171–1174.

Church, K. E., J. R. Sauer, and S. Droege, 1993. Population trends on quails in north america. *Proceedings of the National Quail Symposium* **3**:44–54.

Church, K. E. and J. S. Taylor, 1992. Management and research of northern bobwhite (*Colinus virginianus*) in north america: An overview. *Gibier Faune Savage* **9**:787–796.

Coltman, D. W., J. G. Pilkington, J. A. Smith, and J. M. Pemberton, 1999. Parasite mediated selection against inbred soay sheep in a free-living, island population. *Evolution* **53**:1259–1267.

Cook, M. P., 2004. Northern Bobwhite Breeding Season Dispersal, Habitat-Use, and Survival in a Southeastern Agricultural Landscape. Master's thesis, University of Georgia.

Couvet, D., 2002. Deleterious effects of restricted gene flow in fragmented populations. *Conservation Biology* **16**:369–376.

DeVos, T., Jr and D. W. Speake, 1995. Effects of releasing pen-raised northern bobwhite on survival rates of wild populations of northern bobwhites. *Wildlife Society Bulletin* **23**:267–273.

Don, R. H., P. T. Cox, B. J. Wainright, K. Baker, and J. S. Mattick, 1991. 'touchdown' PCR to circumvent spurious priming during gene amplification. *Nucleic Acids Research* **19**:4008.

Ellsworth, D. L., J. L. Roseberry, and W. D. Klimstra, 1988. Biochemical genetics of wild, semi-wild, and game-farm northern bobwhites. *Journal of Wildlife Management* **52**:138–144.

Ellsworth, D. L., J. L. Roseberry, and W. D. Klimstra, 1989. Genetic structure and gene flow in the northern bobwhite. *Auk* **106**:492–495.

Eo, S. H., 2008. Integrating Phylogenetic Relationships and Population Structure for Conservation Planning in Galliformes. Ph.D. thesis, University of Georgia.

Ernst, H. B., W. M. Boyce, V. C. Bleich, B. May, S. J. Stiver, and S. G. Torres, 2003. Genetic structure of the mountian lion (*Puma concolor*). *Conservation Genetics* **4**:353–366.

Evanno, G., S. Regnaut, and J. Goudet, 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. *Molecular Ecology* **14**:2611–2620.

Faircloth, B. C., 2006. GMCONVERT: File conversion for GENEMAPPER output files. *Molecular Ecology Notes* **6**:968–970.

Faircloth, B. C., 2008. An Integrative Study of Social and Reproductive Systems in Northern Bobwhite (*Colinus virginianus*): A Non-Migratory, Avian Species Bearing Precocial Young. Ph.D. thesis, University of Georgia.

Faircloth, B. C., T. M. Terhune, N. A. Schable, T. C. Glenn, W. E. Palmer, and J. P. Carroll, 2008. Ten microsatellite loci from northern bobwhite (*Colinus virginianus*). *Conservation Genetics* .

Falush, D., M. Stephens, and J. K. Pritchard, 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* **164**:1567–1587.

Fies, M. L., K. M. Puckett, and B. Larson-Brogdon, 2002. Breeding season movements and dispersal of northern bobwhites in fragmented habitats in virginia. In *Proceedings of the National Quail Symposium*, volume 5, pages 173–179.

Fisher, R. A., 1930. The genetical theory of natural selection. Oxford University Press, London, first edition.

Folk, T. H., 2006. Population Ecology of Northern Bobwhites. Ph.D. thesis, Auburn University.

Frankham, R., 1996. Relationship of genetic variation to population size in wildlife. *Conservation Biology* **10**:1500–1508.

Frankham, R., J. D. Ballou, and D. Briscoe, 2002. A primer of Conservation Genetics. Cambridge University Press, New York.

Frankham, R., J. D. Ballou, and D. A. Briscoe, 2004. A Primer of Conservation Genetics. Cambridge University Press, Cambridge, United Kingdom.

Frye, J. O. E., 1942. The comparative survival of wild and pen-reared bob-whites in the field. *Transactions of North American Wildlife Natural Resources Conference* **7**:169–178.

Glenn, T. C. and N. A. Schable, 2005. Isolating microsatellite dna loci. *Methods in Enzymology* **395**:202–222.

Goudet, J., 1995. Fstat (ver 2.9.3) a computer program to estimate and test gene diversities and fixation indices. *Journal of Heredity* **86**:485–486.

Guinand, B., 1996. Use of multivariate models using allele frequency distributions to analyze patterns of genetic differentiation among populations. *Biological Journal of Linnean Society* **58**:173–195.

Hardy, O. J. and X. Vekemans, 2002. Spagedi: a versatile computer program to analyze spatial genetic structure at the individual or population level. *Molecular Ecology Notes* **2**:618–620.

Hoffman, J. I. and W. Amos, 2005. Microsatellite genotyping errors: Detection appraoches, common sources and consequences for paternal exclusion. *Molecular Ecology* **14**:599–612.

Hughes, D. W., T. M. Terhune, D. C. Sisson, and H. L. Stribling, 2005. Demographics of northern bobwhite on agricultural and intensively managed bobwhite plantation landscapes. *Proceedings of the Annual Southeast Association of Fish and Wildlife Agencies.* .

Kalinowski, S. T., M. L. Taper, and T. C. Marshall, 2007. Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**:1099–1106.

Kimura, M. and G. H. Weiss, 1964. The stepping-stone model of population structure and the decrease of genetic correlation with distance. *Genetics* **49**:561–576.

Kuvlesky, W. P., Jr., B. D. Leopold, J. L. Roseberry, and T. Hutton., 1993. Population dynamics and effects of hunting. *Proceedings of the National Quail Symposium* pages 180–181.

Lacy, R. C. and D. B. Lindenmayer, 1995. A simulation study of the impacts of population subdivision on the mountain brushtail opossum (*Trichosurus caninus ogilby*), in south-eastern australia: Loss of genetic variation within and between populations. *Biological Conservation* **73**:131–142.

Lande, R., 1988. Genetics and demography in biological conservation. *Science* **241**:1455–1460.

Lander, E. S. and P. Green., 1987. Construction of multilocus genetic linkage maps in humans. *Proceedings of the National Academy of Sciences* **84**:2363–2367.

Leberg, P. L., 1992. Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. *Evolution* **46**:477–494.

Litvaitis, J. A., 1993. Response of early successional vertebrates to historic changes in land use. *Conservation Biology* **7**:866–873.

Madge, S. and P. McGowan, 2002. Pheasants, Partridges, and Grouse: A Guide to the Pheasants, Partridges, Quails, Grouse, Guineafowl, Buttonquails, and Sandgrouse of the World. Princeton University Press, Princeton, NJ, USA.

Marshall, T. C., J. Slate, E. B. Krunk, and J. M. Pemberton., 1998. Statistical confidence for likelihood based paternity inference in natural populations. *Molecular Ecology* **7**:639–655.

Mills, L. S. and F. W. Allendorf, 1996. The one-migrant-per-generation rule in conservation and management. *Conservation Biology* **10**:1509–1518.

Nedbal, M. A., R. L. Honeycutt, S. G. Evans, R. M. Whiting, Jr., and D. R. Dietz, 1997. Northern bobwhite restocking in East Texas: A genetic assessment. *Journal of Wildlife Management* **61**:854–863.

Nei, M., T. Maruyama, and R. Chakraborty, 1975. The bottleneck effect and genetic variability in populations. *Evolution* **29**:1–10.

Palmer, W. E. and S. Wellendorf, 2007. Effects of radiotransmitters on northern bobwhite annual survival. *Journal of Wildlife Management* **71**:1281–1287.

Pritchard, J. K., M. Stephens, N. A. Rosenberg, and P. Donnelly, 2000. Association mapping in structured populations. *American Journal of Human Genetics* **67**:170–181.

Raymond, M. and F. Rousset, 1995a. An exact test for population differentiation. *Evolution* **49**:1280–1283.

Raymond, M. and F. Rousset, 1995b. Genepop (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* **86**:248–249.

Reed, D. H. and R. Frankham, 2003. Correlation between fitness and genetic diversity. *Conservation Biology* **17**:230–237.

Rice., W. R., 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.

Robinson, S. K., I. Thompson, Frank R., T. M. Donovan, D. R. Whitehead, and J. Faaborg, 1995. Regional Forest Fragmentation and the Nesting Success of Migratory Birds. *Science* **267**:1987–1990.

Roseberry, J. L. and W. D. Klimstra, 1984. Population ecology of the Bobwhite. Southern Illinois University Press, Carbondale, Illinois, U.S.A., first edition.

Roth, R. R. and R. K. Johnson, 1993. Long-term dynamics of a wood thrush population breeding in a forest fragment. *Auk* **110**:37–48.

Sala, O. E., F. S. I. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oeserheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall, 2000. Global biodiversity scenarios for the year 2100. .

Sauer, J. R., J. E. Hines, and J. Fallon, 2008. The north american breeding bird survey, results and analysis 1966-2007. **Version 5.15.2008**.

Schable, N. A., B. C. Faircloth, W. E. Palmer, J. P. Carroll, L. W. Burger, L. A. Brennan, C. Hagen, and T. C. Glenn., 2004. Tetranucleotide and dinucleotide microsatellite loci from the northern bobwhite (*Colinus Virginianus*). *Molecular Ecology Notes* **4**:415–419.

Sisk, T. D., N. M. Haddad, and P. R. Ehrlich, 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecological Applications* **7**:1170–1180.

Slatkin, M., 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* **47**:264–279.

Slatkin, M., 1995. A measure of population subdivision based on microsatellite allele frequencies. *Genetics* **139**:457–462.

Smith, J. N. M. and J. J. Hellman, 2002. Population persistence in fragmented landscapes. *Trends in Ecology and Evolution* **17**:397–399.

Spencer, C. C., J. E. Neigel, and P. L. Leberg, 2000. Experimental evaluation of the usefulness of microsatellite dna for detecting demographic bottlenecks. *Molecular Ecology* **9**:1517–1528.

Stangel, P. W., M. R. Lennartz, and M. H. Smith, 1992. Genetic variation and population structure of red-cockaded woodpeckers. *Conservation Biology* **6**:283–292.

Stoddard, H. L., 1931. The Bobwhite Quail: Its Habits, Preservation, and Increase. Charles Scribner's Sons, New York, New York.

Tallmon, D. A., G. Luikart, and R. S. Waples, 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution* **19**:489–496.

Temple, S. A. and J. R. Cary, 1998. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* **2**:340–347.

Tewksberry, J. J., S. J. Hejl, and T. E. Martin, 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* **79**:2890–2903.

Valentine, T. L., 2007. Introgression and gene flow of Northern Bobwhites (*Colinus virginianus*) in the Southeastern U.S.A. Master's thesis, University of Georgia.

Walters, J. R., P. D. Doerr, and I. J. H. Carter, 1988. Long distance dispersal of an adult red-cockaded woodpecker. *Wilson Bulletin* **100**:496–499.

Westemeier, R. L., J. D. Brawn, S. A. Simpson, T. L. Esker, R. W. Jensen, J. W. Walk, E. L. Kershener, J. L. Bouzat, and K. N. Paige, 1998. Tracking the long-term decline and recovery of an isolated population. *Sceince* **282**:1695–1698.

Wright, S., 1931. Evolution and mendelian populations. *Genetics* **16**:97–159.

Zanette, L., 2001. Fragment size and the demography of an area-sensitive songbird. *Journal of Animal Ecology* **69**:458–470.

Table 4.1: Distribution of samples for seven study sites located in south Georgia and north Florida. Populations FO, PH, TT, FS1-3 are all located in large blocks of well-managed bobwhite habitat and have not been dramatically influenced by habitat fragmentation. FS1-3 are farm sites with variably levels of connectivity to other sites due to disjunct habitat patches associated with intensive farming practices, but none are isolated and severely limited by dispersal and subsequent gene flow. The BC site is an isolated site where the closest known wild population of bobwhites is >20 km.

Population (acronym)	Sample Size (n)	Sampling Period
Foshale (FO)	30	2002-2003
Pebble Hill (PH)	30	2002-2003
Tall Timbers (TT)	53	2002-2003
Farm Site 1 (FS1)	41	2002-2003
Farm Site 2 (FS2)	58	2002-2003
Farm Site 3 (FS3)	39	2002-2003
Isolated Site (IS)	179	2003
Total	430	2002-2003

Table 4.2: Genetic characterization of northern bobwhites for seven sites sampled in south Georgia and north Florida including total number of individuals analyzed (N), mean number of alleles per locus ($A \pm SE$), allelic richness ($A_R \pm SE$), observed (H_o) and expected (H_e) heterozygosity, and F_{IS} by sample site.

Population (acronym)	N	A (± SE)	A_R	H_o (± SE)	H_e (± SE)	F_{IS}
Foshale (FO)	25	7.583 (± 1.227)	6.411	0.656 (± 0.081)	0.674 (±0.075)	0.133
Pebble Hill (PH)	29	7.813 (± 1.362)	6.543	0.582 (± 0.079)	0.676 (± 0.078)	0.144
Tall Timbers (TT)	51	9.416 (± 1.416)	6.466	0.757 (± 0.048)	0.766 (± 0.045)	0.037
Farm Site 1 (FS1)	41	9.166 (± 1.313)	6.546	0.742 (± 0.060)	0.754 (± 0.050)	0.098
Farm Site 2 (FS2)	58	9.666 (± 1.606)	6.682	0.718 (± 0.060)	0.726 (± 0.059)	0.153
Farm Site 3 (FS3)	39	8.916 (± 1.311)	6.311	0.727 (± 0.054)	0.738 (± 0.045)	0.104
Buck Creek (BC)	176	11.160 (±1.664)	6.310	0.730 (± 0.055)	0.733 (± 0.054)	0.086
Total	419	9.142 (± 0.531)	6.638	0.715 (± 0.024)	0.726 (± 0.022)	0.0871

Table 4.3: Inter-population differentiation estimated by R_{ST} for northern bobwhite populations sampled in south Georgia and north Florida. Acronyms correspond to those in Table 4.1. R_{ST} values in bold are represent significant differentiation.

	FO	PH	TT	FS1	FS2	FS3
FO	*					
PH	0.0513	*				
TT	0.0239	-0.0043	*			
FS1	**0.0482**	-0.0117	-0.0077	*		
FS2	**0.0981**	-0.0077	-0.0027	-0.0023	*	
FS3	**0.0994**	-0.0014	-0.0020	0.0009	-0.0110	*
BC	-0.0090	**0.0549**	**0.0448**	**0.0954**	**0.0546**	**0.1053**

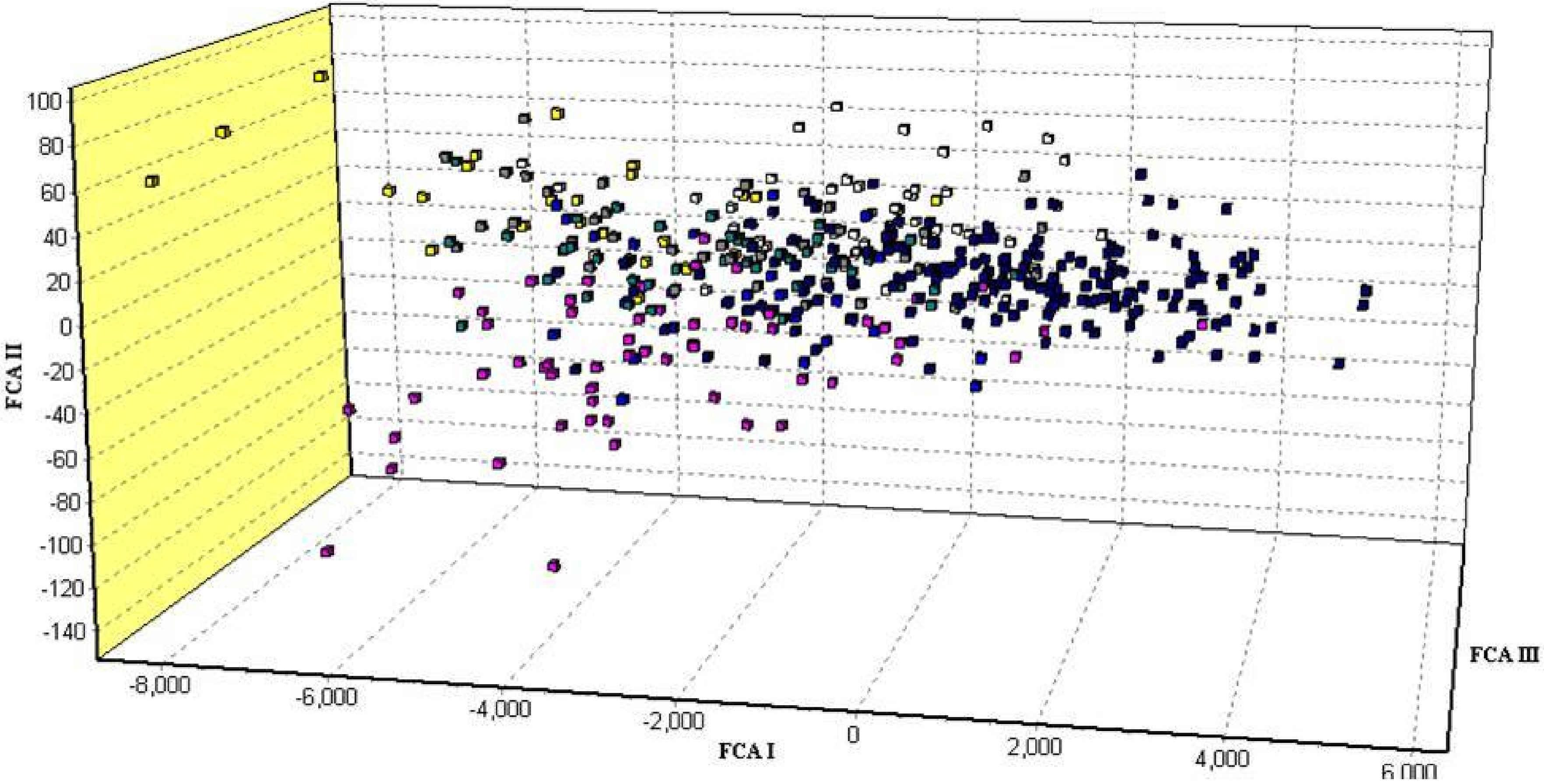

Figure 4.1: Factorial Correspondence Analysis of northern bobwhite genotypes using 15 microsatellite loci. FC I, FC II and FC III represent 33.7%, 17.0% and 15.53%, respectively.

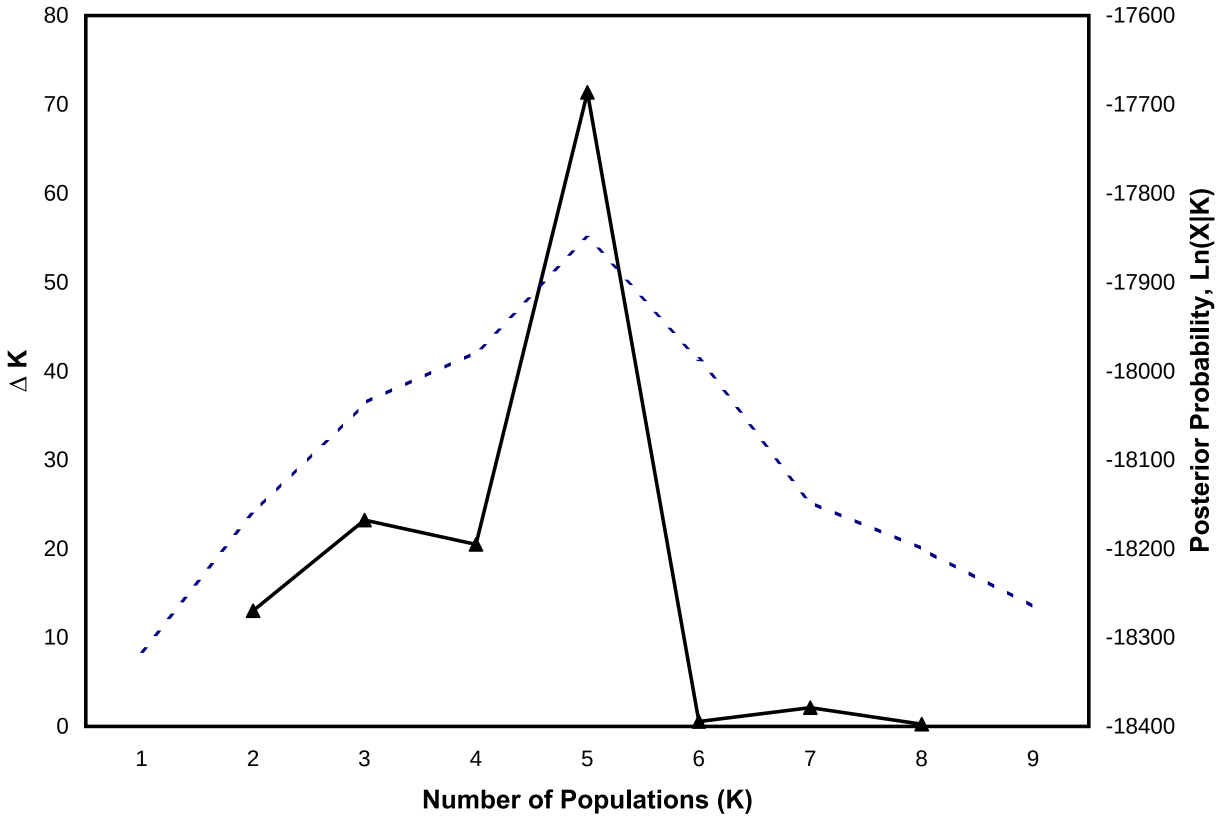

Figure 4.2: Idenfication of K=5 as the most likely genetic clusters based on the log posterior probability Ln (X—K) and second order rate of change (Δ K), estimated as model averages from 10 independent runs of STRUCTURE at theoretical cluster ranging from K=1-10.

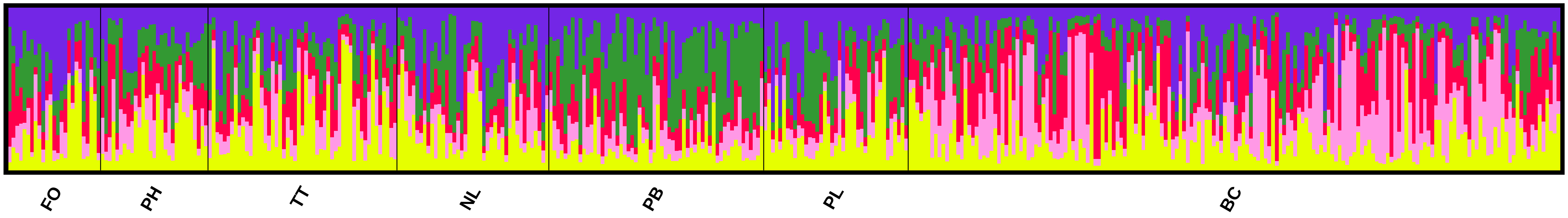

Figure 4.3: Proportion of membership for northern bobwhites inferred via Bayesian clustering using program STRUCTURE without using a priori population information and plotted with DISTRUCT. Each vertical line represents a separate individual partitioned into K = 5 clusters where each distinct color depicts a different cluster. Sections demarcated by the solid black lines distinguish groups of individuals with respect to their geographical sampling location.

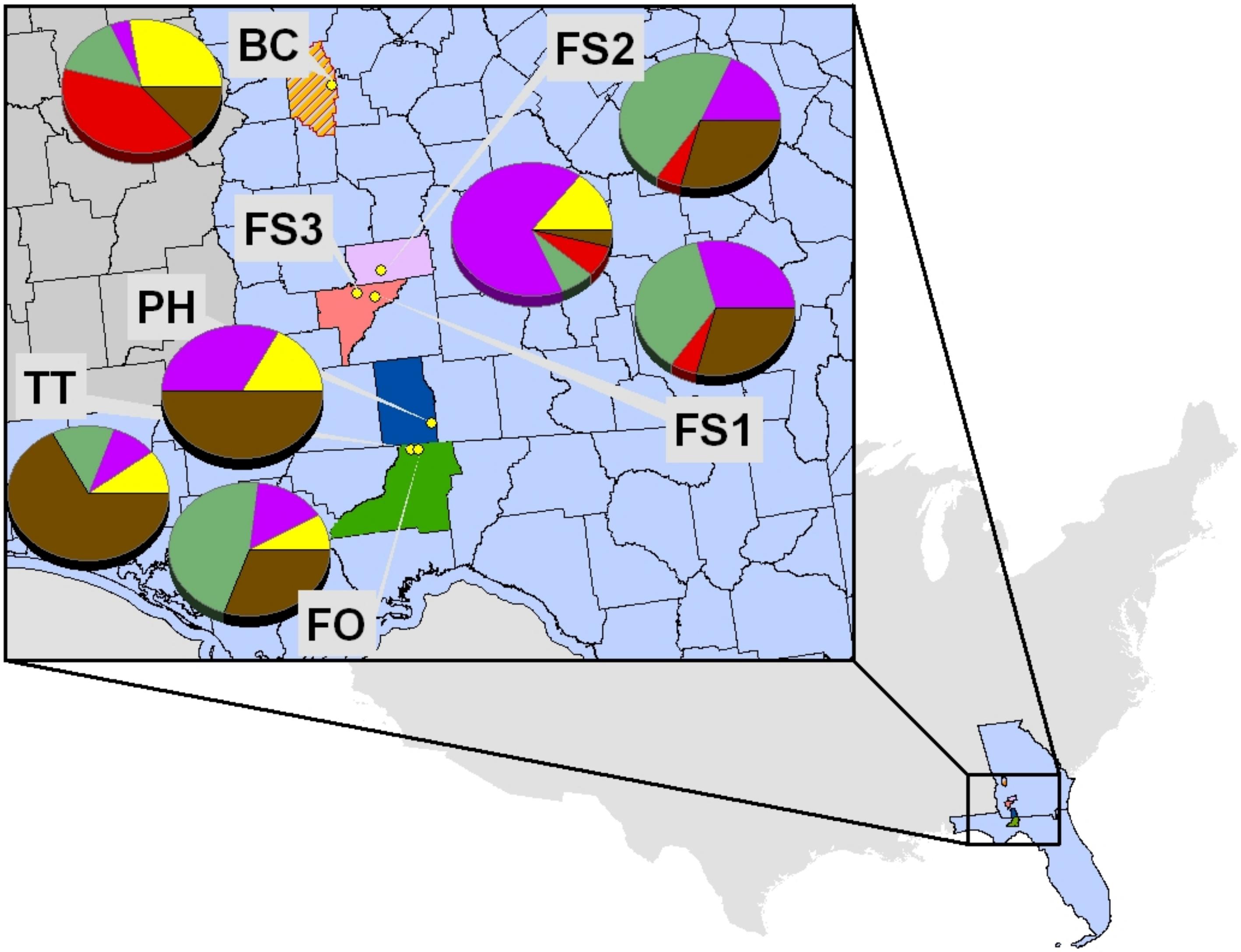

Figure 4.4: South Georgia and north Florida region illustrating sites where genetic sampling occurred during 2002-2003. Pie charts show the proportion of assigned individuals (>50% ancestry) from program STRUCTURE to each cluster delineated by geographically sampled sites (Site acronyms correspond to Table 4.1). Sampling sites are designated as follows: Buck Creek (BC) located in Marion county (orange-hatched), Georgia; Farm Site 1 (FS1) and Farm Site 3 (FS3) located in Baker county (coral shaded area), Georgia; Farm Site 2 (FS2) located in Dougherty county (lavender shaded area), Georgia; Pebble Hill (PH) located in Grady county (dark-blue shaded area); and Tall Timbers (TT) and Foshale (FO) located in Leon county (green shaded area), Florida.

CHAPTER 5

SUMMARY, RECOMMENDATIONS & CONCLUDING REMARKS

Summary

> "With the increase of the human population and the expansion of the livestock industry, came conditions less favorable to the species [bobwhite]."
>
> *Herbert L. Stoddard*

The plight of the northern bobwhite dates back many decades and is inextricably linked to anthropogenic influence. Although northern bobwhites adapted to an ephemeral ecosystem-type and inhabit variable environments that are often created by humans (Brennan 1999, Roseberry and Klimstra 1984, Stoddard 1931), the intensity of recent human influence is more ominous today than previously observed (*see Chapter 1*). Historically, bobwhites have been found in both large and small habitat patches in contiguous blocks as well as fragmented landscapes (Brennan 1999, Stoddard 1931). However, habitat fragmentation and loss due to intensification of land-use (e.g. silviculture and agriculture) and a general reduction of other beneficial practices (e.g. prescribed fire) has constrained bobwhites to isolated and small habitat patches (Brennan 1999, Brennan et al. 1998, Burger 2002). Translocation has been assumed to mitigate the potential deleterious effects associated with species residing among these habitats and has even become a common technique for conservation and restoration purposes, but its implementation has often lacked reliable scientific investigation (Griffith et al. 1989, Seddon et al. 2007). In this study, I set out to assess the efficacy of translocation in the context of genetic and demographic contribution of northern bobwhites to an isolated site in Marion county, Georgia.

The efficacy of translocation is conditional on the ability of translocated individuals to remain on the study site, survive and successfully reproduce. I did not detect differences in survival or movement between translocated and resident bobwhites, but I did identify a decrease in stratum-specific survival which was seemingly correlated with declining habitat conditions outside the target release area and off the study site altogether (*see Chapter 2*). The source of wild bobwhites did not negatively affect survival whereby survival of individuals from all three source-sites was similar to or higher than their resident counterparts. In addition, site fidelity of translocated bobwhites to the overall study site remained high, but those few individuals dispersing off the study site suffered high mortality rates. This finding suggests that habitat management is an important consideration to the success of translocation.

Translocated bobwhites nested and renested earlier than resident bobwhites, but overall reproductive effort was similar between groups (*see Chapter 3*). Nest survival and production was also similar between groups. As a result of these successes, bobwhite abundance increased throughout the study site during years following translocation and was most evident within the treatment (target) area (see Figure 5.1). However, fall abundance during 2005 on both the treatment and buffer areas declined slightly whereas the control continued to increase. This slight decline may be a result of individuals redistributing themselves evenly across the managed property, but the maintenance of fall abundance, as a whole, without an additional translocation is encouraging.

Despite the study site being located among a highly fragmented landscape, genetic variation was high and was not limited by inbreeding depression or gene flow prior to instituting translocation (*see Chapter 4*). Evaluation of multi-locus genotypes on the study site as compared to other non-isolated sites revealed that bobwhites are much more resilient to the landscape than previously thought. Although genetic variation was high among all sampled sites, some evidence of sub-structuring was identified and was more evident in the study site considered most isolated as compared to other non-isolated sites. However, substantial cluster overlap was also evident. The high genetic variation and apparent, but cryptic genetic sub-structuring observed in all of the sampled sites suggests that bobwhite genetics is complex and the identification of distinct hybrids beyond F_1 individuals is difficult following translocation - this was likely confounded by multiple releases occurring in subsequent years. Nevertheless, introgression was apparent between resident and translocated bobwhites during both years whereby the number of Bayesian clusters increased (from 1 cluster pre-release to 5 clusters following the initial translocation to 7 clusters following the final release) in subsequent sampling occasions on the study site and a reduction in the number of novel alleles unique to translocated individuals pre-release was observed among the sampled juvenile population following a single breeding season post-release. The complexity and enigmatic genetic structure observed among bobwhite populations in this study may, in part, be explained by any one or a combination of the following: long-term historical and current releases of pen-reared bobwhites, historical translocations (Stoddard 1931), the flexible mating strategy and high propensity to reproduce (Burger et al. 1995, Faircloth 2008), and recent but temporally limited population bottlenecks in some areas. Perhaps it should not be too surprising that genetic variation of bobwhites remained high even following extreme habitat fragmentation and purported population bottlenecks because the northern bobwhite adapted to and thrive in an ephemeral ecosystem-type.

This project was successful by not only improving a local bobwhite population (see Figure 5.1) but also in generating the necessary knowledge to refine the technique of translocation and answer questions regarding its pragmatic application. I believe that the success of translocation in this study was attributed more to the demographic than genetic contribution of translocated bobwhites. The demographic contribution to the fall population is largely a result of the successful breeding of translocated bobwhites. On average, the annual contribution of progeny by transolcated individuals was 287 and if only 50% (a conservative estimate) of these individuals survive to the Fall, this translates to roughly 4.5 birds per 10 ha on a 405 ha site (or a 2.4 birds per 10 ha on a 607 ha site) added to the Fall population. Because genetic variation was high on the study site prior to translocation, the hypothesis that translocation would benefit genetically depauperate populations and serve in the capacity of a "genetic rescue" could not be adequately investigated [i.e., the study site was not in need of a genetic rescue; (Tallmon et al. 2004)]. However, the identification of introgression between translocated and resident bobwhites in this study may portend that translocation may be beneficial in infusing novel alleles into populations suffering from low genetic diversity, but further research is warranted to investigate these effects. The successes observed in this study was not without: intensive habitat management occurring on the study site prior to translocation; the relatively large target-release site; and a reliable source of bobwhites available for translocation. Additionally, whereas this study did not adequately investigate the timing of release, I believe that translocation of bobwhites should be implemented prior to breeding season to improve the probability of individuals surviving long enough to reproduce.

Recommendations

> "More than 85,000 [quail] were imported in 1927 and nearly as many in 1928. . . . quail were brought into the Thomasville-Tallahassee region at least as far back as 1922, not because the native stock was depleted and restocking was necessary in consequence, but simply in the belief that to do so would improve the shooting by replacing a portion of the birds shot."
>
> *Herbert L. Stoddard*

Stoddard (1931) was perhaps the first to investigate translocation and at the time he suggested that translocating bobwhites was conducted to merely augment hunting populations. However, today the utility of translocation in most circumstances highlights the imperiled status of bobwhites. The use of translocation as a luxury (to have more birds for sport) has shifted to that of necessity (to even have birds at all). Therefore, the gravity with which we make decisions regarding the implementation of translocation should be biologically sound and empirically corroborated to ensure that it is used to complement and not become an alternative to management. The latter would without doubt exacerbate the declines rather than abate them. That said, translocation should not be applied capriciously or even be made available to everyone owning property and "wanting" a covey of quail; rather we should view translocation as a conservation tool and not a broadly-applied management tool. For instance, if, on a given site, repeated and continuous translocation is necessary to maintain a population of bobwhites then other factors are likely limiting that population and translocation should not be continued as that site may be indicative of a "habitat-sink". As biologists, we should make every attempt to avoid such scenarios.

Below I outline a few considerations and criteria derived from this study and others (Terhune et al. 2006, 2005) to help guide decisions and develop state protocols for implementing translocation as a conservation tool.

- *Legality and Permitting.* Laws regarding translocation vary by state and these laws are often confusing for landowners. Therefore, states should make available an easy-to-read document explaining the laws associated with translocation, necessary permits required, and state-developed protocols or procedures for implementing translocation. Knowledge of and compliance with state laws should ultimately be left up to individual landowners.

- *Management Plan.* To ensure proper habitat conditions on potential recipient sites and to mitigate political influence, third-party consultation (Non-profit organizations, Certified Wildlife Biologist consultants, etc.) should be a requirement to make sure that all criteria outlined in the state translocation protocol are adhered to. A management plan documenting historical and projected land-use objectives should be provided for each applicant's property. Within the management plan the following criteria should be documented:

1. *Adequate Source of Birds.* Given the declining status of bobwhites throughout much of their range, a sufficient source of wild birds may be hard to come by. It is probably most realistic for it to be the individual landowner's responsibility to identify a source of bobwhites available for translocation; however, birds being translocated should not compromise the genetic integrity of the species and therefore potential stocks should be evaluated and approved. Releases of 30 pairs (60 individuals) was used in this study and thus the release of smaller groups may not produce the expected results.
2. *Property Size.* Based on movement and site fidelity analysis in this study, I propose that the property size should minimally be 607 ha (1500 acres) and the property should additionally be contiguous. However, this is merely a lower bound and depending on the shape of the property the minimal size may need to be increased to reduce dispersal of translocated individuals off the site.
3. *Monitoring Plan.* A valid monitoring protocol should be included in the management plan prior to approval of a translocation project. Monitoring the bobwhite population on the recipient site would provide a valuable resource to track the successes and failures of translocation and help to guide future translocation protocols, refine the process of translocation and identify potential caveats to successful implementation of translocation. Monitoring should include information on the date of translocation, number of individuals released, type of release and the total number of planned releases.

- *Future Bobwhite Donor.* In order for translocation to work as a conservation tool and to increase the number of source populations available, landowners receiving bobwhites should in the future be required to provide bobwhites for future translocations.

- *Timing of Translocation.* Translocation in this study was conducted 3-4 weeks prior to breeding season, during March, and previous research (Terhune et al. 2006, 2005) proposes that this is the best time to implement translocation. However, future research investigating the timing of release and its effects on the success of translocation may be warranted to substantiate this assertion. Although I cannot discard the implementation of translocation during other periods of the year (e.g., Fall) as unsuccessful, I can submit that when translocation occurs prior to breeding season the results have proven successful.

- *Number of Translocations.* In this study, 2 translocations employed prior to breeding season during consecutive years was sufficient to elicit a population response necessary to reach a threshold where population levels were maintained without continued translocation in the third year (see Figure 5.1). Although it is ideal that no more than 2 translocations per property should be necessary, some sites may warrant more translocations to reach a threshold where population persistence occurs without the need of additional releases. However, it is important to note that the need for repeated translocation(s) may be indicative of other ecological problems limiting the recipient bobwhite population. The continued investment of translocated bobwhites to such sites ostensibly negates the utility of translocation to conserve bobwhites, as a whole, and therefore should be implemented with caution.

Concluding Remarks

> "...it is best where possible to work for the improvement of indigenous stock, for with little doubt thousands of generations of quail subjected to the laws of natural selection produce the stock best adapted to survive in any region."
>
> "Field observations show that there is a super-abundance of suitable animal life whereever the vegetation is kept in proper condition for quail ..."
>
> *Herbert L. Stoddard*

In reading his classic work, *The Bobwhite Quail: its habits, preservation and increase*, I have come to realize that H. L. Stoddard was right more times than he was not! Once again, I find myself in agreement with Stoddard (1931) regarding the notion that when habitat is properly managed, bobwhites inhabiting those habitats will have all that they need to fulfill daily and seasonal requirements as well as population persistence. Ironically, whereas human alteration of the landscape has caused the precipitous declines of bobwhites and other grassland obligates during recent decades, the onus of species preservation rests on humans to make sound decisions regarding the natural resources we enjoy to consume. The best strategy to ensure landscape-level population persistence is to preserve habitat; and the less we preserve and more we fail to manage the habitat currently supporting bobwhites, the more common local population extinction will become.

The role of translocation, while appealing, is not a panacea to northern bobwhite management or restoration and should remain *only* a conservation tool. Translocation, as demonstrated in this study, may elicit a positive demographic response and allow a site to reach a population threshold needed for long-term persistence, but its efficacy is predicated on quality habitat. That said, wildlife biologists should make every attempt to employ habitat management fostering future bobwhite populations. When habitat management has been exhausted, only then should translocation be considered. Upon consideration, one should carefully consider the species' ecology and review the criteria posited here as well as those found in other studies to best guide the successful implementation of translocation.

Literature Cited

Brennan, L. A., 1999. The Birds of North America. No. 397. A. Poole and F. Gill, eds., Philadelphia, Pennsylvannia, USA.

Brennan, L. A., Engstrom, R. T., Palmer, W. E., Hermann, S. M., Hurst, G. A., Burger, L. W., Hardy, C. L., 1998. Whither wildlife without fire? Transactions of the North American Natural Resources Conference 63, 1–11.

Burger, Jr., L. W., 2002. Quail management: Issues, concerns, and solutions for public and private lands–a southeastern perspective. Proceedings of the National Quail Symposium 5, 20–34.

Burger, Jr., L. W., Ryan, M. R., Dailey, T. V., Kurzejeski, E. W., 1995. Reproductive strategies, success, and mating systems of northern bobwhite in missouri. Journal of Wildlife Management 59, 417–426.

Faircloth, B. C., 2008. An integrative study of social and reproductive systems in northern bobwhite (*colinus virginianus*): A non-migratory, avian species bearing precocial young. Ph.D. thesis, University of Georgia.

Griffith, B., Scott, J. M., Carpenter, J. W., Reed., C., 1989. Translocation as a species conservation tool: Status and strategy. Science 245, 477–480.

Roseberry, J. L., Klimstra, W. D., 1984. Population ecology of the Bobwhite., 1st Edition. Southern Illinois University Press, Carbondale, Illinois, U.S.A.

Seddon, P. J., Armstrong, D. P., Maloney, R. F., 2007. Developing the science of reintroduction biology. Conservation Biology 21, 303–312.

Stoddard, H. L., 1931. The Bobwhite Quail: Its Habits, Preservation, and Increase. Charles Scribner's Sons, New York, New York.

Tallmon, D. A., Luikart, G., Waples, R. S., 2004. The alluring simplicity and complex reality of genetic rescue. Trends in Ecology and Evolution 19 (9), 489–496.

Terhune, T. M., Sisson, D. C., Stribling, H. L., 2006. The efficacy of relocating wild northern bobwhites prior to breeding season. Journal of Wildlife Management. 70, 914–921.

Terhune, T. M., Sisson, D. C., Stribling, H. L., Carroll, J. P., 2005. Home range, movement, and site fidelity of translocated northern bobwhite (*Colinus virginianus*) in southwest georgia,USA. European Journal of Wildlife Research 51, 119–124.

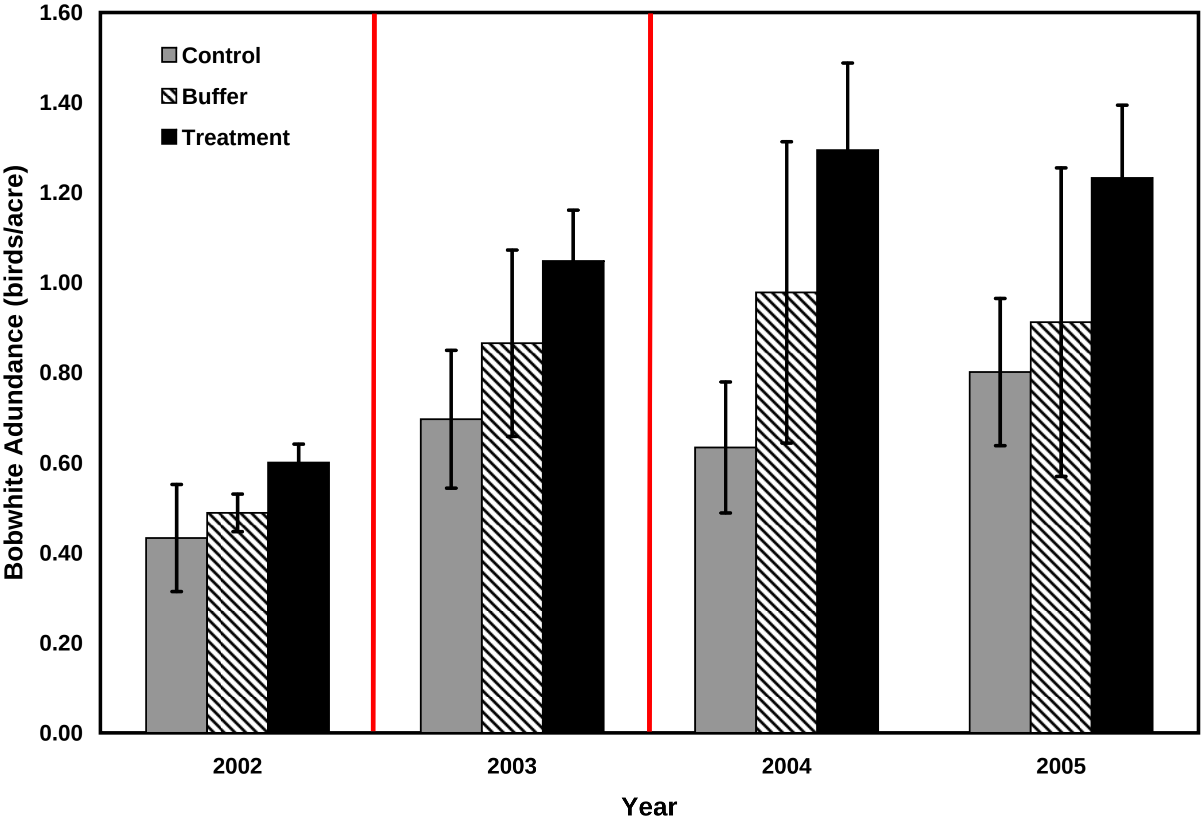

Figure 5.1: Fall abundance estimates for Buck Creek Plantation, Marion county, Georgia, prior to and following translocation. Treatment is the target area receiving translocated bobwhites prior to breeding season and red-lines indicate when translocations occurred.

APPENDIX A

ESTIMATES OF THE GENOTYPE ERROR RATE.

Table A.1: Per-locus estimates of the genotype error rate during 2003-2006 determined using a randomly selected and blindly genotyped subset of the bobwhite genetic samples collected during 2003-2006 on Buck Creek Plantation, Marion County, Georgia. Asterisks indicate markers removed from the set of candidate markers due to linkage.

Locus		Error Rate
CV-P1A7		0.000
CV-P1F2		0.022
CV-P1F3		0.011
CV-P1H12		0.000
CV-P2D7		0.000
CV-PA12A	**	0.000
CV-PA12G		0.022
CV-PA1C		0.000
CV-PA1F	**	0.033
CV-P13E		0.010
CV-PA3F		0.000
CV-PA3G		0.019
CV-PA5F		0.011
CV-PBA4		0.000
CV-PBH5		0.000
CV-PCF5		0.011

APPENDIX B

ESTIMATED WEIGHTS OF NORTHERN BOBWHITES.

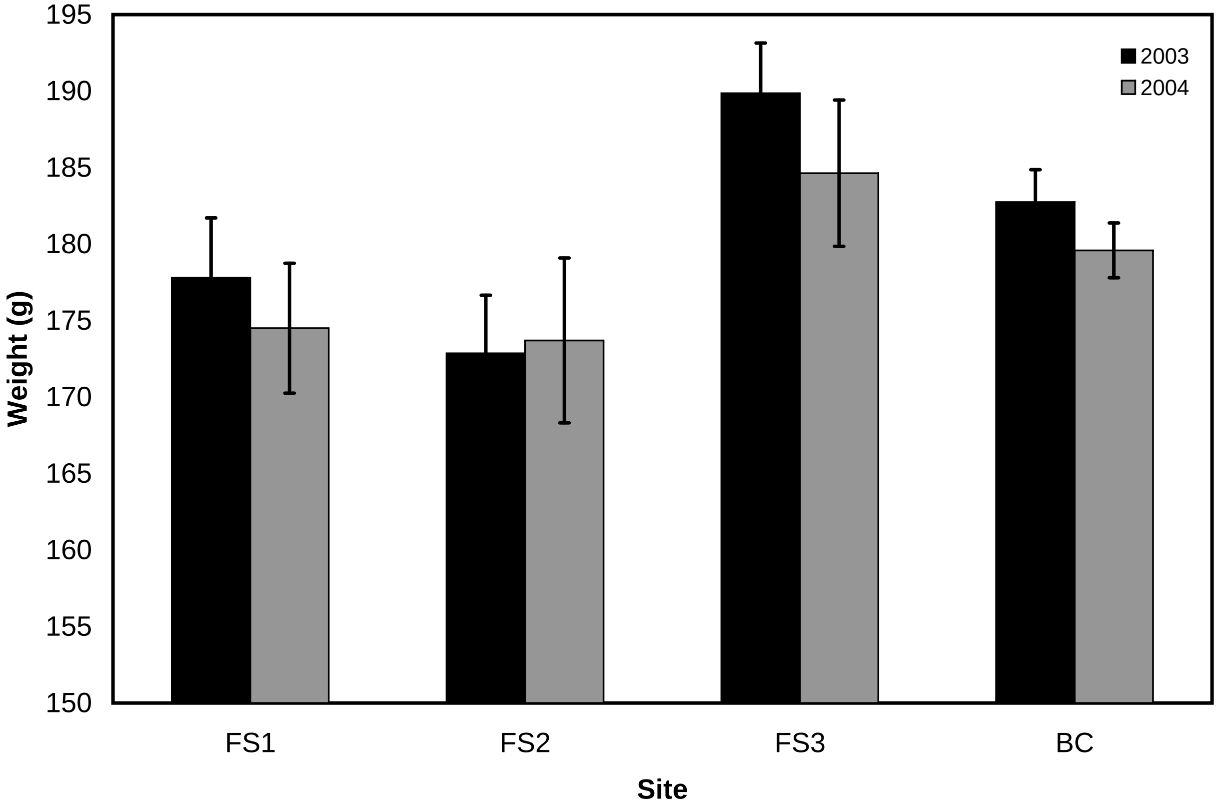

Figure B.1: Mean weights of translocated and resident bobwhites delineated by source sites (Farm Site 1 [FS1], Farm Site 2 [FS2], Farm Site 3 [FS3] and the study site, Buck Creek [BC]).