

POPULATION AND LANDSCAPE ECOLOGY OF NORTHERN BOBWHITES ON FLORIDA RANGELANDS

by

JAMES A. MARTIN

(Under the direction of John P. Carroll)

ABSTRACT

Northern Bobwhite (*Colinus virginianus*) evolved under natural disturbance regimes that constantly changed and recreated the environment. Due to anthropogenic influences, many ecosystems are different today and bobwhites likely are affected in unpredicted ways by disturbances. I investigated how disturbance size (i.e. prescribed fire size) affects bobwhite survival, reproduction, and abundance. Furthermore, I investigated nest habitat selection at multiple scales and described the ecology of bobwhites on an altered agriculture landscape. My results suggest that fire size does affect bobwhite demography and should be considered by habitat managers. I offer evidence that bobwhites fair better on pastureland than previously thought.

INDEX WORDS: *Colinus virginianus*, density, disturbance, fire, Florida, hazard rates, Northern Bobwhite, rangelands, reproduction, scale, size

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B.S., University of North Carolina Asheville, 2003

A Dissertation Submitted to the Graduate Faculty  
of The University of Georgia in Partial Fulfillment  
of the  
Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2010

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## DEDICATION

*For Skeeter, a distinguished gentleman, whose character and smile graced the presence of humanity. His passion for bobwhites was only matched by his zeal for polo. Your dedication to something larger than yourself is one measure of your kindness. May the birds flush to your side more times than not...*

*To my grandfathers, one who I never met in person, but try to live up to his name. And the other who stoked my internal passion for the outdoors. Both supply daily inspiration to walk down the path least traveled.*

*To those children out there that flip over rocks to catch crawdads, yank on vines to scare out squirrels, climb trees just because, try to catch rabbits with poorly constructed traps, and enjoy the company of an ol' dog. Keep it up. Nature's little wonders are the key to sanity. Don't be afraid to be a wolf among sheep.*

*To the bird hunter—Game you yourself have gotten . . . is food for the soul. In it are the sights, the sounds, and the smells of a landscape, the weather of a day, the companionship of a friend, your rapport with the dogs and theirs with each other, the moment when their ranging bells suddenly fall silent as they freeze on point, the memory of the rush of your blood as you walk in to make the flush and the heart-stopping instant when the bird bursts from cover and towers, the shot, the puff of feathers on the air, and, yes, that ineffable moment, compounded in equal parts of self-satisfaction and self-reproached, when the dog brings it to you and you hold in your hand the creature you both love and love to kill. William Humphrey, *Birds of a Feather**

## PREFACE

It is ironic how things tends to evolve and mutate into something very different than what you started with. That is very much the case with my graduate studies and this dissertation. The same can be said for much of central and south Florida. I came to know this place very intimately over a 5 year time span. I refer to the region as a land of contradiction. Fire often sweeps across wetlands that are full of water. A land parcel here may have been manipulated a thousand times over by man, while just across the fence, that parcel may resemble "pristine" conditions. In the winter the prairie is dry enough to build sand castles, but in the summer wet enough to jet-ski. The region is known for its quantity of beef cattle, but the soils are some of the poorest on earth. Rabbits are larger there than in northern regions, apparently one of the rare exceptions to Bergmann's rule. I have watched a turkey's head move forward while gobbling through binoculars, but heard nothing. Deer rut in the summer, but hunting season is in the winter. Nonetheless, even a farm-boy from rural North Carolina holds a small place of his heart for south Florida rangelands.

This document is a sketch of my research in the region. It is not exhaustive. The rest will hopefully appear in other avenues in the near future. Would I have done things differently? Yes, indeed. But we had to paint a wide swath on the first swipe. Little was known of the area regarding northern bobwhite ecology and how they interact with their environment. Plenty was known about bobwhites, but not in the context of this ecosystem. Dogmas and old wife's tales run deep through the region—but few address the important issues threatening bobwhites and the rangelands. Agriculture intensification (conversion of native ground to tame ground) and development threaten much of what is left of the prairie and flatwoods, making it much more complex to manage the remaining habitat

patches. Bobwhites are perhaps the only species with a large enough cultural following to make a difference. Time will only tell.

## QUOTATIONS

*The grass-after it gets old and tough-it's not much good. There's a lot of wiregrass, and when it's real good grazing [sic]. Then, I guess it kept down the palmetto some—And when the palmetto's young and tender, they would eat it.*

—Alderman 1982

*...flat and sandy with mile on mile of straight pine timber, each tree an exact duplicate of its neighbortree, and underneath the scrub palmettoes, the twisted brakes, and hammocks, and the gnarled water oaks...the land gives only a tough wiregrass, and the poor little cattle, no bigger than a donkey, wander half starved and horribly emaciated in search of it.*

—Remington 1895

*Two emaciated Texas ponies pattered down the street bearing wild looking individuals whose hanging hair, drooping hats, and generally bedraggled appearance would remind you at once of the Spanish moss which hangs so quietly and help-lessly to the limbs of the oaks out in the swamps...They had about four dollars' worth of clothes between them, rode McClellan saddles with saddlebags, and guns tied on before.*

—Remington 1895

*It is always wise to consider statements regarding the "good old days" rather carefully.*

*Nevertheless, it seems reasonable to believe that quail are not generally as abundant at present as they were several years ago...*

–Frye 1954

*The term dry prairie is somewhat of a misnomer...Dry prairies are dry only when considered relative to the other typically treeless communities of Central Florida-wet prairies...*

–Excerpt from Multi-Species Recovery Plan for south Florida

*What have we gotten ourselves into?...Well, Bill says it will work out in the slop...*

*[speaking about working on the flooded dry prairie]*

–J.A. Martin to A.B. Butler 2005

## ACKNOWLEDGMENTS

Many Native American cultures believe that it takes a village to raise a child. Completing a doctorate degree and dissertation is no different—many people helped raise this child.

Karl Miller contributed much to my appreciation of applied wildlife management and the value of teaching students about habitat. He also kept me grounded and didn't let me lose sight of the art of wildlife management. Bob Cooper instilled a logical approach to data analysis and experimental design. His gentle demeanor was always a good antidote for John's chaos. I think there are two approaches to selecting a major professor, choose one that is the most similar to one's personality and philosophy or choose the one at the other end of the spectrum. John Carroll and I are on two ends of the spectrum, but somehow we met in the middle to make it work. John, thanks for the opportunity to follow dreams I didn't know I had.

No one has influenced my professional career as much as Bill Palmer. I appreciate the long phone conversations with Bill about quail management and research. I am thankful to him for the many opportunities to expand our projects. I appreciate his candor about things I could do better. He also was inspiration on how to balance work and home life—I don't feel guilty for the hunting excursions because of Bill. Finally, Bill sold my wife and I our first English Cocker spaniel which ignited a life long compassion for the little pocket rockets.

I thank the PhD students in the Carroll lab when I arrived: Brant Faircloth, Jeff Thompson, and Theron Terhune. Collectively, they showed me the ropes and set a precedent on how to be the best over-achiever possible. Through the years Brant was helpful

with computer and software issues. Theron was helpful with analysis, Latex, and philosophical dilemmas. Theron and I continue to stay in touch and bounce ideas off of each other.

Many other students in the Carroll lab have been helpful or at least entertaining through the years: Patrick Cook, Tom Bliss, Elizabeth Doxon, Susan Felege, Seth Stapleton, Tina Hannon, Kim Sash, Bok Lee, Jena Hickey, April Conway, Rick Hamrick, Randy Cass and Jessica Rodriguez (sorry if I missed someone, there have been a lot!). Thanks for the fellowship.

Thanks to the folks in the clerical offices at Warnell and Tall Timbers for keeping me going in a somewhat straight direction when it comes to administrative duties.

A hardy thank you to Butch and Scott Beyer at Escape Ranch for their support and companionship through the years. We learned a lot together. Thanks for the tips on training bird dogs. Special thanks to Scottie for the hard work with burning. Butch and Flow, thanks for being like family to me while I was a way from home. Thanks to the rest of the Escape Ranch crew for your hard work.

Thanks to Barbara Carlton and Pat and Brady Pfeil of 2x4 Ranch for getting our research kicked off in south Florida. Its hard to believe it has been so long since it began. I was a fired up 22 year old back then and learned a lot from being around folks of your wisdom.

Thanks to Tommy Hines of the Florida Wildlife Commission for the mentorship and political support within the state. Also, thanks to Chuck McKelvy and Kurt Hodges for your support.

To all my technicians and interns through the years for your hard work and putting up with my idiosyncrasies about data collection (listed in no particular order): Ed Potter, Laura Smith, Matt "Buzz" McKinney, Josh Agee, Stephen "Tex" McDowell, David Martin, Justin Smith, Josh Harn, Page Applin, Jason "The Scrambler" Diaferio, Paul "Diet Coke" Grimes, Charlie "Chick" Plush, Justin "Penguin" Fletcher, Audrey Sweet, Jennifer Good, Chris "Paco" Yarborough, Michele Prasek, Sonny Mowbray, and Andrew Saunders.

Shane Wellendorf deserves special thanks for the multitude of logistical support given through the years and teaching me how to do telemetry. Gee thanks Shane.

On a personal level, there are so many people to thank for the opportunity and ability to complete my degrees. I became a man working on a tobacco farm for Jimmy Wilkins. Much of what I know about land and land management came from him. Also, from Jimmy I developed my work ethic. Thanks for making me pull those ragweeds up by hand in the tobacco fields in 100 degree heat at the age of 10. His partner in crime, Jim Pentecost, a retired wildlife biologist, helped lead me in the direction of wildlife management.

TR Russ, Mike Juhan, and Adam Butler deserve credit as friends throughout the last several years. Our hunting and fishing adventures helped maintain my sanity and kept me grounded on what is important in life.

I have a family that is as tight nit as they come. They have been supportive of my education from day one. It is an honor to be a member of the Martin family. I have too many relatives to list and thank but all of you deserve thanking.

To my wife, Nevena, who I ironically met only 2 days after deciding to get a PhD. That was a good week. I appreciate her love and understanding through my times of extended field seasons. She also tolerates my ever calculating mind that rarely rests even at home. She is strong willed enough to make me realize that at times I need to just be James Martin the husband and not thinker.

Lastly, my parents are responsible for every good quality I may possess while I take credit for the bad ones. My parents worked a full-time and an additional part-time job each to support my sister and I through our college years. More than money, my parents have always been there to be supportive in times of struggle and rejoice in the good times. Neither one had the opportunity to attend college, but they realized that their children needed a good education. Thanks for everything!

FUNDING SUPPORT

Mr. and Mrs. Orrin Ingram

Mr. Summerfield Johnston, II and III (Skee and Skeeter)

USDA Bobwhite Restoration Project–Mississippi State University

Tall Timbers Research Station and Land Conservancy

University of Georgia Graduate School–Graduate Recruitment Grant

Dr. Barbara Carlton and Family

Florida Wildlife Foundation

Florida Wildlife Commission

Quail Unlimited

Thank you all.

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## CHAPTER 1

### INTRODUCTION AND LITERATURE REVIEW

#### 1.1 THE NORTHERN BOBWHITE AND SOUTH FLORIDA HISTORY

[South Florida]... *a perfect place for Indians, alligators, serpents, frogs, and every other kind of loathsome reptile.*

–A surgeon for the U.S. Army fighting Seminole Indians in 1838

The peninsular region of Florida, colloquially referred to as south Florida, encompasses the 30 southernmost counties in Florida and is home to many endemic species and unique ecosystems. The high levels of endemism and uniqueness are driven by the areas's relative geographic isolation and climatic conditions (Obeysekera et al. 1999). For simplification, we will focus on the areas of south Florida that contain habitats historically and presently suited for northern bobwhites (*Colinus virginianus*); therefore, the Everglades region will not be discussed throughout this work.

Post-Columbian South Florida boasts a culturally rich tradition of "cracker cowboys" and cattle ranching in combination with other emerging agriculture pursuits. Furthermore, natural resources are typically considered valuable resources by property owners either through personal or commercial interests. Two main upland habitats are important and managed for bobwhites—dry prairie and pine flatwoods (*Pinus* spp.). These two habitat types are significant ecologically and culturally within the context of bobwhite management and research (Frye 1954). Therefore, it is important to highlight the ecological and cultural evolution of these habitats to gain a historical appreciation of the landscape changes.

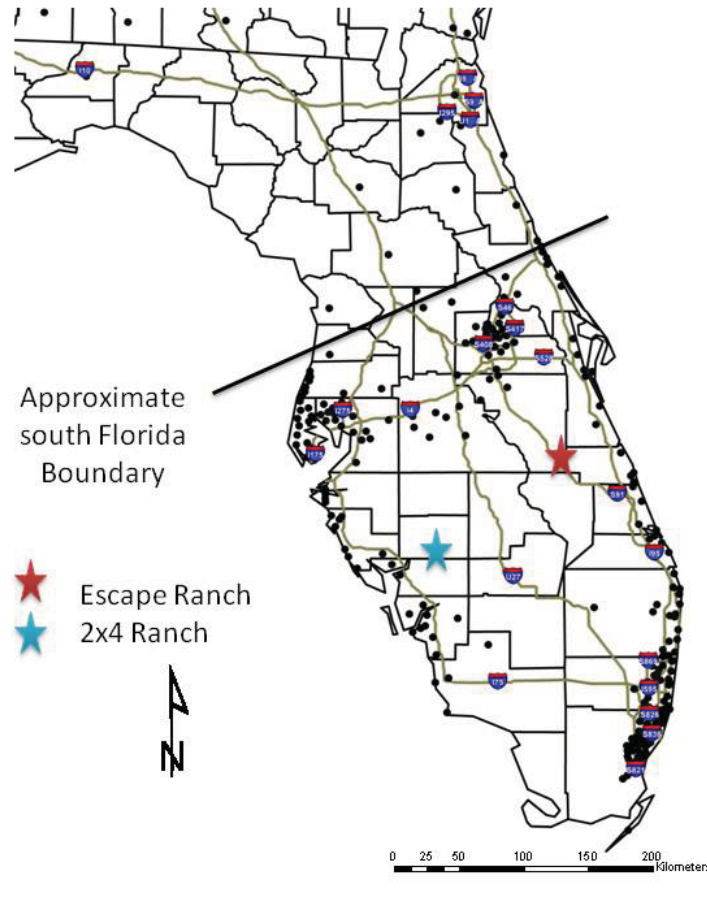


Figure 1.1: Map of south Florida referred to throughout dissertation. Solid black line indicates the fuzzy boundary that separates north and south Florida.

### 1.1.1 CATTLE INDUSTRY HISTORY

Ponce de Leon brought the first cattle to Florida in 1521 near the present day port of Ft. Meyers, but these herds of cattle were short-lived as the colonization was a failure (Yarlett 1985). There were other attempts to colonize Florida over the next several decades, but most were unsuccessful. It was not until the mid-1600s that cattle became established in present day Florida. During that time most cattle were owned by Spanish settlers for the purpose of providing beef for the Spanish military garrisons throughout the state

(Yarlett 1985). The primary areas for cattle production located near present day Tallahassee, Gainesville, St. Augustine, and along the St. Johns River. The Spanish control of the cattle industry was short-lived. In 1792, battles between England and the Spanish for control of Florida disrupted much of the Spanish progress within the area. Concurrently, Native Americans began to expand their herds of cattle (Sievers et al. 1985). By the early 1800s the cattle industry expanded dramatically as many settlers came to Florida to purchase land for cattle ranching. Large numbers of cattle were sold to Cuba for gold out of Ft. Meyers. During the Civil War, Florida's cattle was a significant asset to the Confederate army, although, this consumption reduced the cattle herds substantially. These low cattle levels were maintained until the 1920s (the onset of tick fever and eradication) and continued until 1935.

Concurrent with the eradication of tick fever, ranchers began using fences to separate herds, a necessity for the eradication effort. These fences were novel to Florida because ranching up to that point was open-range. Fence laws did not come into effect until 1949. Open range ranching is quite different than contemporary ranching (Mealor and Prunty 1976). Open range ranching negated the necessity of owning large tracts of land. Typically, a cattleman owned an average of 160 acres (Mealor and Prunty 1976), but the cattle were able graze over several square miles of range. This system required the cattlemen be able to hunt the cattle several times a year for health checks and head counts (Yarlett 1985). Therefore cattlemen, locally identified as cracker cowboys, needed to be excellent horsemen and often needed the assistance of cattle dogs. In addition to the occasional round-up, prescribed fire was the predominant management tool used by the traditional rancher (Mealor 1973). Ranchers typically burned one-third of the range each year in the late fall and early winter. Winter burns were used because of the favorable weather conditions to safely conduct burns. Burning the range in this fashion would have created a mosaic of habitats on the landscape. Cattle would have preferentially grazed the recent burned areas and left the unburned areas virtually untouched (Vinton et al. 1993).

The change from open-range ranching to fenced cattle production impacted the vegetation structure on grazed acres (Mozley 1985). Indisputably, with the advent of fencing came the emergence of "improved pastures"—a misleading term for acreage converted from native vegetation to an exotic forage to increase carrying capacity. Many exotic grasses were introduced such as carpetgrass (*Axonopus* spp.), common bermudagrass (*Cynodon dactylon*), and bahia grass (*Paspalum notatum*). By the late 1950s, cattle numbers were increasing and overall beef production was on the rise. Simultaneously, the early exotic grasses were being replaced by higher yielding species including Pangola grass (*Digitaria* spp.), star grasses (*Cynodon nlemfuensis*), and *Hemarthria*. During the next 20 years, the cattle industry successfully eradicated screw worm (*Cochliomyia hominivorax*) and cattle weights increased by almost 100 percent through breeding programs and improved husbandry. However, during the 1970s costs of managing improved pasture were increase and many ranchers began to view their native range as a valuable grazing resource. Many ranchers began an integrated system of grazing native range and improved pasture with the same cow herds. In south Florida, the improved pasture acreage changed from vast acreage of Pangola, stargrass, and *Hemarthria* grasses to bahia grass. Bahia required fewer inputs to maintain and therefore remains the dominant grass on improved pasture today.

Cattle ranching and bobwhite management were synonymous for most of the last century (Frye 1954). The tools used for forage production were complimentary to those used for bobwhite habitat management (e.g. prescribed fire). In fact, little directed management was conducted specifically for bobwhites. Hunttable bobwhite numbers (>1 quail/5 acres; William E. Palmer, personal communication) were an accidental by-product of applying prescribed fire to the landscape for cattle production. However, with the conversion of native rangeland to "improved pasture", cattle production and bobwhite management diverged. The remaining native patches received little management attention, and the grazing pressure on these areas began to show chronic signs of degrading their suitability

for bobwhites. Currently, the ability of ranchers to manage for bobwhites and cattle is a matter of personal objectives and economic constraints.

### 1.1.2 ECOLOGICAL BACKGROUND

The pre-Columbus extent of the dry prairie was believed to be approximately 0.83 million ha (USFWS 1999), but now likely covers only half of the historical range and is decreasing at a rapid pace. This destruction of native flatwoods and dry prairie is the equivalent of cutting down virgin old-growth timber, but receives much less attention among ecologists and conservationists.

Some debate exists on the ecological differences between pine flatwoods and dry prairie, and the possibility that these two communities may have been naturally similar. However, recent investigations concluded that dry prairie and pine flatwoods are indeed different natural communities—dry prairies are not just flatwoods that were cut-over. However, the ecological factors driving the differences between dry prairie and flatwoods are not well understood. Soil types explain little variation in the occurrence of the two communities—both occur on alfisols and spodosols (Bridges 2006). The current model being used to discern differences in the two habitat types is based upon climatic conditions and fire history (Bridges 2006, Platt et al. 2006). Pine advancement into current dry prairies has been stymied by landscape fires and the changing south Florida climate over the last 10-15,000 years. Evidence based on pollen cores suggest that up 5,000 years B.P. south Florida was more xeric and was dominated by oaks (*Quercus* spp.). Around 5,000 years B.P., pines became more prevalent and began to expand in range (Bridges 2006). However, the advancement of pines was slowed by frequent fires and hydrological factors (Bridges 2006, Platt et al. 2006). This struggle between dry prairie and flatwoods would likely continue today; however, landscape fragmentation and alterations to the fire and hydrological regime prohibits the natural change (Walker et al. 1997). Functionally, flatwoods and dry prairie are ecological equivalents for bobwhites with the exception of flatwoods that have

reached excessive timber volume ( $> 25 \text{ m}^2/\text{ha}$ )—conditions that are very rare even under today's management scenarios.

## 1.2 LITERATURE REVIEW

### 1.2.1 NORTHERN BOBWHITE DECLINE

The decline in northern bobwhite decline is well documented for the past 40 years (Brennan 1991, Sauer et al. 2005). However, prior to the North American Breeding Bird Survey, there is little empirical evidence regarding the population trend for northern bobwhites. This is unfortunate because some anecdotal evidence suggests that bobwhite populations have been in decline for over a century (Guthery 2002). Early bobwhite biologists (see Stoddard, Errington, and Frye) reported regional declines in bobwhite populations in the early part of the 20th century. Therefore, what we are experiencing today is likely only a snap-shot in time of a long-term decline. It is plausible that some of the decline today is a reflection of a longer-term ecological phenomenon in bobwhite populations. However, scientists agree that the recent trends are much steeper and are directly tied to anthropogenic change in the landscape (Brennan 1991, Brennan and Kuvlesky 2005, Rollins and Carroll 2001, Roseberry and Sudkamp 1998).

Although a casual relationship for the and bobwhite population decline has not been elucidated by the research community, correlative data exists. Throughout the range of bobwhites habitats have changed dramatically. (Brennan 1991, Brennan and Kuvlesky 2005) due to agricultural intensification, agricultural extensification, disruptions of natural disturbance regimes, afforestation of the southeast through pine plantations, and urbanization. These factors have been exacerbated by an increase in predation pressure [(Rollins and Carroll 2001); William E. Palmer, personal communication]. Within south Florida it is likely that all these factors have contributed to bobwhite decline with perhaps afforestation being the only exception. However, the flatwoods and dry prairie of Avon Park Bombing Range have been planted to thousands of hectares of slash pine plantations.

Row crop agriculture is an important land use in south Florida, but differs from the classical agriculture found throughout much of the US (Hodges et al. 2006). Vegetable farming is the predominant row crop within the region. However, most of it occurs on muck soils in drained marshes that historically would not have been bobwhite habitat. The vegetable farming conducted in upland settings is fugacious and is normally immediately followed by planting to pasture. Ranchers used farmers as a low cost conversion instrument to convert native rangeland to pasture. Therefore, agricultural intensification affects bobwhites in a different context. Cattle stocking rates (Capece et al. 2007) have increased in time with the advent of fencing and supplemental food resources. The increase in cattle density like has affected plant communities within native habitats, although little data exists on this subject.

Agriculture extensification has affected bobwhite habitat within the region via the conversion of native habitats to pastureland. Pastureland has replaced over half of the once existing flatwoods and dry prairie ecosystem. Ecologically, pastureland is in direct odds with bobwhite adaptations (Flanders et al. 2006). The exotic grasses that make up the pastureland provide little food or cover for bobwhites. Bobwhite mobility is affected by these grasses, and is inhospitable under high temperatures (Burkhart 2004). On the landscape level, pasturelands are typically juxtaposed with native habitats creating patches of habitat throughout large landscapes. This fragmentation of native habitats has likely degraded the viability of populations within remaining habitat patches.

Much debate exists on the definition of natural disturbance regimes regarding grassland habitats in the Southeast. Because wildlife management should be objective based (Burger 2006), tools such as prescribed fire should be used to reach a pre-defined objective for vegetation and subsequently bobwhite populations. However, the evolution and adaptation of vegetation should be considered regarding disturbance regimes. South Florida has a very defined season when lightning occurs, beginning in late March and peaking in June (Platt et al. 2006). Concurrently, for the first 6-8 weeks of lightning onset rainfall is

limited, creating a situation of dry fuels and an ignition source (see Figure 1.2). Fire scar records from Avon Park Bombing range indicate that lightning season fires were common and occurred on average every two growing seasons (Wayne Taylor, unpublished data), suggesting that lightning season fire was important in the evolution and adaptation of south Florida vegetation. However, anthropogenic ignition is equally important in fire history. As previously stated, European colonization occurred approximately 500 years ago in south Florida, and settlers adapted the landscape for cattle production via fire. Before Europeans, Native Americans used prescribed fire throughout Florida for various objectives. Substantial evidence exists on the role of Native American fire throughout much of the eastern US and the tall grass prairie of the Midwest (Abrams and Nowacki 2008, Nowacki and Abrams 2008). However, in south Florida, Native Americans were associated with the coastline, perhaps negating the need of prescribed fire. Therefore, south Florida may be one area of the Southeast that lightning season fire shaped vegetation more so than anthropogenic sources of ignition.

### 1.2.2 FIRE EFFECTS ON BOBWHITES

As previously mentioned, Stoddard (1931) was the first to establish empirical evidence that bobwhite populations respond favorably to frequently burned pine forests. Frye (1954) was the next investigator to report on the overall benefits that burning can have for bobwhite populations in south Florida. Rosene (1969) and Speake (1966, 1967) soon followed with investigations in the plantation country of South Carolina, Florida, Georgia, and Alabama. With the exception of Stoddard, these author's work have largely been overlooked in the cited literature. This is likely because their work was never published in mainstream peer-refereed literature. Furthermore, most their work was mensurative and lacked experimental rigor that we today perceive as necessary. But these works helped to develop a body of evidence supporting the idea that bobwhites and fire are compatible under most conditions, especially in the southeast.

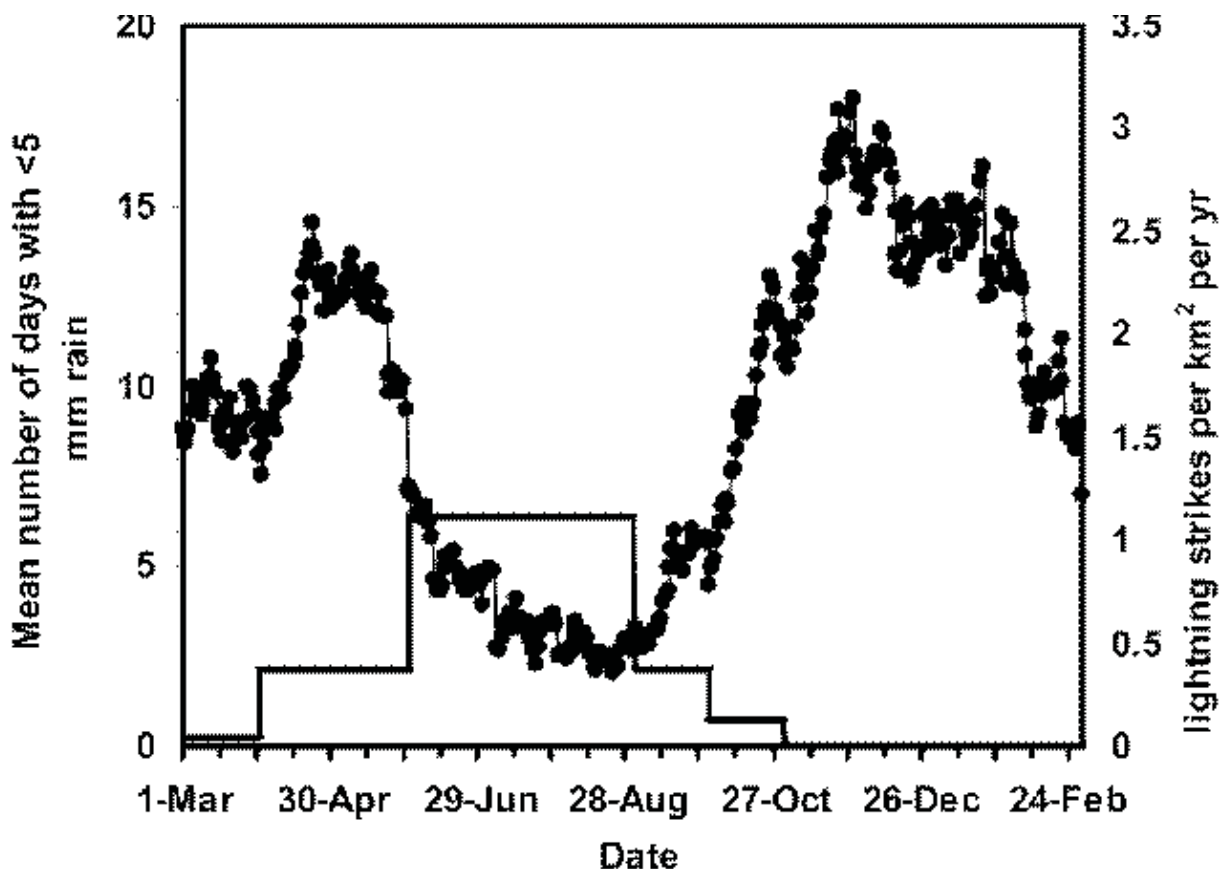


Figure 1.2: The mean number of successive days with <5 mm rainfall for a given day of the year (black dots) plotted against the successive dates in a year. The histogram is the mean number of cloud-ground lightning strikes per km<sup>2</sup>. Data was taken near Sarasota, Florida for the period 1944-1997. Graph taken from Platt et al. 2006.

The frequency that fire is applied to a given area for the purpose of bobwhite habitat management has been mostly based on anecdotal evidence and on the growth rates of the vegetative communities normally managed for bobwhites. Typically, fire is applied on an every other year basis to any given patch of habitat. However, some variation exists from region to region and property to property (Landers and Mueller 1986). In areas of higher soil productivity fire return intervals may be 18-24 months at maximum, while at lower soil productivity fire return intervals may be >36 months. Fire frequency dictates the seral stage of the vegetation which in turn dictates what is optimal for bobwhite

fitness (Spears et al. 1993). Nonetheless, a casual relationship between fire frequency and bobwhite populations has not been developed in the published literature.

The effects of growing season fire versus dormant season fire have been investigated on multiple occasions (Brennan et al. 2000, Engstrom et al. 1996, Folk 2006). However, these studies were not necessarily experimental, and they conflict on the impacts of growing season fire on bobwhite populations. Brennan et al. (2000) suggested that growing season fire resulted in higher hunting success the following fall. While Engstrom et al. (1996) reported preliminary findings that growing season fire had adverse effects on bobwhite relative abundance. Anecdotal evidence exists for negative effects of growing season on bobwhite abundance (Rosene 1969, Stoddard 1931), but others including this author report thriving populations in areas managed with growing season fire (see Escape Ranch and Disney Wilderness Preserve). The effects of fire season on other grassland ground nesting birds is more understood (Howell et al. 2008, Thatcher et al. 2006, Tucker Jr et al. 2004, 2006). Most studies indicate a positive or neutral response of the population metric of interest to growing season fire. This is no surprise considering many grassland birds evolved in pyrogenic ecosystems that likely experienced lightning-induced fire events (Brennan and Kuvlesky 2005).

Perhaps the most overlooked aspect of prescribed fire management for wildlife is the scale or extent (fire size) to which fire is applied. Fire size and scale are two slightly different issues. Fire size is simply the land area burned contiguously at one time. Scale is slightly different because it is related to how large the fire is in relation to the amount of habitat available to a given species in the immediate landscape. For example, consider two habitat patches of unequal size, 100 ha and 1000 ha. If a 10 ha fire was applied to each patch the fire size would be the same for both burns (i.e. 10 ha), but on the larger patch the fire would be on a much smaller scale (i.e. 1% versus 10% for the smaller property). The terms fire extent, scale, size will be used interchangeably from this point forward, but note the slight differences in the terms.

Theoretically, an individual's fitness (plant or animal) is likely related to disturbance extent and therefore for a species an optimal disturbance size should exist (Miller 1982). In practice, we will likely never know to which scale or extent animals are most adapted to, but can establish a range of conditions to manage under (see Figure 1.3). We have little empirical data regarding what range of fire extent values bobwhites are best suited. Conventional bobwhite management on plantations apply fire at small extents of 5 to 25 ha with some outliers at larger extents (50-100 ha; William E. Palmer, personal communication). However, public land managers conduct fires at much larger extents, > 1000 ha, but typically manage at larger operational scales. It has been argued that these larger fires are more natural and mimic conditions that bobwhites and other disturbance dependent species evolved (Perera et al. 2007). The argument of what constitutes a "natural" fire is an argument itself, but the issue of fire scale is worth further discussion. Under conditions of large "natural" fires the burned patches were an island in a sea of habitat, but today the burned patches are on an island of habitat in a sea of non-habitat. The paradigm needs to shift from acres burned counting (ABC) to applying fire at scales and sizes that meet ecological objectives for the given area (EOFM: ecological objective-driven fire management). Simple ABC management can result in habitat for a number of species, but likely is inefficient in providing habitat for the most species across a variety of spatial and temporal scales.

### 1.3 JUSTIFICATION AND PURPOSE OF STUDY

A plethora of research exists on northern bobwhite ecology throughout most of its distribution. However, little research exists for bobwhites in south Florida. Given the uniqueness and isolation of south Florida bobwhite populations it is important to investigate the ecology of bobwhites in the region, and provide scientific evidence for the over-arching theories of bobwhite ecology. Bobwhite management is still culturally important within the region. Furthermore, the Florida Wildlife Commission (FWC) manages several large

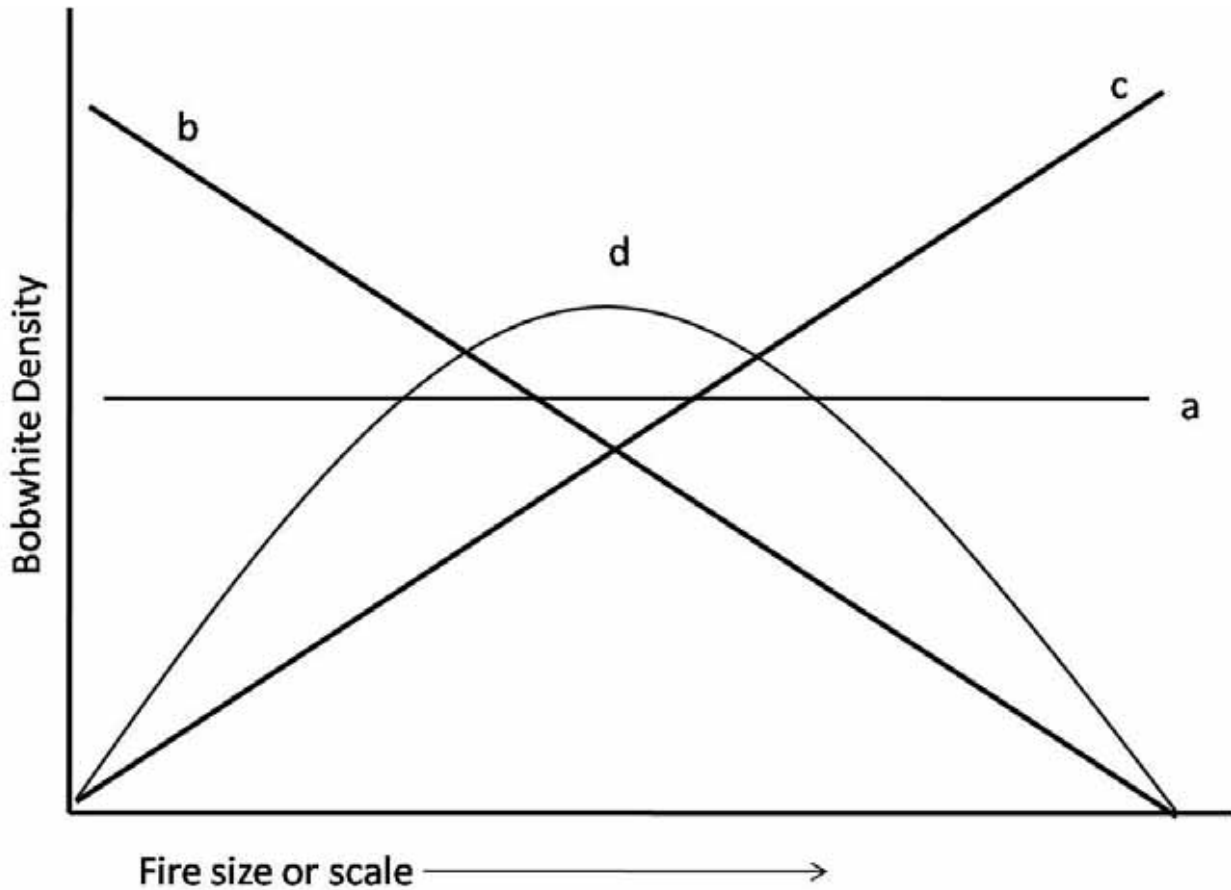


Figure 1.3: Four possible models of the relationship between fire size or scale and bobwhite density. Each letter indicates a different relationship.

wildlife management areas (WMAs; >10,000 ha) for bobwhites. However, these WMAs struggle to meet the hunting demand of the hunting constituency because of high demand and low bird supply. Results from this study will likely be used to improve management on those areas. Throughout this research, I cooperated with over a dozen ranch managers or owners representing over 100,000 ha. It is perceived that these individuals will use a great deal of the information gathered from the research to improve their management for bobwhites. Lastly, the United States Department of Agriculture Natural Resource Conser-

vation Service (USDA-NRCS) is keenly interested in incorporating this research into their programs.

#### 1.4 OBJECTIVES

The studies described in this dissertation were designed to address the following objectives:

1. Establish baseline population level parameters for northern bobwhites in south Florida.
2. Investigate the effects of fire extent on northern bobwhite nest survival.  
Ecological hypothesis: Nest survival will decrease with increasing fire size.
3. Investigate the effects of fire extent on northern bobwhite adult survival  
Ecological hypothesis: Adult survival will decrease with increasing fire extent.
4. Describe nesting habitat used and preferred by northern bobwhites  
Ecological hypothesis: Bobwhite's nest will be constructed at random regarding habitat conditions and structure, with some evidence that more dense vegetation is preferred.
5. Investigate northern bobwhite densities in relation to fire size  
Ecological hypothesis: Bobwhites will be more abundant on sites managed with small fires opposed to larger fires.

## 1.5 STUDY PLAN

### 1.5.1 STUDY AREAS

Two study areas were used for the research described throughout this dissertation, 1) a five-county focal area centered around Arcadia, FL, USA, and 2) a 5,000 ha private ranch approximately 1 km east of Kenansville, FL, USA.

The climate in south Florida is subtropical and humid with average annual temperatures in the mid-20s C, ranging from about 16 C in midwinter to about 27 C in summer. Rainfall averages about 137 cm, with 50 to 60 % of it occurring from June to September (USFWS 1999).

#### FOCAL AREA

The five county focal area included Desoto, Sarasota, Hardee, Highlands, and Charlotte counties. These counties were part of a Federal and State government focal area for bobwhite restoration using Farm Bill programs, specifically the Environmental Quality Incentive Program (EQIP). These counties were chosen because they included some of the historical range of dry prairie, and a perceived landowner interest in bobwhite management. My research was conducted on six selected properties throughout the focal area which totaled over 50,000 ha. The nature and extent of the study region did not allow for random selection of study ranches—we cooperated with every willing landowner. Five of the properties were privately-owned cattle ranches, and the other was a state-owned park. Management was very similar on all properties except for the presence of livestock on the private property, and the park used lightning season fires in addition to dormant season fire. Dry prairie and exotic grass pasture were the dominate habitat types on the properties. The cattle operations were cow-calf systems with stocking rates (AU) ranging from 0.2-1.0 AU/ha.

## PRIVATE RANCH

The private property is managed predominately for bobwhite habitat and hunting. Cattle were excluded from the quail management areas, and had been for approximately 7 years. The predominant habitat type on the ranch is mesic-pine flatwoods, and exotic grass pasture (i.e. improved pasture). The quail management areas have historically been burned on a 2-3 year return interval within the traditional winter season (January-early March). However, in the 2-3 years prior to my study the burning program had become lackadaisical. Therefore, the understory vegetation had shifted towards a shrub community dominated by saw palmetto (*Serenoa repens*). The flatwoods had an over-story of predominately longleaf pine (*Pinus palustris*) and some pockets of South Florida slash pine (*Pinus elliottii* var.*densa*). The ranch supplementally feeds bobwhites on a two week interval at approximately 1-2 bushels/ha/year with grain sorghum (*Sorghum* spp.). Predators were removed throughout the year using live-traps at a rate of 30,000 trap nights per year. Bobwhite hunting on the ranch occurred approximately 2 days a week for the duration of the hunting season—a hunting course was rarely hunted more than once per week. The harvest rate never reached above 10 % of the pre-hunting season population. Upon initiation of the study, I developed a prescribed fire plan for the entire study area. The study area was broken down into three main units that represented a level of fire scale: small (10 ha), med (20 ha), and large (40 ha). Within each unit each patch was randomly assigned a fire season: dormant (January-April 15th) or growing season (April 15th - August 15th). The burn plan was determined for each year of the study and was adapted slightly each year to accommodate pragmatic issues of implementing the burns. Any given patch was burned on average twice during the three years of the study, and optimally burned in two different seasons. The burn plan, not the known presence of nesting bobwhites or other extraneous considerations in a given patch, guided the implementation of burns on a daily basis.

## 1.6 GENERAL METHODS

### 1.6.1 DATA COLLECTION SUMMARY STATISTICS

Data included in this dissertation was collected from March 2004 to December 2008, which encompasses four breeding and non-breeding seasons for bobwhites. During this time 365 covey call surveys were conducted with 1280 covey detections. Also, 1047 bobwhites were captured, of those 409 radio-tagged (119 males and 290 females); 17,130 telemetry locations, of those 3,512 are brood locations, and 140 nests monitored.

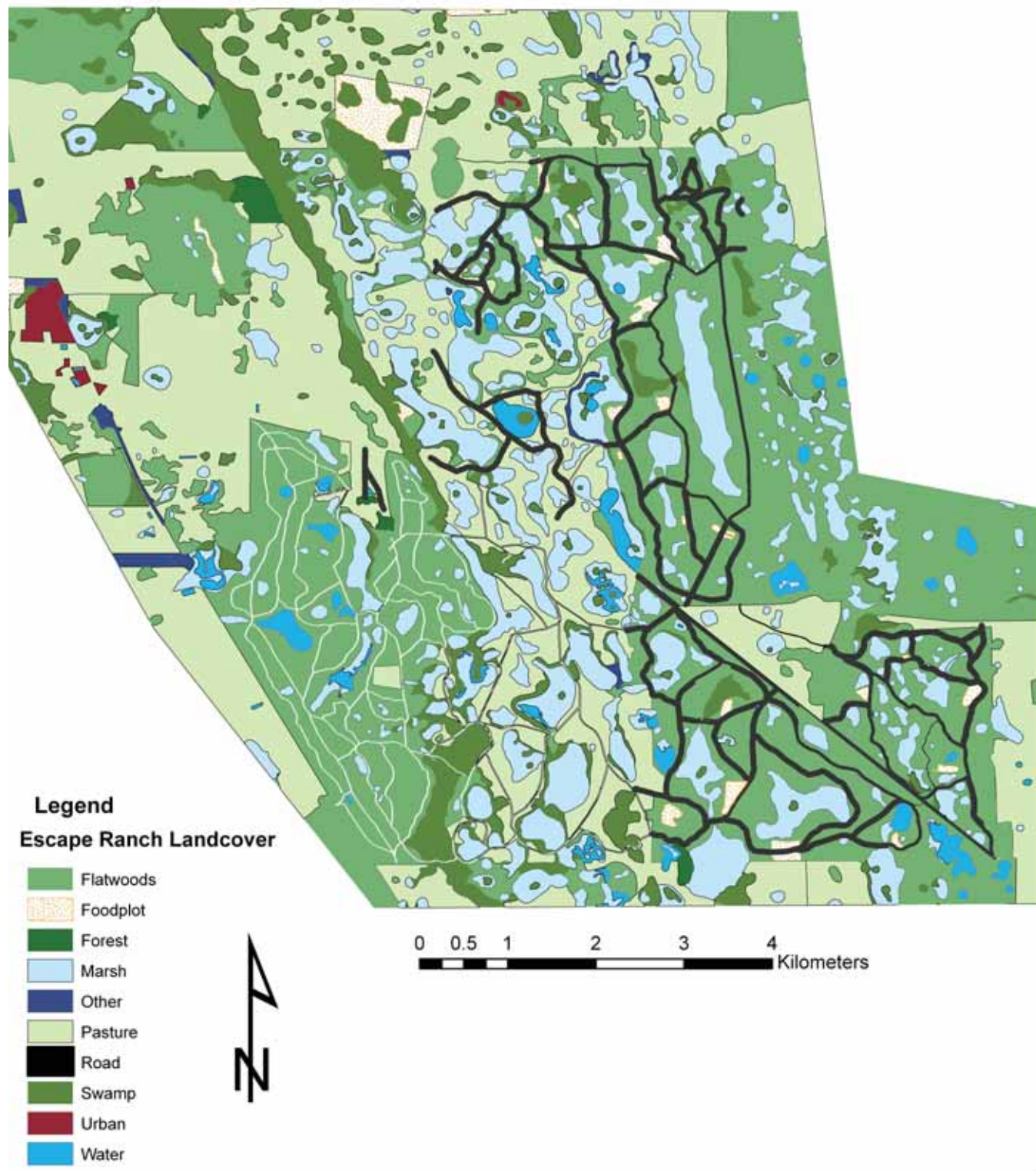


Figure 1.4: Landcover map for Escape Ranch, Florida, US, 2008. Mapping data came from digitizing aerial photos and Landsat 2004 imagery.

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## CHAPTER 2

# REPRODUCTIVE ECOLOGY OF NORTHERN BOBWHITES ON SOUTH FLORIDA RANGELANDS: AN ANALYSIS OF BURN SIZE<sup>1</sup>

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<sup>1</sup>J.A. Martin, W. E. Palmer, and J. P. Carroll. To be submitted to: *Journal of Applied Ecology*.

## 2.1 INTRODUCTION

Prescribed fire is an often used habitat management tool for northern bobwhites (hereafter, bobwhites; *Colinus virginianus*), especially for pine (*Pinus* spp.) savannahs of the Southeast (Brennan et al. 1998, Buckner and Landers 1979, Christensen 1981, Outcalt 2008, Platt et al. 2006, Stoddard 1931). The use of fire for bobwhite management is based on cultural, practical, and some empirical evidence that without fire bobwhites would not be able to persist (Engstrom et al. 1984, Folk 2006, Speake 1966, Stoddard 1931). However, the use of fire in most contexts is typically guided by historical tradition (Putz 2003), and less so by objective-driven land management. This type management is advantageous for most species adapted to the pyrogenic pine forests, but can be deleterious under some circumstances. Furthermore, fire management guided by tradition will not be optimal in today's environment.

The spatial and temporal patterns of prescribed fire are driving factors at any spatial scale, because they likely determine successional status, age distribution, and grain of the vegetation covering the landscape (Niklasson and Granstromm 2000). The spatial pattern dictates the dispersal distances for colonizing organisms (Moloney and Levin 1996, Turner et al. 1997) and the survival of those organisms. The proportion of area burned may be a key variable describing bobwhite demography. Niklasson and Granstromm (2000) made a key assertion that the proportion of the area burned per time unit is affected by two variables: the number of fires per unit time, and the size of the individual fires.

We believed factors other than fire would influence bobwhite nest survival; therefore, we included covariate information into our models. The published literature is scant on information regarding bobwhite nest survival, especially in the eastern portion of the population range (however, see Parnell 2002, Puckett et al. 1995, White et al. 2005). In the Mid-west and Southwest, several authors have described the importance of numerous fine scale habitat features for nest survival (Lusk et al. 2006, Rader et al. 2007, Taylor et al. 1999, Townsend et al. 2001). But it is likely that differences exist between the ecological

drivers for survival between subtropical or temperate areas of the Southeast versus more arid ecosystems of the Southwest. Nest survival in subtropical systems is likely driven by fine scale habitat characteristics, climatic conditions, coarser scale habitat conditions, habitat management, and interactions among those drivers (White et al. 2005). Under most circumstances, eastern subtropical habitats do not lack sufficient cover for nesting bobwhites, but may lack the quality of cover they potentially seek. In the Southwest, it is believed that > 600 nest sites/ha is a minimum amount of nesting cover (Hernandez et al. 2003). This threshold can be met on a majority of old-field or native ground cover settings in the Southeast. Lastly, landscape context has been found to be important for survival of other ground nesting species as well with bobwhites (Staller et al. 2002, Stephens et al. 2005, White et al. 2005).

In conjunction with habitat structure (small and large scales), weather factors likely play a role in nest survival. Rader et al. (2007) in southern Texas found that bobwhite nest survival was positively affected by the cumulative amount of precipitation and temperature. However, in south Florida these parameters are likely to affect nest survival in an opposite fashion because of regional habitat characteristics. Nonetheless, it is plausible that nest survival is driven by climatic conditions. Historically, these variables would have been viewed as "nuisance" parameters and unrelated to management. However with global climate change scenarios, predicting demographic responses to climatic conditions will likely prove an important exercise as managers are forced to manage in the future under changing conditions. Furthermore, these factors are even more relevant to south Florida. The natural hydrology regimes of south Florida have been severely compromised in the last century (Obeysekera et al. 1999). Much of the habitats used by bobwhites have been affected by an altered water flow during the rainy season (i.e. nesting season). We hypothesized that the cumulative rainfall experienced by a nest would be related to local flooding and wetland water levels that would influence predator movements.

In an manipulative experiment, we studied bobwhite nest survival and reproductive rates in response to changes in the size of fires while keeping the proportion of the area burned constant. Additionally, the season of fire for each patch of habitat was considered a quasi-experimental component to our study. The percentage of growing season and dormant season burns were kept constant to avoid confounding effects of season. The objectives of our study were to, (1) describe factors that drive nest survival and (2) compare fecundity of bobwhites in response to prescribed fire size.

## 2.2 METHODS

### 2.2.1 STUDY AREA

The climate in south Florida is subtropical and humid with average annual temperatures in the mid-20s C, ranging from about 16 C in mid-winter to about 27 C in summer. Rainfall averages about 137 cm, with 50 to 60 % of it occurring from June to September (Obeysekera et al. 1999, USFWS 1999).

The study area is managed predominately for bobwhite habitat for hunting. Cattle were excluded from the quail management areas, and had been for approximately 7 years. The predominant habitat type on the ranch is mesic-pine flatwoods, and exotic grass pasture (i.e. improved pasture). The quail management areas have historically been burned on a 2-3 year return interval within the traditional dormant season (January-early March). However, the 2-3 years prior to our study the burning program had become less consistent. Therefore, the understory vegetation had shifted towards a shrub community dominated by saw palmetto (*Serenoa repens*). The flatwoods had an over-story of predominately longleaf pine (*Pinus palustris*) and some pockets of South Florida slash pine (*Pinus elliotii* var. *densa*). The ranch supplementally feeds bobwhites on a two week interval at approximately 1-2 bushels/ha/year with grain sorghum (*Sorghum* spp.). Predators were removed throughout the year using live-traps at a rate of 30,000 trap nights per year. Bobwhite hunting on the ranch occurred approximately 2 days a week for the duration

of the hunting season—a hunting course was rarely hunted more than once per week. The harvest rate never reached above 10 % of the pre-hunting season population.

### 2.2.2 PRESCRIBED FIRE PLAN

Upon initiation of the study, we developed a three-year prescribed fire plan for the entire study area. The study area was broken down into three main units that represented a level of fire size [Figure 3.1: small (10 ha), med (20 ha), and large (40 ha)]. Each unit was assigned a fire size at random. Within each unit each patch was randomly assigned a fire season: dormant (January-April 15th) or growing season (April 15th - August 15th) for the first year of the study, subsequently the next time that a patch was burned in a different season than the previous occasion. The burn plan was determined for each year of the study and was adapted slightly each year to accommodate pragmatic issues of implementing the burns. Any given patch was burned on average twice during the three years of the study. The burn plan guided the implantation of burns on a daily basis and not the known presence of nesting bobwhites or other extraneous considerations in a given patch.

### 2.2.3 FIELD DATA COLLECTION

We captured bobwhites using standard wire walk-in funnel traps (February - April, 2006 - 2008) baited with grain sorghum (Stoddard 1931). Birds were banded and fitted with 6.4-6.9 g pendant-style radio transmitters and released (American Wildlife Enterprises, Monticello, FL, USA). All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists' Union 651988) and those of the University of Georgia, Institutional Animal Care and Use Committee (IACUC Protocol No. 2001-GB-01). Radio-marked bobwhites were located using homing techniques (White and Garrott 1990) 3 - 5 days per week and approached to within 10 - 25 m. Locations were taken using a programmable telemetry receiver and a three-element hand-held yagi

antenna. We approximated the bobwhite's location using geometric calculations which required a GPS position of the observer, distance to the bird in meters, and compass bearing. We assumed that birds were nesting if in the same location on 2 consecutive days (Burger et al. 1995b). Once the nest had been initiated it was flagged. Nests were checked twice daily, once in the morning to detect depredations from the previous night and in the afternoon to detect if bird was on recess. Egg counts were recorded when birds were on recess. Nests were monitored until termination (Burger et al. 1995a). Upon nest termination, the fate of the nest was determined by visual inspection of the nest bowl and egg fragments. If nests were successful, the number of successful eggs that hatched was recorded. We did not attempt to determine cause specific failure of nests based upon findings by Staller et al. (2005).

#### 2.2.4 VEGETATION DATA COLLECTION

We collected vegetation characteristics at all known nest sites and random locations. The random site was determined by a random azimuth and predetermined distance from the nest (20 meters). We quantified visual obstruction, and canopy cover of numerous vegetation functional groups (i.e., grass, forb, woody, saw palmetto, litter, vine, and bare ground) at each location. We measured visual obstruction from the mean of four observations from the four cardinal directions using a Robel pole (Robel et al. 1970) placed at the center of the nest bowl or at a random location. Observations were recored at a distance of 3 m and height of 1 m. The mean obstruction value was used for each location. We estimated percent canopy cover at each nest and random site using a modified 1 m Daubenmire frame (Daubenmire 1959). The disc of vulnerability [adapted from Kopp et al. (1998)] for each location was determined by placing a tennis ball within the nest bowl or random location and estimating the maximum distance the ball could still be seen from the four cardinal directions. The mean of the four values was used to calculate the area of a circle (i.e. disc), this value can be interpreted as an index for nest concealment. Furthermore, the

distance to nearest human created edge (e.g. road, tractor trail, or fence-line) was determined by pacing from each location. However, using an Geographic Information System and the *Near* tool these distances were also estimated to test the accuracy and validity of the observers values (ESRI 2009)

### 2.2.5 LANDSCAPE METRICS

We selected four landscape metrics that may explain variation in nest survival at a larger scale. We constructed a 450 m buffer around each nest to calculate landscape configuration metrics within the buffer. This buffer was chosen based on home range and movement data specific to this study area (James A. Martin, unpublished data). The metrics were selected from those possible within Fragstats (McGarigal et al. 2002) based on our understanding of bobwhite ecology.

## 2.3 DATA ANALYSIS

Prior to modeling, a Pearson Correlation procedure was conducted for each pair of predictor variables. Variables that were deemed correlated if  $r > 0.30$ , thus, were eliminated from the analysis to avoid multicollinearity. Multicollinearity creates unnecessary redundancy and over-fitting in models. We also plotted scatter plots and box plots of each variable to inspect the data's distribution and relationships with other variables. If variables were correlated or depicted a noticeable relationship in the scatter plots, they were not included in the same models.

### 2.3.1 NEST SURVIVAL MODELING

Recent advances have been made in modeling nest survival to add more flexibility in modeling covariates (see Dinsmore et al. 2002, Hazler 2004, Rotella et al. 2004, Shaffer 2004). We modeled nest survival using the logistic-exposure method described by Shaffer (2004). This method allows for flexible modeling of survival times, and requires no assumptions

about when the nest losses occur. Furthermore, this method can be conducted in readily available software (e.g. SAS and R). We used program R to conduct the nest survival modeling (Team 2009). This required a user-defined logistic-exposure link function within the built-in general linear model (GLM) function of R (Mark Herzog, personal communication; see appendix). Instead of the traditional binary response variable, successful or not, this procedure requires the response variable to be a continuous variable—exposure days. The number of exposure days was derived from the number of days the nest was under observation. Throughout modeling, convergence issues were common and this was circumvented by providing starting values for parameter estimates.

### 2.3.2 MODEL SELECTION AND VARIABLE REDUCTION

We used a modified information theoretic-approach (Burnham and Anderson 2002) to evaluate how plausible the models were at explaining variation in nest survival. We had a total of 21 explanatory variables that could be loosely categorized into five groups 1) micro-habitat vegetation characteristics, 2) edge measures, 3) landscape metrics, 4) fire regime, and 5) miscellaneous variables. Within each one of the groups, we created various models that had ecological basis and were simple to interpret. We ran univariate models (i.e. one variable) because habitat managers often can easily interpret these type of models. We used the STEP function in R to reduce the number of variables within each group. The STEP function fits combinations of the variables and retains only the variables that reduce the AIC value. Akaike's Information Criterion (AIC) is an extension of likelihood theory, and AIC is a relative distance between model pairs (Burnham and Anderson 2002). The distance is related to the Kullback-Leibler distance of information theory (Burnham and Anderson 2002). This distance is a measure of entropy (i.e. information lost) for models used to approximate truth (Burnham and Anderson 2002). The relative fit of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002), which can take a value from 0 to 1, with the best-fitting candidate model having

the greatest Akaike weight. The number of parameters used to estimate AIC included the fixed effects.

The variables retained by the variable reduction process were then used to build models with variables from other categories. These composite models represent ecological hypotheses that may explain variation in nest survival.

### 2.3.3 REPRODUCTION

We measured a multitude of reproductive metrics for each subpopulation and overall reproductive effort within each treatment by year and pooled estimates.

Fecundity is the number of young successfully raised during a defined interval, generally one year (Gill 2000); annual fecundity reflects the number of nesting attempts and the success of each attempt, clutch size, and the experience of the breeding individual (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 ( $\pi$ ) multiplied by mean brood size ( $\gamma$ ) and mean number of nests produced per year ( $\psi$ ). Thus, the estimator for  $F$  is:

$$\hat{F} = (\pi) * \left(\frac{\gamma}{2}\right) * (\psi) \quad (2.1)$$

where  $\hat{F}$  is the number of juvenile females hatched;  $\pi$  is the estimated probability that a breeding female successfully hatches a clutch (i.e. nest success rate);  $\gamma$  is the estimated mean brood size (see equation 5.6); and  $\psi$  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, Williams et al. 2002):

$$\hat{var} = \left( var(\hat{\pi}) * (\hat{\gamma}\hat{\psi})^2 \right) + \left( var(\hat{\gamma}) * (\hat{\pi}\hat{\psi})^2 \right) + \left( var(\hat{\psi}) * (\hat{\pi}\hat{\gamma})^2 \right) \quad (2.2)$$

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:

$$\hat{P} = \hat{H} * \bar{x} \quad (2.3)$$

where  $\hat{H}$  is the probability that a breeding female produces a successful clutch and  $\bar{x}$  is the mean clutch size. Because equation 2.3 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:

$$\hat{P} = \hat{h}_1 \hat{b}_1 + \hat{h}_2 \hat{b}_2 + \hat{h}_3 \hat{b}_3 \quad (2.4)$$

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

$$\hat{b} = \frac{1}{y_i} \sum_{j=1}^{y_i} b_{ij} \quad (2.5)$$

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

$$b = \hat{CS} * \hat{HR} \quad (2.6)$$

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, Williams et al. 2002).

## 2.4 RESULTS

Average fire size within each treatment were near our pre-determined goals for each treatment ( $\bar{x}_{small} = 10.00$  ha, SD = 4.08 ha;  $\bar{x}_{medium} = 21.07$  ha, SD = 4.52 ha;  $\bar{x}_{large} = 43.30$  ha, SD = 11.92 ha). A total of 139 nests were monitored throughout the three years (2006-2008) of study, including: 48 in the small fire size, 52 in the medium, and 39 in the large fire size treatment. A total of 212 hens were monitored during the study, including: 66 in the small fire size treatment, 76 in the medium, and 70 in the large fire size treatment. The average number of exposure days for each nest was 13.61 (SE= 0.63) and a total of 1,864 days (Table 2.2). Female bobwhites incubated the majority of the nests ( $n = 130$ ), whereas males only incubated 9 total nests. Five male attending nests were detected in the small scale treatment, three in the medium, and one in the large treatment.

### 2.4.1 NEST SURVIVAL

Data reduction procedure for the vegetation variables yielded two variables: DOV and BARE. Among the edge variables, edge density (EDGEDENS), was the only variable retained. Three landscape metric variables were retained: mean proximity index (MPI), interspersed juxtaposition index (IJI), and patch richness density (PRD). Within the fire variable subgroup all potential variables were retained including: FIRESIZE, YEAR, and SEASON. Other miscellaneous variables that were retained included: clutch size (CLUTCH), day of the nesting season (DAY), and the cumulative amount of rainfall (RAIN). Using these twelve variables (Table 2.6) we constructed 18 composite models. The top ranking model, as indicated by AIC ( $w_i = 0.39$ ), contained 7 variables including: DAY, RAIN, DOV, BARE, EDGE, SEASON, and FIRESIZE (Table 2.3). This model also had a modest  $r^2$  of 0.17. The next best fitting model was the global model ( $w_i = 0.25$ ), and had a  $r^2$  of 0.21. This model was 1.5 times less likely than the top model. The third best fitting model ( $w_i = 0.18$ ;  $r^2 = 0.17$ ) included the same variables as the top model with the addition of YEAR, and was 2.2 times less likely than the top fitting model.

The relative importance weights ( $\sum w_{Variable}$ ) for the variables indicated that numerous variables were important (Table 3.2). The two vegetation variables, DOV and BARE, had high relative importance wt. values  $\sum w_{DOV} = 0.94$  (9) and  $0.89$  (8), respectively (the number in parenthesis indicates the number of models the variable was included). The experimental variable, FIRESIZE, had a high relative importance wt.  $\sum w_{FIRESIZE} = 0.89$  (10), also. The quasi-experimental variable, SEASON, had the 3rd highest relative importance wt.  $\sum w_{SEASON} = 0.95$  (12). Lastly, DAY and RAIN had the highest importance weights,  $\sum w_{DAY} = 0.99$  (12) and  $\sum w_{RAIN} = 0.98$  (10), respectively.

The model-averaged parameter estimates had a high amount of variation (Table 2.5). However, several variables had the majority of the estimate mass outside of zero and were thought to be biologically significant. The medium fire size had a negative influence on nest survival, and these nests were 2.3 times less likely to survive (large scale fires were the baseline). Nests within the small treatment were 1.3 times less likely to survive compared to the large scale treatment. Winter or dormant season fires elicited a greater positive response as opposed to summer fires; however, both were positive compared to the absence of fire. Also, for every day progression in the nesting season, nests were 1.02 times less likely to survive. For each additional 2.54 cm of rain nest survival declined by 18%. Nests with an additional square meter of viewing space by predators were 1.17 times less likely to survive, and similarly with each increase in bare-ground nests were 1.30 times less likely to survive.

#### 2.4.2 REPRODUCTIVE EFFORT

Estimates of reproductive output were highly variable among years and within the treatments (Table 2.6). The productivity index suggested small fire size produced more chicks per hen than the other two treatments [ $P_{small} = 4.02$  (CI = 0.96); see Figure 2.5]. This was corroborated by the fecundity estimates which also suggested the small fire size produced

more female chicks (see Figure 2.4). As suggested by the nest survival analysis, nest success was highest in the large fire size treatment ( $0.59 \pm 0.02$ ),  $0.50 \pm 0.01$  in the small fire size, and  $0.33 \pm 0.01$  in the medium size fire treatment. The similarity between the nest survival (each exposure day modeled as an independent Bernoulli trial) and nest success (simple moments estimator) estimates suggest for bobwhites the moments estimate is sufficient to describe nest success probabilities.

## 2.5 DISCUSSION

### 2.5.1 NEST SURVIVAL

The top ranking models suggest that bobwhite nest survival is not affected by single variables or a single category of variables (e.g., micro-site vegetation, weather, etc.). These models indicated that combinations of variables at different scales and contexts explained the most variation in nest survival. Stephens et al. (2005) found similar results with duck nest survival in the Missouri Coteau of North Dakota. We only considered two spatial scales in our analysis that corresponded to micro-site habitat and habitat structure within a home range size buffer around each nest. We had little *a priori* information to believe nest survival could be affected by habitat structure at a larger scale in this landscape. We believed that comparisons at larger scales would only increase unexplainable variation in our results because the landscape outside of the extent of the study area is much different than within. Furthermore, many landscape metrics are sensitive to scale and not applicable in this context (Hargis and David 1998).

Landscape metrics that measure landscape structure were not well supported in explaining nest survival. White et al. (2005) found landscape metrics were significant predictors of nest placement within a fragmented landscape—as fragmentation increased likelihood of bobwhite nesting decreased. But our models did not support the findings of White et al. (2005) which can likely be explained by the dramatic differences in landscape contexts (Donovan et al. 1997). More important than the landscape metrics, the amount of

edge has long been considered an important factor regarding avian nest survival (Martin 1995). Our models demonstrated that edge density was an important indicator of nest survival, concordant with other ground nesting bird studies (Keyser et al. 1998, Potts 1986). However, the type of edge considered in our models was mostly natural, not human-induced or resulting from habitat fragmentation. The preliminary models, prior to variable reduction, included variables related to human-induced edges, such as roads, trails, and food plots; however, these variables were not retained in the subsequent analysis. Perhaps bobwhites, even in non-fragmented habitat, select areas with limited edge to reduce predation (J. A. Martin, unpublished data). Conversely, edge habitat in natural landscapes may be poor surrogate for predation and bobwhite response to such edge is neutral (Tewksbury et al. 1998).

Our models provided support for previous work conducted with micro-site characteristics and bobwhite nest survival (Klimstra and Roseberry 1975, Lusk et al. 2006, Rader et al. 2007, Stoddard 1931, Taylor et al. 1999). Klimstra and Roseberry (1975) and Stoddard (1931) were the first to describe nest construction and concealment in bobwhites, Klimstra and Roseberry (1975) demonstrated that "excellent concealed nests" were more likely to be successful. Similarly, Lusk et al. (2006) found that nest survival was mostly affected by vegetation canopy height, shrub cover, and bare-ground exposure—all indicators of nest concealment. Our data suggested that nest concealment, encapsulated by the single variable—DOV, had the most profound variable at this scale. Concordant with Lusk et al. (2006), bare-ground had a negative influence on nest survival. Habitat management dictates the vegetative structure, hence nest concealment; therefore, vegetation structure can be affected and monitored by habitat managers.

Fire is an important habitat management tool for bobwhites and it can dictate vegetative structure dependent upon the season of fire (Engstrom et al. 1996, Platt et al. 1988, Sparks et al. 1999, Streng et al. 1993). Our models suggest that season of fire was important in describing nest survival. Winter or dormant season fires elucidated a greater

positive response as opposed to summer fires; however, both were positive compared to the absence of fire. We did experience direct nest losses from summer fire, but this was limited to only three nests in three years. Indirectly, fires conducted during the breeding season for bobwhites likely reduce available space for nesting and reduce the search area by nest predators. The effect size of winter season burning was much more compelling than summer fires. Winter burning creates areas that have ample time to recover from fire prior to the nesting season in the same year of the fire. Furthermore, the absence of fire is likely not conducive for nest survival because those areas lacking fire become overgrown with rank vegetation. Unburned areas on our study site were rare, especially in the latter years of observation, suggesting bobwhites chose unburned sites over recently burned sites for nesting. This decoupling of selection and fitness is likely a result of the increased concealment of nests in the unburned sites, but predation is likely higher in unburned sites where other food sources for predators are prevalent (Jones et al. 2004).

Fire size, the experimental treatment, was not as important as season of fire. However, the medium fire treatment displayed biologically significant negative effects on nest survival. Fires of this size may create a perimeter/area ratio that is more suited to predator movements than that of small or large fires. Horn et al. (2005) found in the grasslands of North Dakota that nest survival was highest in large and small fields, and lowest in medium size fields—congruent with our findings. We agree with the explanation of Horn et al. (2005) that predators are less efficient in searching large patches, but lack a plausible explanation for increased survival in small patches compared to medium sized patches.

### 2.5.2 REPRODUCTIVE EFFORT

Our hypotheses regarding the effects of fire size on reproductive effort for northern bobwhites were supported by the data. However, the medium fire size was an anomaly in the overall relationship that as fire size increases reproductive measures decrease. Based on nest success or nest survival alone, the large size fire treatment would have been deemed

the most suitable for bobwhites. But when other reproductive metrics are included, the productivity and fecundity metrics indicate large fires are detrimental to overall reproductive output for bobwhites relative to smaller fires. Wellendorf and Palmer (2009) presented similar results with fires of much smaller sizes, they found that nest success was highest on large fires (ca. 8 ha) but had lower overall productivity.

The model by Miller (1982) predicted that colonizing (high rates of reproduction and high dispersal abilities) species respond more favorable to large disturbances; conversely, competitive species may respond more favorable to smaller disturbances. Bobwhites can loosely be defined as a colonizing species, but perhaps have limited dispersal abilities compared to the species Miller (1982) described (e.g., wind dispersed plants). But some authors have suggested bobwhites can disperse long distances (Cook 2004, Folk 2006). Nonetheless, our results show that initially large scale fires increased reproduction, concordant with the theoretical models (Davis and J.E. Cantlon 1969, Miller 1982). But in latter years reproduction rates were lower in the large fires compared to small fires. Previous authors have describe this phenomenon as the "new ground" effect (Palmer et al. 2001). Bobwhites likely responded to the large amounts of habitat created (i.e. more food, better cover) and were under less predation pressure from competitive species, albeit at a cost, because the number of nests produced per hen declined through time at a greater rate than smaller fires. Overall the highest rates of reproduction occurred the year the treatments were applied, further suggesting the initial pulse of reproduction from the application of the disturbance.

Much like most large scale manipulative experiments, our study suffered from lack of spatial replication of the experimental units (Block et al. 2001, Eberhardt and Thomas 1991). We only had one unit for each of the three fire treatments, but did have multiple years of data. The costs and logistical constraints did not allow multiple replicates. However, the treatments were randomly applied upon initiation of the study. Furthermore, our experimental units were adequate in size (>300 ha) our study organism was virtually

unaffected by fragmentation or edge effects of the surrounding landscape. We acknowledge the limitations of our study design which somewhat prohibits the extrapolation of our results to other study areas; however, we feel our results, if tested, would be replicated under similar circumstances and very likely within the south Florida rangeland ecosystem.

## 2.6 CONSERVATION IMPLICATIONS

Bobwhites can be used as a surrogate for other non-migratory, ground-nesting, disturbance-dependent species as to how disturbance sizes, in this case fire, will affect reproduction. The large fire sizes represented in our experiment are small relative to those used by public land management agencies throughout the Southeast. Avian response to even larger fires will likely be more dramatic, suggesting existing low abundances of bobwhites on those areas of perceived suitable habitat structure are an artifact of a disturbance regime not aligned with bobwhite adaptations. Habitat managers are in a conundrum between logistical and biological objectives on the application of fire to a given landscape. To some extent larger fires are more logistically efficient, but are likely not biologically optimal for many species of birds. We encourage planners and managers to consider fire size as a constraint in their fire management plans. However, we do caution that the creation of new fire breaks (edge) may have other deleterious effects on the targeted species. The creation of new fire breaks could be circumvented with the use of natural fire breaks and changing firing techniques to create a mosaic of unburned and burned fuel (habitat) on large fires. However, more research is needed on this topic because typically those unburned patches will be areas of low habitat quality. These remnant patches may act as ecological traps for bobwhites in this context (Schlaepfer et al. 2002).

## 2.7 ACKNOWLEDGMENTS

We would like to thank our private donors for supporting this research through funding and land access. We would also like to thank the USDA-Bobwhite Restoration Project, Tall Timbers Research Station and Land Conservancy, Inc., and the University of Georgia Graduate School and Warnell School of Forestry and Natural Resources for funding. We thank the many technicians and interns that braved the elements in the pursuit of this data. We thank the helpful comments of peers and committee members that improved this draft.

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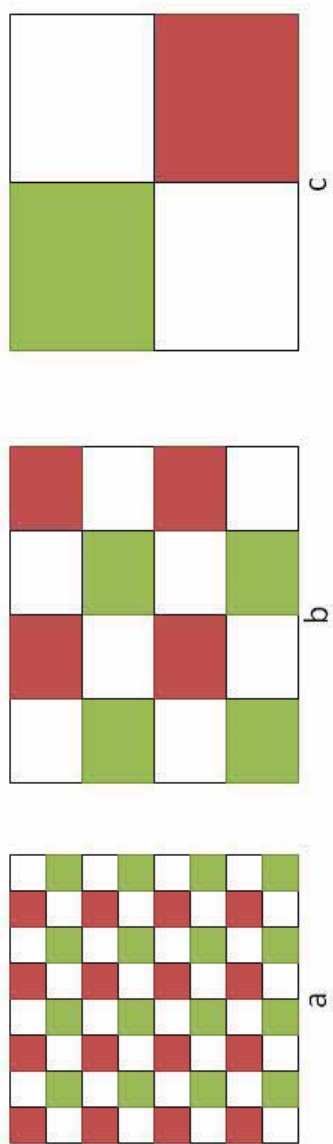


Figure 2.1: A simplified schematic of the prescribed fire size treatments: (a) small ca. 10 ha, (b) medium ca. 20 ha, and (c) 40 ha. Red squares indicate fires in the growing season and green squares indicate dormant season fires.

Table 2.1: Explanatory variable descriptions and possible relationship with nest survival. Only variables that were retained after variable reduction are included.

Explanatory Variable	Definition and Ecological Importance
DOV	Disc of vulnerability : an index of nest concealment; as this value increases the nest can be seen from ground level at a farther distance
BARE	Bare ground: the amount of bare ground around the nest bowl; more bare ground likely indicates less nest concealment
EDGE	Edge density; amount of edge per unit area in the 450 m buffer around nest; more edge likely increases predation
MPI	Mean Proximity Index; a measure of the degree of isolation and fragmentation of a patch, an increase in this value indicates more fragmentation; more fragmentation likely indicates more predation
IJI	Interspersion Juxtaposition Index; as the number increases patches of habitat are more adjacent;
PRD	Patch richness density; number of patch types in 450 m buffer;
FIRESIZE	The experimental treatment of fire size to the landscape; large fire size was used as the baseline within models
YEAR	Year of the study; year 1 was used as the baseline
SEASON	The season of fire that was last applied to the patch of habitat containing each nest; No fire was compared to dormant and growing season fires
CLUTCH	The clutch size of the nest; more eggs in nest may decrease concealment and increase scent from nests
DAY	The day of the nesting season; More cover later in nesting season may lead to increased survival; however, predators may learn to detect nests more easily the later in the nesting season
RAIN	The cumulative amount of rainfall during incubation; Increased amounts of rainfall may increase predation risk

Table 2.2: Mean ( $\pm$  SE), minimum (MIN), and maximum (MAX) values for all explanatory variables used throughout modeling. Data are from a private ranch in south Florida, USA, 2006-2009.

Variable	$\bar{x}$	SE	MIN	MAX
RAIN	7.42	0.71	0.00	36.73
EXPOSURE DAYS	13.61	0.63	1.00	38.00
DAY	57.63	2.71	0.00	142.00
WETDIST	80.51	4.52	0.00	276.59
ROADDIST	73.26	5.36	0.60	288.85
OPNWTRDIS	251.03	11.03	30.00	600.00
TRLDIST	48.52	4.37	0.68	364.72
MPI	28.52	1.06	0.32	63.53
MNN	89.89	2.48	44.70	208.70
IJI	62.03	0.64	35.63	89.58
TE	14416.86	184.43	8220.00	19350.00
EDGE	226.67	2.90	129.92	303.67
PRD	11.01	0.11	6.30	12.66
MSIEI	0.55	0.01	0.15	0.88
GRASS	7.94	0.15	0.00	10.00
WOOD	2.87	0.19	0.00	8.00
SAW	3.52	0.23	0.00	10.00
LITT	7.09	0.21	0.00	10.00
BARE	3.61	0.19	0.00	9.00
DISTEDGE	21.77	1.79	0.00	100.00
DOV	2.00	0.10	0.00	6.50

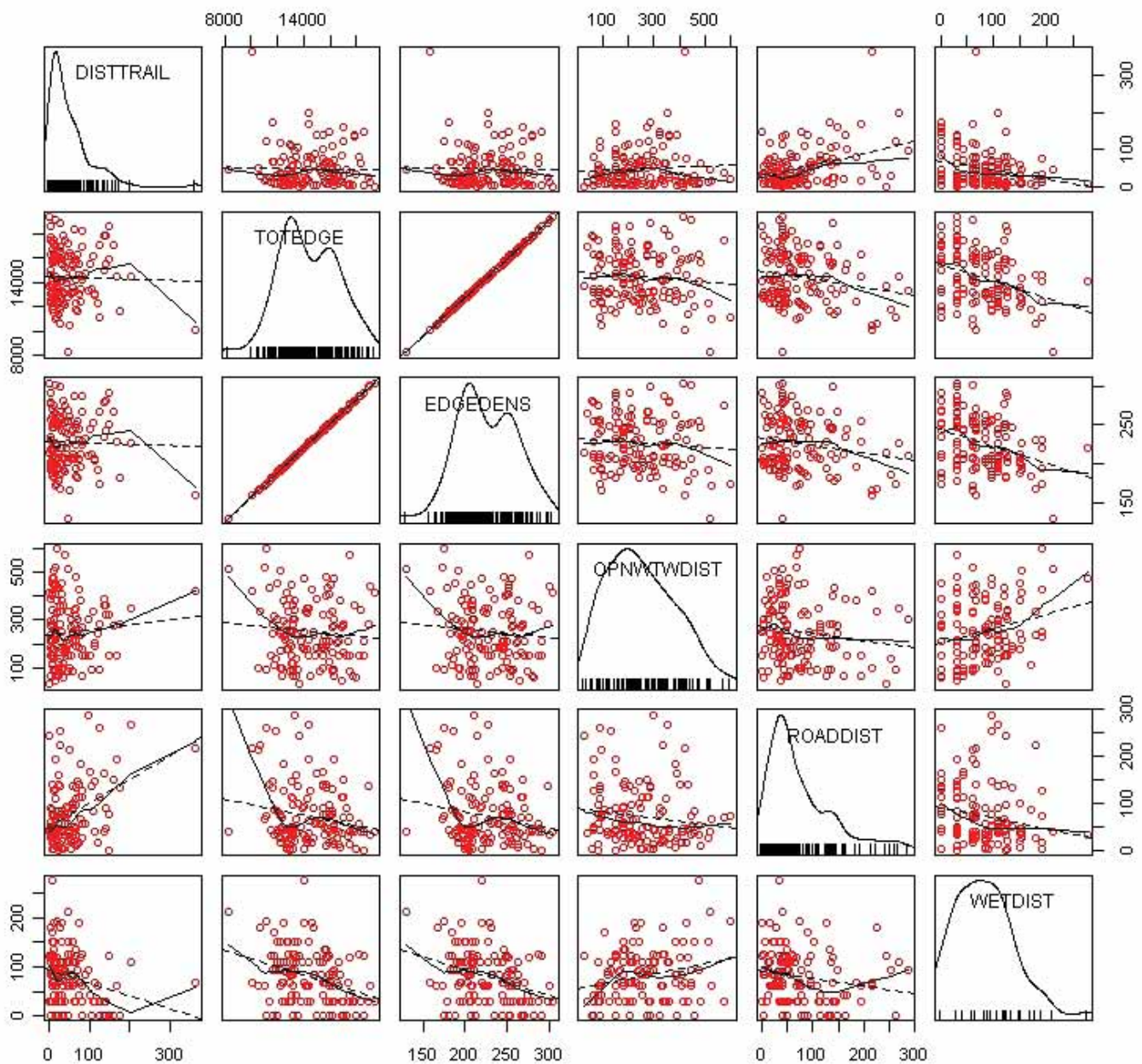


Figure 2.2: Scatter plot diagram depicting relationships between pairs of edge and distance type parameters variables south Florida during 2006-2008. All variables are measured in meters. Graphs on the diagonal are the distribution of the data. The remaining cells are scatter plots with a linear trend line (dotted line) and a non-parametric spline (solid line).

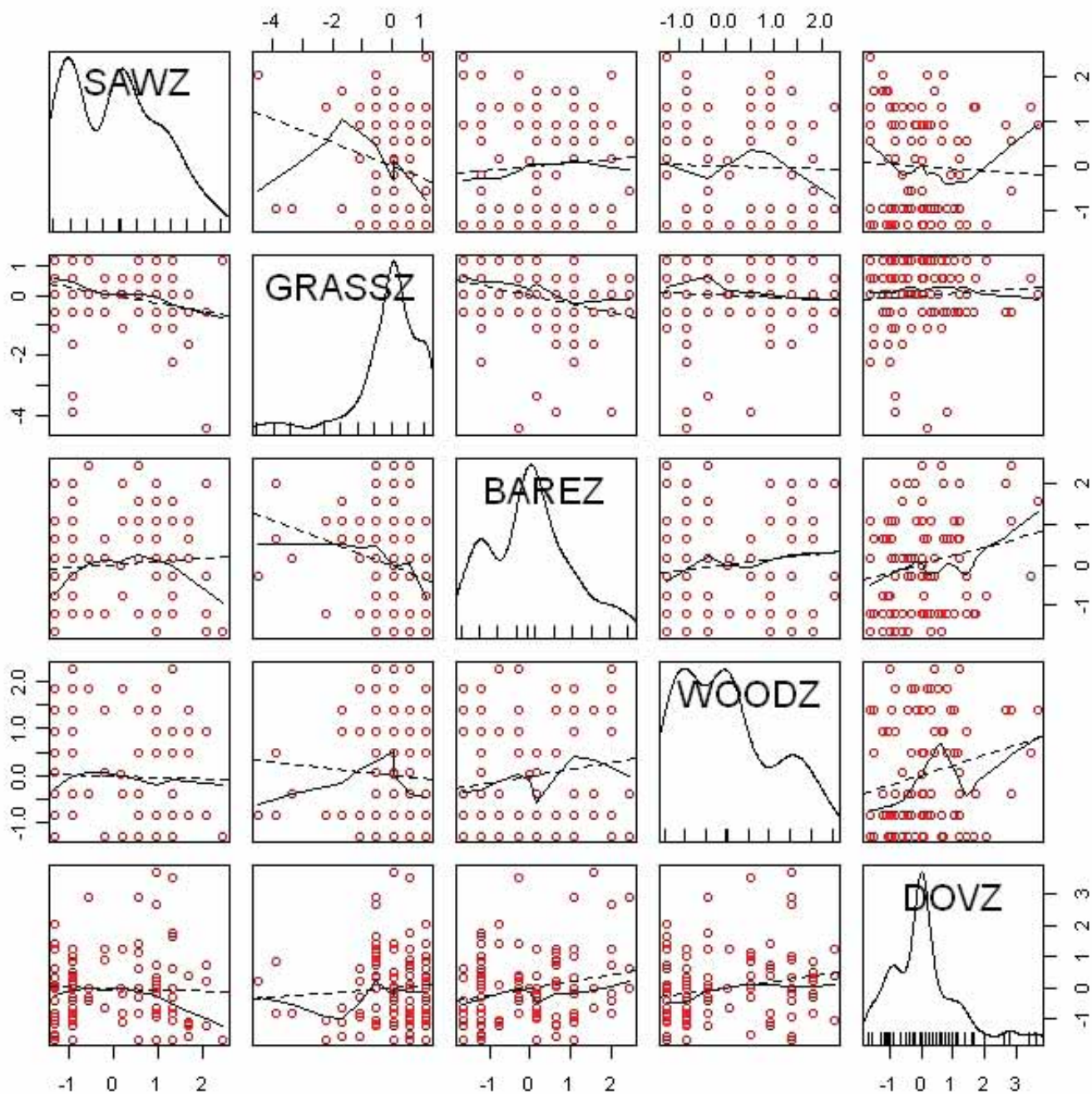


Figure 2.3: Scatter plot diagram depicting relationships between pairs of vegetation parameters variables south Florida during 2006-2008. These variables have been standardized. Graphs on the diagonal are the distribution of the data. The remaining cells are scatter plots with a linear trend line (dotted line) and a non-parametric spline (solid line)

Table 2.3: Models describing variation in nest survival for northern bobwhites in Florida, USA, 2006-2008. Models are ranked by differences in AIC values.

Composite Models	K	AIC	Deviance	$\Delta AIC$	$W_i$	$r^2$
DAY+RAIN+DOV+BARE+EDGE+SEASON+FIRESIZE	9.00	255.55	235.00	0.00	0.39	0.17
Global	17.00	256.42	224.42	0.87	0.25	0.21
DOV+BARE+SEASON+FIRESIZE+YEAR+DAY+RAIN	11.00	257.16	235.00	1.61	0.18	0.17
DAY+RAIN+DOV+BARE+EDGE+SEASON	8.00	259.33	243.33	3.78	0.06	0.14
FIRESIZE+DAY+RAIN+DOV+EDGE+CLUTCH+SEASON	10.00	259.75	239.75	4.20	0.05	0.16
DAY+RAIN+SEASON	5.00	262.09	252.09	6.54	0.01	0.11
MPI+PRD+IJI+DAY+RAIN+CLUTCH	7.00	262.21	248.21	6.66	0.01	0.13
FIRESIZE+DAY	4.00	262.79	254.79	7.24	0.01	0.10
DAY+RAIN+DOV+BARE	5.00	262.90	252.90	7.35	0.01	0.11
FIRESIZE+SEASON+YEAR+DAY	7.00	263.12	247.12	7.57	0.01	0.13
MPI+PRD+IJI+DAY+RAIN+CLUTCH+EDGE	8.00	263.95	247.95	8.40	0.01	0.13
DAY+RAIN+DOV+BARE+EDGE	6.00	264.55	252.55	9.00	0.00	0.11
MPI+PRD+IJI+DOV+BARE	6.00	275.00	263.14	19.45	0.00	0.07
FIRESIZE*SEASON	9.00	278.66	260.66	23.11	0.00	0.08
FIRESIZE+SEASON+YEAR+MPI+IJI+PRD	10.00	278.73	258.73	23.18	0.00	0.09
MPI+PRD+IJI+EDGE	5.00	279.26	269.26	23.71	0.00	0.05
FIRESIZE+SEASON+YEAR+DOV+BARE	9.00	279.51	261.51	23.96	0.00	0.08
FIRESIZE+SEASON+YEAR+EDGE	8.00	282.97	266.97	27.42	0.00	0.06

Table 2.4: Importance weights  $\sum w_{Variable}$  for explanatory variables used to model northern bobwhite nest survival on private ranch, Florida, USA, 2006-2008.

Explanatory Variable	N <sup>1</sup>	Relative Importance Wt. ( $\sum w_{Variable}$ )
DAY	12	1.00
RAIN	10	0.99
SEASON	12	0.96
DOV	9	0.95
BARE	8	0.90
FIRESIZE	10	0.89
EDGE	8	0.77
YEAR	4	0.44
CLUTCH	4	0.32
MPI	6	0.27
IJI	6	0.27
PRD	6	0.27

<sup>1</sup>Number of models variable was included.

Table 2.5: Unconditional model-averaged parameter estimates and Odds Ratio for explanatory variables included in northern bobwhite nest survival models on a private ranch, Florida, US, 2006-2008.

Parameter	$\beta$	SE	Odds Ratio	95% CL
Intercept	4.47	1.26	—	—
DOV	-0.18	0.14	0.83	(1.08,0.64)
BARE	-0.36	0.16	0.70	(0.96,0.51)
EDGE	-0.11	0.16	0.90	(1.23,0.66)
MPI	-0.02	0.01	0.98	(1.00,0.96)
IJI	0.02	0.02	1.02	(1.06,0.98)
PRD	-0.17	0.15	0.85	(1.13,0.63)
FIRESIZE(SMALL)	-0.30	0.44	0.74	(1.77,0.31)
FIRESIZE(MEDIUM)	-0.86	0.39	0.42	(0.90,0.20)
YEAR2	-0.20	0.46	0.82	(2.02,0.33)
YEAR3	-0.03	0.57	0.97	(2.98,0.32)
SEASON(Summer)	0.42	0.44	1.53	(3.65,0.64)
SEASON(Winter)	0.79	0.38	2.21	(4.62,1.06)
CLUTCH	0.03	0.06	1.03	(1.16,0.91)
DAY	-0.02	0.00	0.98	(0.99,0.97)
RAIN	-0.21	0.13	0.81	(1.05,0.62)

<sup>1</sup>Baseline was LARGE. <sup>2</sup>Baseline was YEAR1. <sup>3</sup>Baseline was NOBURN.

Table 2.6: Reproductive parameters for northern bobwhites under three different fire size treatments observed on a private ranch in south Florida, US, 2006-2008.

Parameter		Small		Medium		Large	
		$\bar{x}$	90% CI	$\bar{x}$	90% CI	$\bar{x}$	90% CI
<b>Nests per hen<sup>1</sup></b>							
	2006	0.71	0.34	0.58	0.24	0.82	0.23
	2007	0.77	0.24	0.52	0.20	0.46	0.24
	2008	0.70	0.27	0.93	0.26	0.42	0.19
	Pooled	0.73	0.16	0.68	0.14	0.56	0.13
<b>Overall Clutch Size<sup>2</sup></b>							
	2006	11.09	0.98	11.72	1.27	13.23	1.24
	2007	12.50	0.94	12.83	0.47	9.50	2.21
	2008	11.40	1.35	10.08	1.00	11.5	0.97
	Pooled	11.74	0.68	11.27	0.65	11.88	0.90
<b>Hatched clutch size<sup>3</sup></b>							
	2006	9.00	1.93	11.4	1.55	12.10	0.69
	2007	11.54	1.16	10.2	1.32	7.80	1.44
	2008	11.42	0.65	7.10	0.57	6.60	0.68
	Pooled	11.04	0.68	9.43	0.73	9.50	0.84
<b>Nest Success<sup>4</sup></b>							
	2006	0.58	0.07	0.33	0.05	0.56	0.05
	2007	0.59	0.05	0.42	0.07	0.60	0.08
	2008	0.37	0.04	0.28	0.03	0.64	0.07
	Pooled	0.50	0.02	0.33	0.01	0.59	0.02
<b>Hatches per hen<sup>5</sup></b>							
	2006	0.41	0.38	0.19	0.14	0.46	0.23
	2007	0.46	0.26	0.22	0.17	0.27	0.35
	2008	0.26	0.16	0.26	0.10	0.27	0.31
	Pooled	0.36	0.14	0.22	0.07	0.33	0.16

<sup>1</sup>Calculated using (Number of total nests produced / total number of hens in population April 15th). <sup>2</sup>Mean clutch size for each bobwhite nest. <sup>3</sup>Mean number of chicks hatched per each hatched nest. <sup>4</sup>Proportion of successful (> 1 egg hatch) nests to total nests. <sup>5</sup>Number of successful nest hatches per hen in population April 15th.

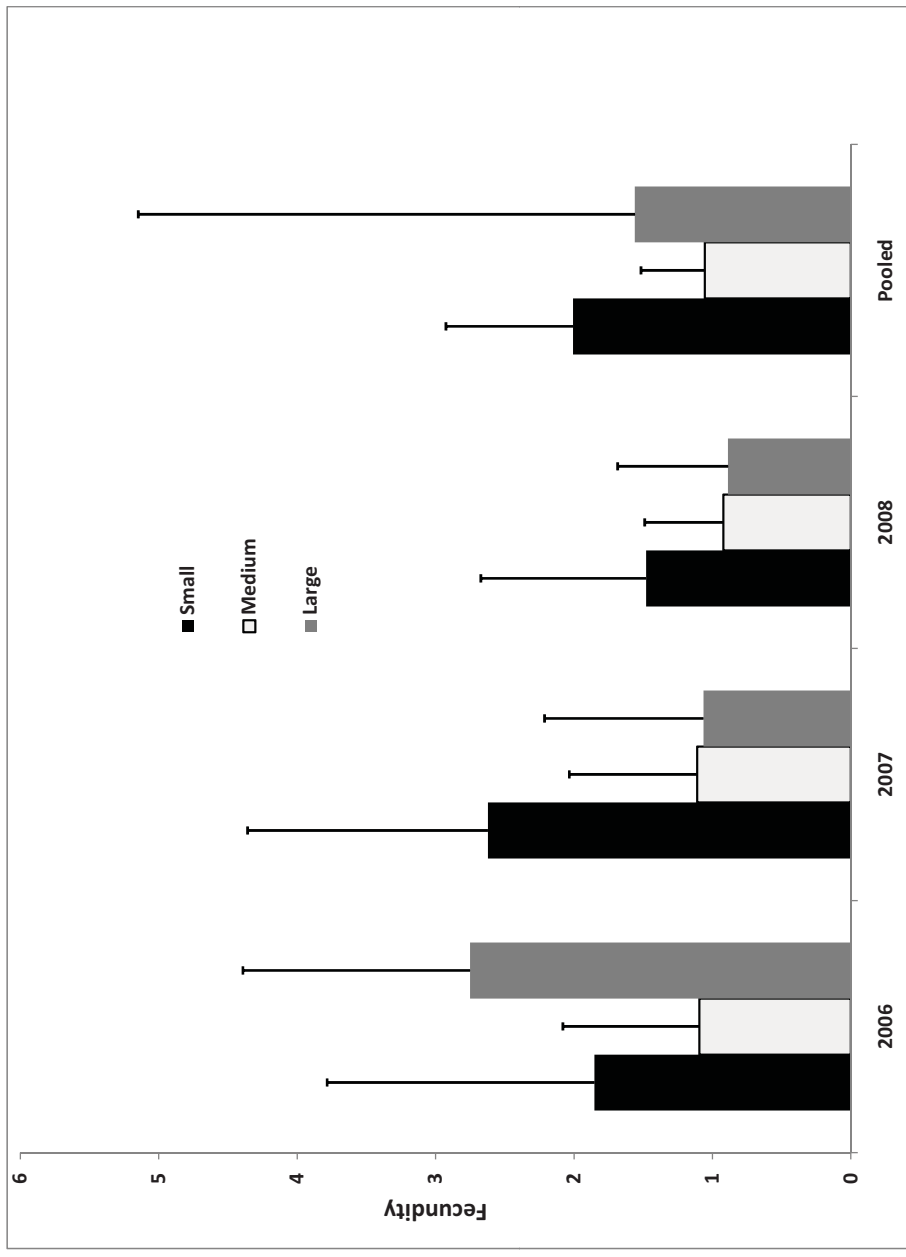


Figure 2.4: Fecundity ( $\pm$  95 % CL) for northern bobwhites under three fire size treatments [small (10 ha); medium (20); and large (40)] in south Florida, US, during 2006-2008.

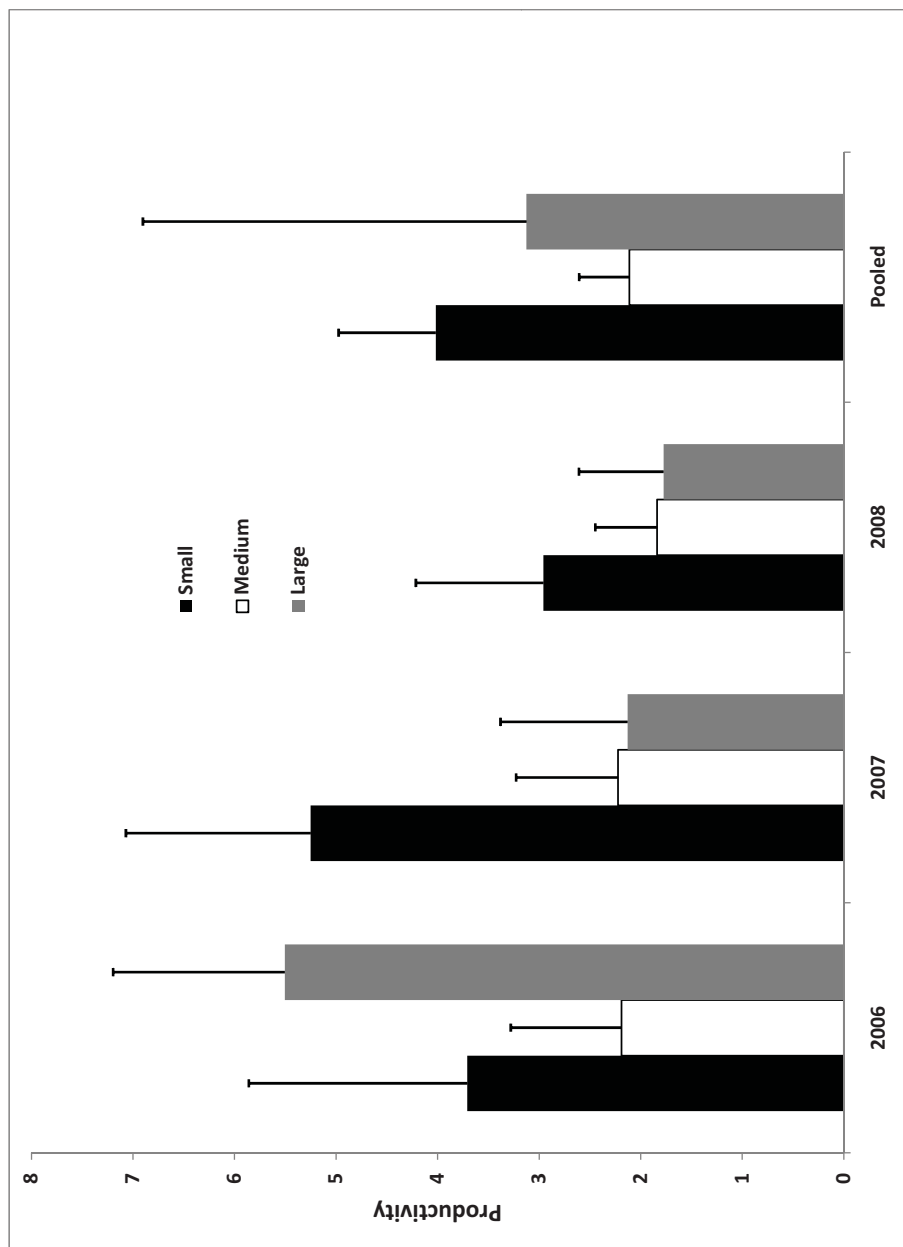


Figure 2.5: Productivity ( $\pm$  95 % CL; the number of chicks hatched per hen) for northern bobwhites under three fire size treatments [small (10 ha); medium (20); and large (40)] in south Florida, US, during 2006-2008.

## CHAPTER 3

### THE EFFECTS OF FIRE SIZE ON NORTHERN BOBWHITE HAZARD RATES AND POPULATION SIZE<sup>2</sup>

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<sup>2</sup>J.A. Martin, W. E. Palmer, and J. P. Carroll. To be submitted to: *Journal of Wildlife Management*.

### 3.1 INTRODUCTION

Habitat managers often use natural disturbances in artificial ways to mimic natural heterogeneity in habitat. Information can be lacking regarding the effects of disturbances on species in today's landscape. Habitat managers often use prescribed fire to create the proper seral stages for northern bobwhites (*Colinus virginianus*), especially for the pine (*Pinus* spp.) savannahs of the Southeast (Brennan et al. 1998, Buckner and Landers 1979, Christensen 1981, Outcalt 2008, Platt et al. 2006, Stoddard 1931). The use of fire for bobwhite management is based on cultural, practical, and some empirical evidence that demonstrates without fire bobwhites would not be able to persist (Engstrom et al. 1984, Folk 2006, Speake 1966, Stoddard 1931). However, we lack empirical evidence on the effects of some aspects of fire management on bobwhite ecology.

The way that fire is applied to a landscape is variable and the practitioner has control over several key factors that affect the outcomes of applying fire. These factors include: (1) season of fire, (2), ignition techniques (i.e. fire behavior), (3) frequency or fire return interval, and (4) size of burned patches. These factors change over time and space. The resulting landscape is heterogeneous and is a main driver of species diversity in some landscapes (Brawn et al. 2001, Platt and Connell 2003). An adequate amount of research exists in regards to the season of fire and its effects on bird and vegetative communities (Brennan et al. 2000, Engstrom et al. 1996, Hanula and Wade 2003, Howell et al. 2008, Platt et al. 1988, Robbins and Myers 1992), and most agree that in general that seasonality has a weak influence on bird diversity while some species have a multitude of responses. Similarly, fire frequency changes bird community diversity while individual species respond differently based upon different life history traits (Breininger and Smith 1992, Collins 2000, Davis et al. 2000). Bobwhites respond favorably to more frequent fires (Brennan et al. 1998, Engstrom et al. 1984) in highly productive sites, but Spears et al. (1993) reported that less frequent disturbances are warranted in the arid Southwest. The ignition techniques (e.g. backing, flanking, or head) has a direct influence on fire behavior (Albini 1976) and the

removal of fuel. Little research has been done on fire behavior or severity effects on animal communities, but Smucker et al. (2005) provides compelling evidence that *wildfire* severity and time-since-fire has direct implications for post-fire bird assemblages.

Perhaps the last frontier of research regarding fire effects on wildlife is the issue of fire size, extent, and scale (Miller 1982, Niklasson and Granstromm 2000). Early ecologists (Armstrong 1988, Coffin and Lauenroth 1988, Davis and J.E.Cantlon 1969, Denslow 1980, Levin and Paine 1974, Miller 1982, Osman 1977, Sousa 1979) established the importance of disturbance patch size on community dynamics. However, much of the published work has been conducted in laboratory setting (Armstrong 1988) or in a marine environment (Paine and Levin 1981, Sousa 1979). Davis and J.E.Cantlon (1969) were the first to establish disturbance size mattered in a terrestrial setting, but involving plants. The consensus view is that larger disturbances favor colonizing species with high rates of reproduction and high dispersal abilities (Davis and J.E.Cantlon 1969, Osman 1977, Sousa 1979).

Fire is a key natural disturbance agent in some ecosystems; therefore, fire patterns likely explain variations in species distributions. The spatial and temporal patterns of prescribed fire are driving factors at any spatial scale, because they likely determine successional status, age distribution, and grain of the vegetation covering the landscape (Niklasson and Granstromm 2000). Spatial pattern dictates the dispersal distances for colonizing organisms (Moloney and Levin 1996, Turner et al. 1997) and the survival of those organisms. The proportion of area burned may be a key variable describing bobwhite demography. Niklasson and Granstromm (2000) made a key assertion that the proportion of the area per time unit is a critically important fire characteristic and is affected by two variables: the number of fires per unit time, and the size of the individual fires.

In an manipulative experiment, we studied bobwhite hazard rates and population size in response to changes in the size of fires while keeping the proportion of the area burned constant. We treated three units with three fire sizes: 10 ha, 20 ha, and 40 ha. Furthermore, the season of fire was a quasi-experimental variable that we monitored the effects on

bobwhite hazard rates. The percentage of growing and dormant season fires was 50% within each treatment to reduce the confounding effects of fire season on demographic parameters.

### 3.2 METHODS

Climate in south Florida is subtropical and humid with average annual temperatures in the mid-20s C, ranging from ca. 16 C in midwinter to ca. 27 C in summer. Rainfall averages about 137 cm, with 50 to 60 % of it occurring during June–September (Obeysekera et al. 1999, USFWS 1999).

The study area is managed predominately for bobwhite habitat and hunting. Cattle were excluded from the quail management areas, and had been for approximately 7 years. The predominate habitat type on the ranch is mesic-pine flatwoods, and exotic grass pasture (i.e. improved pasture). Bobwhite management areas have historically been burned on a 2-3 year return interval within the traditional dormant season (January-early March). However, in the 2-3 years prior to my study the burning program had become lackadaisical. Therefore, understory vegetation had shifted towards a shrub community dominated by saw palmetto (*Serenoa repens*). Flatwoods had an over-story of predominately longleaf pine (*Pinus palustris*) and some pockets of South Florida slash pine (*Pinus elliottii* var. *densa*). The ranch supplementally feeds bobwhites on a two week interval at approximately 1-2 bushels/ha/year with grain sorghum (*Sorghum* spp.). Predators were removed throughout the year using live-traps at a rate of 30,000 trap nights per year. Bobwhite hunting on the ranch occurred approximately 2 days a week during hunting season—a hunting course was rarely hunted more than once per week. Harvest rate never reached above 10 % of the pre-hunting season population.

### 3.2.1 PRESCRIBED FIRE PLAN

Upon initiation of the study, we developed a three-year prescribed fire plan for the entire study area. The study area was broken down into three disjoint units that represented a level of fire size: small (10 ha), med (20 ha), and large (40 ha) [Figure 3.1]. Each unit was assigned a fire size at random. Within each unit each patch was randomly assigned a fire season: dormant (January-April 15th) or growing season (April 15th - August 15th) for the first year of the study, subsequently the next time that patch was burned in a different season than the previous occasion. The burn plan was determined for each year of the study and was adapted slightly each year to accommodate pragmatic issues of implementing the burns. Any given patch was burned on average twice during the three years of the study. The burn plan guided the implantation of burns on a daily basis and not the known presence of nesting bobwhites or other extraneous considerations in a given patch.

### 3.2.2 DATA COLLECTION

We captured bobwhites using standard wire walk-in funnel traps (February–April, 2004–2005) baited with grain sorghum (Stoddard 1931). Birds were banded and fitted with 6.4–6.9 g pendant-style radio transmitters and released (American Wildlife Enterprises, Monticello, FL, USA). All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists' Union 651988) and those of the University of Georgia, Institutional Animal Care and Use Committee (IACUC Protocol No. 2001-GB-01).

Radio-marked bobwhites were located using homing techniques (White and Garrott 1990) 3 - 5 days per week and approached to within 10–25 m. Locations were taken using a programmable telemetry receiver and a three-element hand-held yagi antenna. We approximated the bobwhite's location using geometric calculations which required

a GPS position of the observer, distance to the bird in meters, and compass bearing. We assumed that birds were nesting if in the same location on 2 consecutive days following Burger et al. (1995b). Once the nest had been initiated it was flagged. Nests were checked twice daily, once in the morning to detect depredations from the previous night and in the afternoon to detect if bird was on recess. Egg counts were taken when birds were on recess. Nests were monitored until termination to determine fate (Burger et al. 1995b).

### 3.2.3 HAZARD MODELING

To evaluate the effects of fire size and the other explanatory variables, Cox proportional hazard models were used (Cox and Oakes 1984). Individuals that were lost or their radio failed were right-censored from the data set. Also, individuals that were alive upon termination of the study were right censored from the data set. We assumed that censoring occurred at random and was no indication of treatment effects. We constructed models using combinations of six variables to explain the variation in hazard rates. The variables were as follows:

1. GENDER: We believed that gender could drive the hazard rates of bobwhites because can play a role in bobwhite survival (Palmer and Wellendorf 2007, Terhune et al. 2007).
2. AGE: Younger individuals are likely less familiar with surroundings and likely less experienced with predation pressure at any given point in time.
3. YEAR: Annual differences in survival rates are common with r-select species such as bobwhites. Therefore, it is plausible that hazard rates may fluctuate annually in response to weather, predator pressure, and other seasonally changing factors.
4. RAIN: The cumulative amount of rainfall within the last thirty days of life likely dictate two factors indirectly related to bobwhite hazard rates. Increasing amounts of rain may increase scenting conditions for bobwhite predators. Also, in south Florida

abundant rainfall in relatively short periods of time can reduce habitat space for bobwhites through flooding.

5. **FIRESIZE:** The size of a disturbance (i.e., fire) could affect bobwhite movement patterns, food resources, predator abundances, and habitat space that could be expressed through their ability to survive those conditions. Smaller fires are likely more conducive to bobwhite survival because of decreased movements and more residual cover left in an individual's homerange post-fire.
6. **HABMAX:** Nested within our three treatments, patches of habitat were burned using a varying seasons (dormant and growing season) of the year. Individual locations were assigned a season based on the last known fire occasion, and for each individual the mode habitat (HABMAX) was assigned. The possible mode habitats were as follows: (PDS) burned the previous dormant season (the baseline), (PGS) burned previous growing season, (CDS) burned during current dormant season, (CGS) burned during current growing season, (IB) other areas not capable of being burned (e.g., wetland, road, and food plot), and (NB) not burned in the previous 2 years.

The generic hazard model is:

$$h_i(t) = \alpha(t) + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik} \quad (3.1)$$

where  $t$  is an indicator of time,  $i$  is a subscript for observation, and the  $x$ 's are the covariates. The baseline hazard function is unspecified,  $\alpha(t) = \log h_0(t)$ .

Hazard models were assessed on how well they fit the data using Akaike's Information Criterion [AIC; (Burnham and Anderson 2002)]. The relative fit of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002), which can take a value from 0 to 1, with the best-fitting candidate model having the greatest Akaike

weight. We then calculated AIC values, AIC weights, model-averaged parameter estimates and unconditional standard errors for each effect (Burnham and Anderson 2002).

#### 3.2.4 POPULATION ESTIMATION

We estimated bobwhite density using autumn covey-call point-transects—a type of distance sampling (Buckland et al. 2001, Thomas et al. 2009, Wellendorf and Palmer 2005). Survey locations were assigned at random within each of the three treatment areas. Because the treatment areas were relatively small (< 1,000 ha) and our listening area was large (ca. 80 ha), we enforced a minimum distance between points to minimize overlap. For the first three years of data collection, points were conducted multiple times, but during the final year only conducted once (Len Thomas, personal communication).

Observers in our study were trained at minimum of three mornings prior to collecting actual data. At each point observers recorded distance and time of first call for each unique bobwhite covey (Wellendorf et al. 2004). To account for detection differences by distance, we estimated a detection function using program DISTANCE (Thomas et al. 2009, Wellendorf and Palmer 2005). We binned the data into 4 bins of variable size: 0–50 m, 50–100m, 100–250, and 250–500 m based on previous work by Wellendorf and Palmer (2005). The type of distance function was selected with information theoretic procedures (AIC values; see above for AIC explanation) and by investigating the frequency distributions of the data. We did not try every possible combination of models because our data behaved well and was insensitive to the model chosen (Thomas et al. 2009). Model fit was assessed with  $\chi^2$  model-fit statistics. We used a non-parametric bootstrap (n=999) to estimate the variance associated with density estimates.

### 3.3 RESULTS

#### 3.3.1 HAZARD MODELING

We captured 1046 bobwhites throughout the study period (Male = 540; female=506). We radio-tagged a total 409 bobwhites (Male = 119; female=290) and were able to use 384 of these individuals for modeling (Male = 116; Female= 266)–because of radio failures upon release we did not include the remaining individuals in the sample. Bobwhites were followed on average 132 days ( $\bar{x}$  =132.00, SD = 121.0) until mortality or censored. We right censored 108 bobwhites, of which 26 were alive at the end of the study period.

The top ranking hazard model ( $w_i = 0.60$ ) garnered much of the model weight and was 2.6 times more likely than the second ranking model (Table 3.1). The top model included three categorical variables: GENDER, AGE, YEAR, and the continuous variable RAIN30. The global model was the next best model and had a modest weight ( $w_i = 0.28$ ). The third best model was 6 times less likely to represent the truth than the top model ( $w_i = 0.11$ )–it included: GENDER, HABMAX, and YEAR. The remaining models accounted for only 2% of the total wt.

The relative importance wt. (Table 3.2) was the highest for GENDER ( $\sum w_{GENDER} = 1.0$ ;  $n = 6$ ) and YEAR ( $\sum w_{YEAR} = 0.98$ ;  $n = 6$ ). The treatment, FIRESIZE, received the least amount of wt. ( $w_{FIRESIZE} = 0.98$ ;  $n = 6$ ).

The Cox proportional hazard diagnostics suggested most variables met the constant hazard assumption (P-value for  $\rho$ ,  $> 0.05$ ; Table 3.4). However, the quasi-experimental variable HABMAX had one level that did not meet this criteria, level 5–bobwhites that spent the majority of their time in habitats such as wetlands, roads, and pasture.

Unconditional parameter estimates and hazard ratios indicated several variables have biologically significant effects on hazard rates (Table 3.3). Male bobwhites had a higher hazard than females (HR = 1.72; CL= 1.15,2.57). The third year of study was the most hazardous to bobwhites compared to the first year (HR = 1.37; CL = 0.68,2.75). Bobwhites

that spent the majority of their time within growing season burns of the previous year experienced higher hazard than winter burns of the previous year (HR = 2.67; CL = 1.30,5.50; see Figure 3.3). Parameter estimates for the treatments were highly variable making it difficult to draw conclusions; however, small fires were less hazardous than large fires (HR = 0.73; CL = 1.30,5.50; see Figure 3.2).

### 3.3.2 POPULATION ESTIMATION

We conducted covey call surveys on 46 point-transects with one-half of the those surveyed twice in a single year yielding a total effort of 69. These surveys yielded 469 detections with the majority of those in the outer bin (Figure 3.5). Our data showed no sign of heaping. The half-normal cosine function fit the data the best and required no addition cosine adjustments [AIC = 993.19, Effective detection distance (EDR) =  $275.26 \pm 9.02$  SE, Overall detection probability (P) =  $0.30 \pm 0.01$  SE]. According to the  $\chi^2$  test, model fit was good (P = 0.83). The coefficient of variation for our overall density estimate was acceptable (CV% = 22.9). The overall density estimate pooled for all years and treatments was 3.47 (birds/ha) (Bootstrapped 2.5 and 97.5 quartiles = 2.70,4.84).

Post-treatment densities were consistently highest on the small fire size treatment (Figure 3.6). Furthermore, in most years the medium treatment density was higher than the large with the exception being 2006. The large treatment was the only treatment to have a terminal density lower than the pre-treatment density, suggesting an overall decline in the population. However, we believe the 2006 estimate of density for the large treatment was biased high causing this trend to be exaggerated. Nonetheless, the large treatment population was essentially stagnant during the three years of treatments (i.e. estimated population growth rate,  $\lambda = 1$ ). The medium and small treatments exhibited an increase during the treatment years ((i.e.  $\lambda > 1$ ).

### 3.4 DISCUSSION

Our study led to us to three general conclusions: (1) bobwhite hazard rates were affected by fire size treatments, but were less important than other variables in our models; (2) habitat patches burned with growing season fire were most hazardous to bobwhites; and (3) bobwhite density was affected by the treatments most years. The relationship between hazard rates and fire size was quadratic with the hazard rates were the lowest in the small fire size treatment, lowest in the large treatment, and highest in the medium treatment (although CL centered mostly on 1). Wellendorf and Palmer (2009) found similar results in north Florida; however, their burn sizes were much smaller than this study, but the direction of the relationship depicted was the same. Horn et al. (2005) found comparable results with duck nest survival in grass fields in the Midwest; they found nest survival to be the highest in large and small fields but lowest in medium sized fields. We concur with the explanation of Horn et al. (2005) that predators are less efficient in searching large patches, but lack a plausible explanation for increased survival in small patches compared to medium sized patches. Avian predators of adult bobwhites are more efficient than typical nest predators—changing the dynamics of plausible explanations. Avian predators [e.g., Cooper’s hawks (*Accipiter cooperii*), sharp-shinned hawk (*Accipiter striatus*), and red-shouldered hawks (*Buteo lineatus*)] normally account for the majority of adult bobwhite predation (Burger et al. 1995a, Cox et al. 2004, Sisson et al. 2009). These avian predators are not limited in space as ground dwelling meso-mammals. Hawk species may shift movements throughout their homerange to areas of more bobwhite activity (Turner et al. 2008); however, II and Lima (2006) reported hawk space use was unpredictable and did not focus on prey hotspots. Avian predators may be more efficient at harvesting bobwhites in areas of larger disturbances. Bobwhites are poor fliers, rarely flying at distances greater than 100 m (Kassinis and Guthery 1996). Bobwhites foraging large burns before adequate recovery has occurred are likely beyond a single flight to escape cover. Hypothetically, a circular burn of 40 ha would have a radius of 400 m, 4 times that of the average bobwhite

flight. If an individual bobwhite is molested by a hawk in a large burned patch it is unlikely to make it to safety. Bobwhites in medium sized patches may be under pressure from both edge hunting meso-mammals and avian predators hunting the core areas.

Growing season fire typically reduces the amount of woody cover in pine savanna habitats (Drewa et al. 2006, Outcalt 2008). This outcome may be beneficial depending on the current state of the vegetation and desired objectives. Bobwhites prefer woody vegetation levels ca. 30% (Kopp et al. 1998, Martin et al. 2009). We observed that growing season fires reduced woody vegetation below the 30 % threshold which could decrease the utility of that habitat for escape cover. However, the utility of growing season fire cannot be discounted because those fires can help maintain wood cover near the desired levels once the community shifts past the threshold. Furthermore, growing season fires give habitat managers another tool to manage succession in the high productive forests of the Southeast with minor negative effects to bobwhites.

Contrary to our hypothesis, rainfall amounts reduced the hazard rates for bobwhites. In this context, our metric for rainfall may have not captured the phenomenon we had hoped. Our hypothesis was related to the effects of rainfall and flooding which creates less usable space and subsequently higher hazards from predation. However, as modeled, rainfall likely was a better surrogate for vegetation recovery post-fires. Lusk et al. (2001) reported bobwhite abundance was positively associated with spring rainfall but summer rainfall decreased abundance relative to the mean. We were unable to parse differences in season with this data-set and this likely would have produced more meaningful results.

Reported densities of bobwhites are sparse because techniques that incorporate detection rates have not been readily used in the past. Most studies report relative abundance (coveys/point) or an index value that is assumed to relate to the underlying abundance (Johnson 2008, *sensu*). In the rangeland habitat of Texas, estimated density of bobwhites to be between 0.43 and 0.60 (birds/ha) using line-transect distance sampling (Leif and Smith 1993). In an intensive agriculture landscape, bobwhite densities were found to be less

than 0.36 birds/ha (Smith and Burger 2009). Following habitat restoration of an agricultural landscape, Terhune et al. (2009) demonstrated a 75% increase (0.86 to 1.48 birds/ha) in bobwhite density. On managed sites in Texas, reported bobwhite density ranging between 0.52–2.94 (birds/ha) (Rusk et al. 2007). Our density estimates are higher relative to those reported in the literature but this is plausible considering the intensive management on a large landscape. Our findings were supported by the hunting records during the study period (Palmer et al. 2002).

Fire size played a role in bobwhite abundance during most years of our study. Density does not always related directly to habitat quality or quantity (Van Horne 1983) but should be indicative of demography metrics such as survival and reproduction—with the exception of populations action in a source-sink paradigm (Pulliam 1988). Our density estimates for the treatments mirrored the hazard rates and reproduction for bobwhites within each treatment (see, Chapter 2). The small fire treatment population generally increased during the study and was higher than the other two treatments. Although we felt the pre-treatment estimate of density for the large scale is bias high, the overall growth rate for the treatment was below one.

Much like most large scale manipulative experiments, our study suffered from lack of spatial replication of the experimental units (Block et al. 2001, Eberhardt and Thomas 1991). We only had one unit for each of the three fire treatments, but did have multiple years of data. The costs and logistical constraints did not allow multiple replicates. However, the treatments were randomly applied upon initiation of the study. Furthermore, our experimental units were adequate in size (>300 ha) that our study organism was virtually unaffected by fragmentation or edge effects of the surrounding landscape. We believe our results, if tested, would be replicated under similar circumstances and very likely within the south Florida rangeland ecosystem.

### 3.5 CONSERVATION IMPLICATIONS

Bobwhites can be used as a surrogate for other non-migratory, ground-nesting, disturbance dependent species as to how disturbance sizes, in this case fire, will affect reproduction. The large fire sizes represented in our experiment are small relative to those used by public land management agencies throughout the Southeast. Avian response to even larger fires will likely be more dramatic, suggesting existing low abundances of bobwhites on those areas of perceived suitable habitat structure are an artifact of a disturbance regime not aligned with bobwhite adaptations. Habitat managers are in a conundrum between logistical and biological objectives on the application of fire to a given landscape. Larger fires to some extent are more logistically efficient, but are likely not optimal biologically for most species of birds. We encourage planners and managers to consider fire size as a constraint in their fire management plans. However, we do caution that the creation of new fire breaks (edge) may have other deleterious effects on the targeted species. The creation of new fire breaks could be circumvented with the use of natural fire breaks and changing firing techniques to create a mosaic of unburned and burned fuel (habitat) on large fires. However, more research is needed on this topic because typically those unburned patches will be areas of low habitat quality. These remnant patches may act as ecological traps for bobwhites in this context (Schlaepfer et al. 2002).

### 3.6 ACKNOWLEDGMENTS

We would like to thank our private donors for supporting this research through funding and land access. We would also like to thank the USDA-Bobwhite Restoration Project, Tall Timbers Research Station and Land Conservancy, Inc., University of Georgia Graduate School and Warnell School of Forestry and Natural Resources for funding. We thank the many technicians and interns that braved the elements in the pursuit of this data. We thank the helpful comments of peers and committee members that improved this draft.

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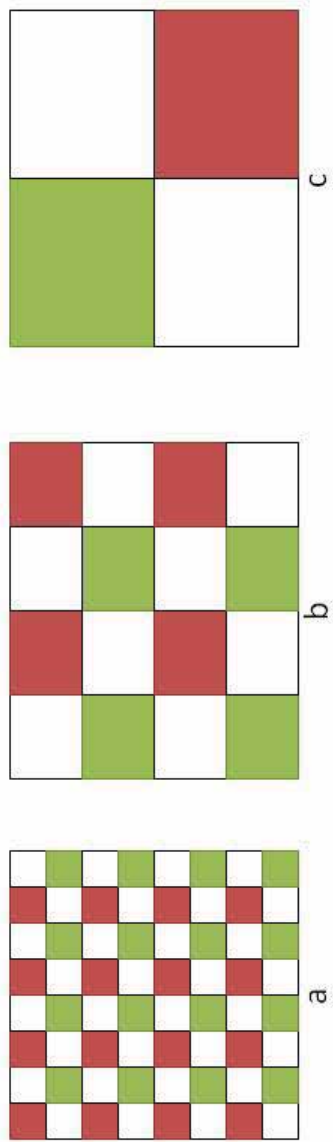


Figure 3.1: A simplified schematic of the prescribed fire size treatments: (a) small ca. 10 ha, (b) medium ca. 20 ha, and (c) 40 ha. Red squares indicate fires in the growing season and green squares indicate dormant season fires.

Table 3.1: Models predicting hazard rates using Cox proportional hazard models for northern bobwhites in Florida, USA. Models are ranked by differences in  $\Delta AIC_c$  values.

Model	k	-2logL	AIC	$\Delta AIC$	$w_i$	$r^2$
GENDER+AGE+YEAR+RAIN30	10	48.53	970.58	0.00	0.5963	0.12
GLOBAL	12	40.50	972.118	1.54	0.2764	0.12
GENDER+HABMAX+YEAR	8	60.88	974	3.42	0.1078	0.10
GENDER+HABMAX+RAIN300	7	69.84	977.747	7.17	0.0166	0.09
FIRESIZE+HABMAX+YEAR	9	54.56	982	11.42	0.0020	0.08
FIRESIZE+HABMAX+RAIN30	8	61.49	983.91	13.33	0.0008	0.08
HABMAX	5	98.70	987	16.42	0.0002	0.05
FIRESIZE+HABMAX	7	70.64	988.986	18.41	0.0001	0.06
GENDER+AGE+YEAR+RAIN30+HABMAX	5	130.60	1306	335.42	0.0000	0.11
FIRESIZE+YEAR+RAIN30	5	130.70	1307	336.42	0.0000	0.11
RAIN30	1	663.00	1326	355.42	0.0000	0.05
GENDER	1	670.50	1341	370.42	0.0000	0.01
FIRESIZE	2	336.50	1346	375.42	0.0000	0.01
AGE	1	673.50	1347	376.42	0.0000	0.00

Table 3.2: Importance weights  $\sum w_{variable}$  for explanatory variables used to model northern bobwhite hazard rates on private ranch, Florida, USA, 2006-2008.

Explanatory Variable	n	Relative Importance $\sum w_{variable}$
GENDER	6	1.00
YEAR	6	0.98
AGE	4	0.87
HABMAX	4	0.40
RAIN	6	0.38
FIRESIZE	6	0.28

Table 3.3: Unconditional model-averaged parameter estimates, odds ratios, and relative survival response to fire size treatments and other variables for northern bobwhites on a private ranch, FL, US, 2005-2008.

Variable	$\beta$	SE	Hazard Ratio	LCL	UCL	Survival Response
SEX(male)	0.54	0.21	1.72	1.15	2.57	-
FIRESIZE(MED)	0.04	0.28	1.04	0.60	1.81	-
FIRESIZE(SMALL)	-0.32	0.29	0.73	0.41	1.29	+
YEAR(2007)	-0.24	0.58	0.79	0.25	2.45	+
YEAR(2008)	0.31	0.36	1.37	0.68	2.75	-
RAIN	-0.06	0.02	0.94	0.91	0.98	+
AGE(JUV)	-0.21	0.21	0.81	0.54	1.23	+
HABMAX(PGS) <sup>1</sup>	0.98	0.37	2.67	1.30	5.50	-
HABMAX(CDS) <sup>2</sup>	-0.02	0.37	0.98	0.47	2.03	+
HABMAX(CGS) <sup>3</sup>	0.44	0.34	1.55	0.79	3.05	-
HABMAX(IB) <sup>4</sup>	-0.60	0.76	0.55	0.12	2.45	+
HABMAX(NB) <sup>5</sup>	0.57	0.40	1.78	0.81	3.91	-

<sup>1</sup>Previous growing season <sup>2</sup>Current dormant season <sup>3</sup>Current growing season <sup>4</sup>Areas not readily available to burn, such as roads, wetlands, and roads. <sup>5</sup>Not burned in previous 2 years

Table 3.4: Diagnostic statistics for variables used in Cox proportional hazard models. The  $\rho$  statistic tests the assumption of constant hazard through time (i.e., not time dependent).

Variable	$\rho$	$\chi_2$	$P$
GENDER	-0.09	1.02	0.31
AGE	0.16	3.34	0.07
HABMAX(PGS) <sup>1</sup>	-0.13	1.62	0.20
HABMAX(CDS) <sup>2</sup>	-0.11	1.18	0.28
HABMAX(CGS) <sup>3</sup>	-0.13	1.68	0.20
HABMAX(IB) <sup>4</sup>	-0.20	4.57	0.03
HABMAX(NB) <sup>5</sup>	-0.16	2.48	0.12
YEAR(2007)	0.12	1.52	0.22
YEAR(2008)	0.03	0.10	0.76
RAIN30	0.16	3.33	0.07
FIRESIZE(Medium)	-0.01	0.01	0.94
FIRESIZE(Small)	-0.13	1.72	0.19

<sup>1</sup>Previous growing season <sup>2</sup>Current dormant season <sup>3</sup>Current growing season <sup>4</sup>Areas not readily available to burn, such as roads, wetlands, and roads. <sup>5</sup>Not burned in previous 2 years

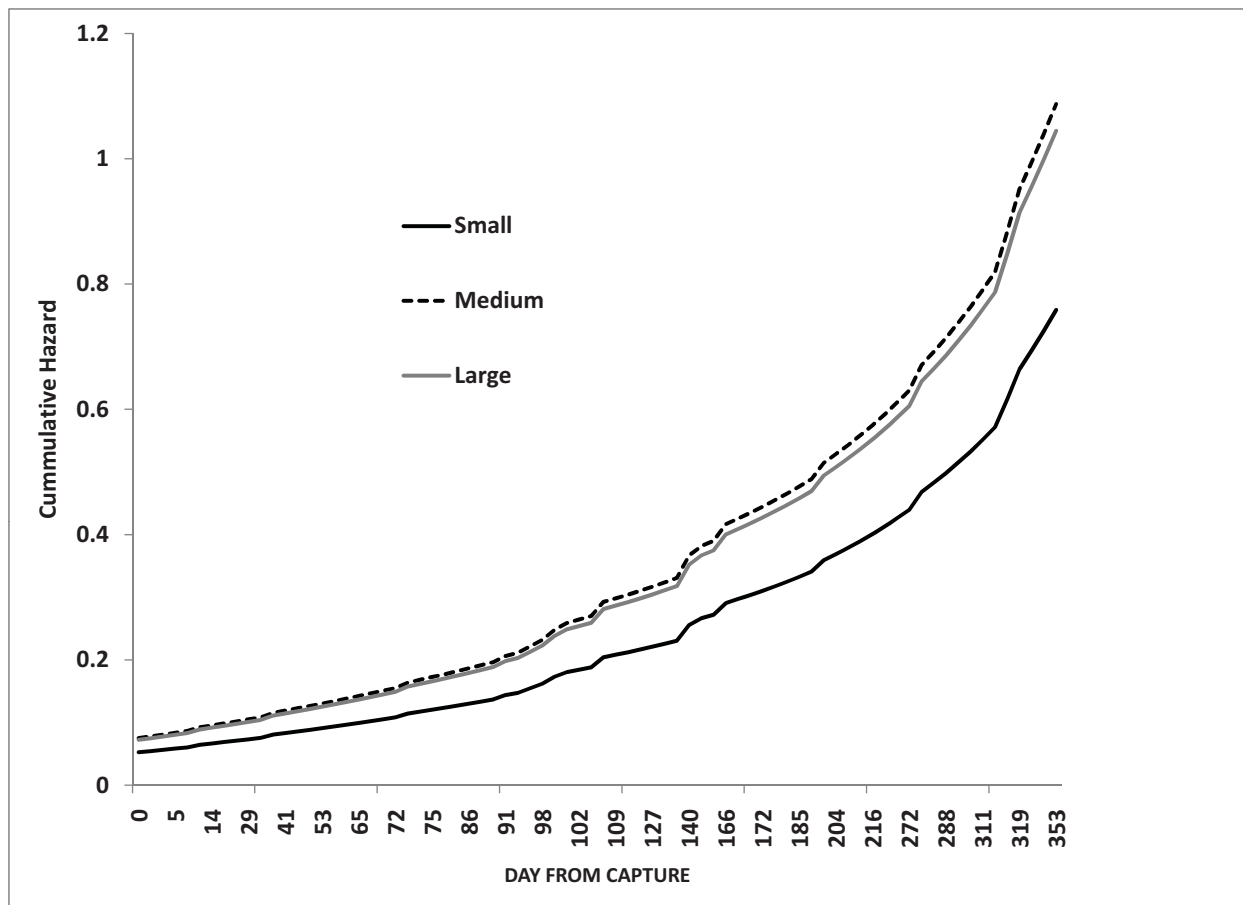


Figure 3.2: Cumulative hazard curves estimated from Cox proportional hazard models for northern bobwhites under three fire size treatments (Small, 10 ha; Medium, 20 ha; Large, 40 ha) in south Florida, US, 2006-2008.

Table 3.5: Density (birds/ha) of northern bobwhites under three different fire size treatments observed on a private ranch in south Florida, US, 2006-2008.

Year	Small		Medium		Large	
	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI
2005 <sup>1</sup>	3.33	1.55	3.95	1.41	6.92	9.45
2006	2.87	1.02	1.98	0.90	2.96	1.46
2007	3.90	1.72	3.07	2.77	2.87	1.60
2008	4.69	3.71	4.42	1.51	3.93	1.52
Pooled <sup>2</sup>	3.82	1.04	3.16	1.39	3.25	0.66

<sup>1</sup>Pre-treatment data. <sup>2</sup>Pooled estimates only includes 2006–2008 data.

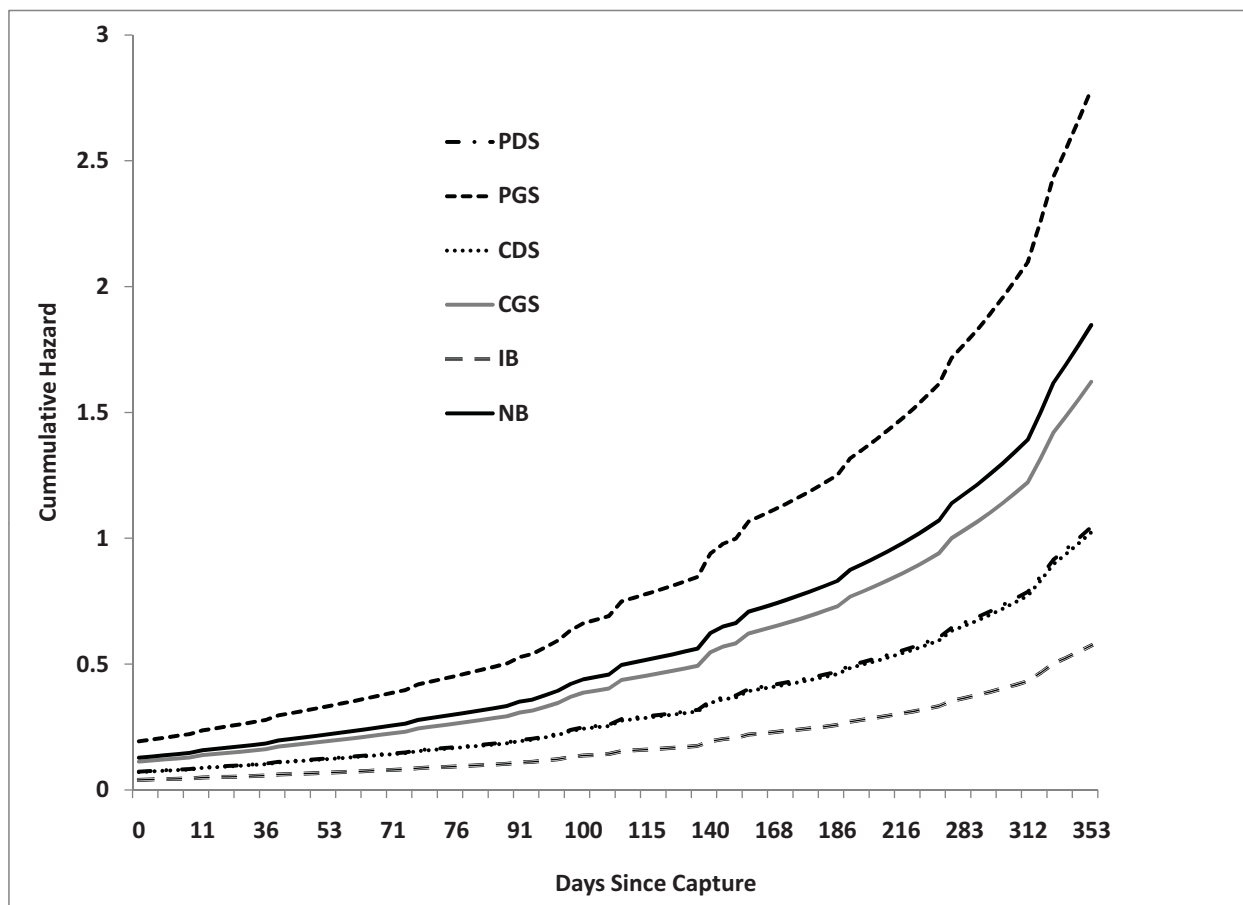


Figure 3.3: Cumulative hazard curves estimated from Cox proportional hazard models for northern bobwhites in response to various seasons of fire in south Florida, US, 2006-2008. Abbreviations = PDS, previous dormant season; PGS, previous growing season; CDS, current dormant season; CGS, current growing season; IB, impossible to burn; NB, not burned in previous 2 years.

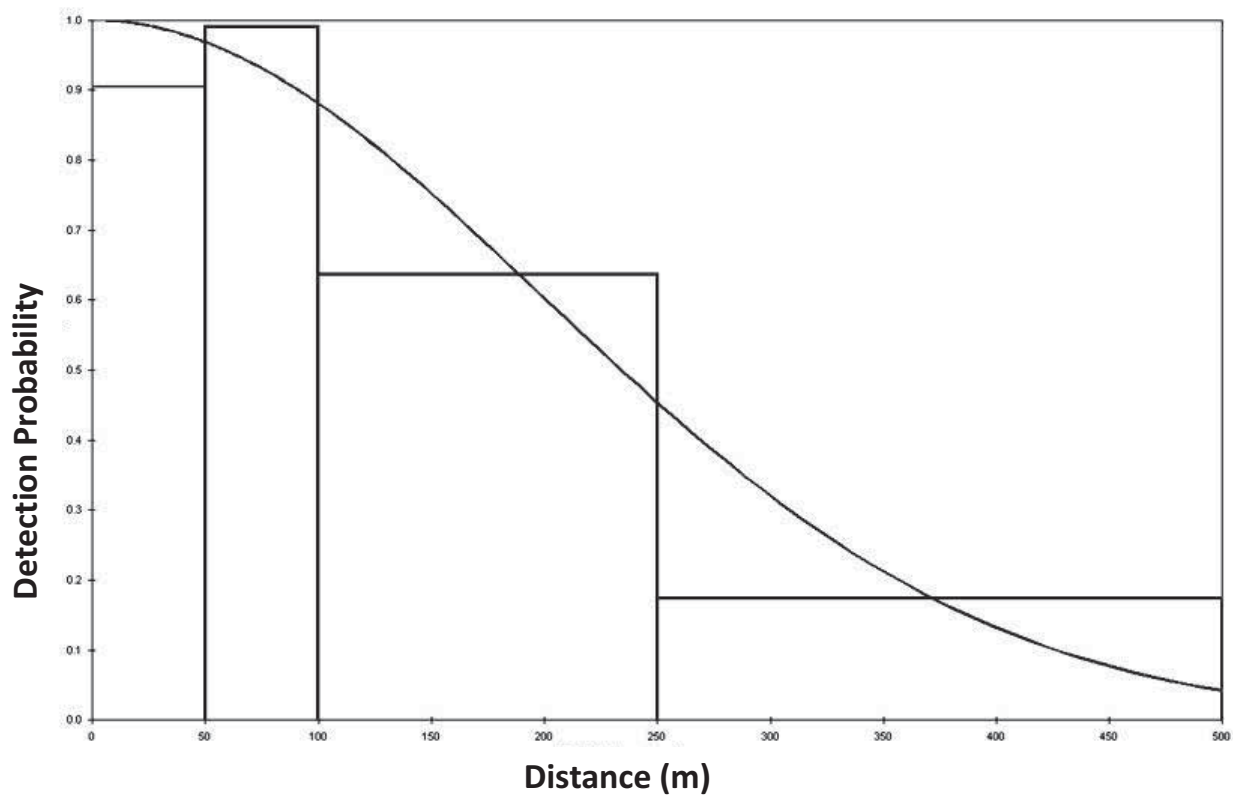


Figure 3.4: Half-normal detection function, best-selected model determined by AIC using program DISTANCE, describing northern bobwhite covey detection in south Florida, US, 2005-2008. Data was placed into four bins: 0–50 m, 50–100, 100–250 m, and 250–500 m.

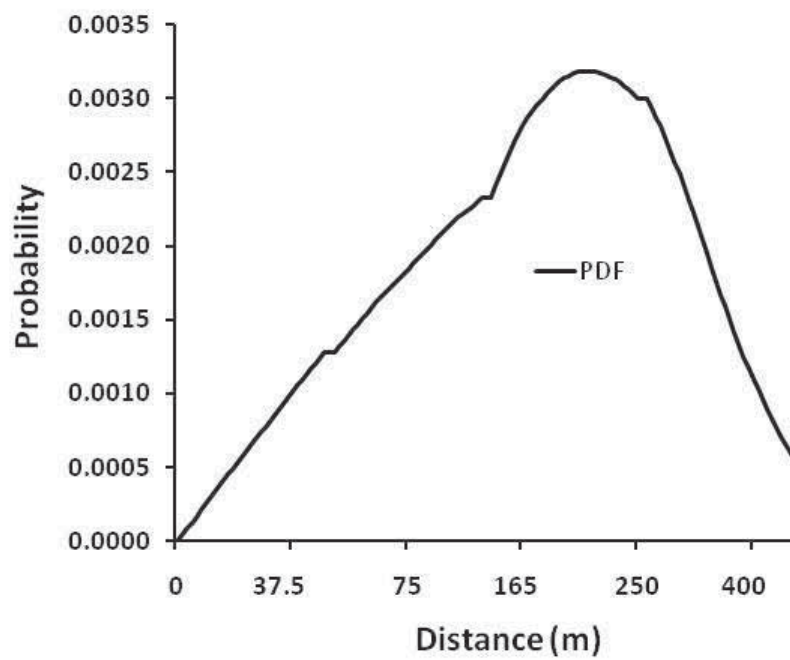


Figure 3.5: Probability density function for covey detections in south Florida, US, 2005-2008.

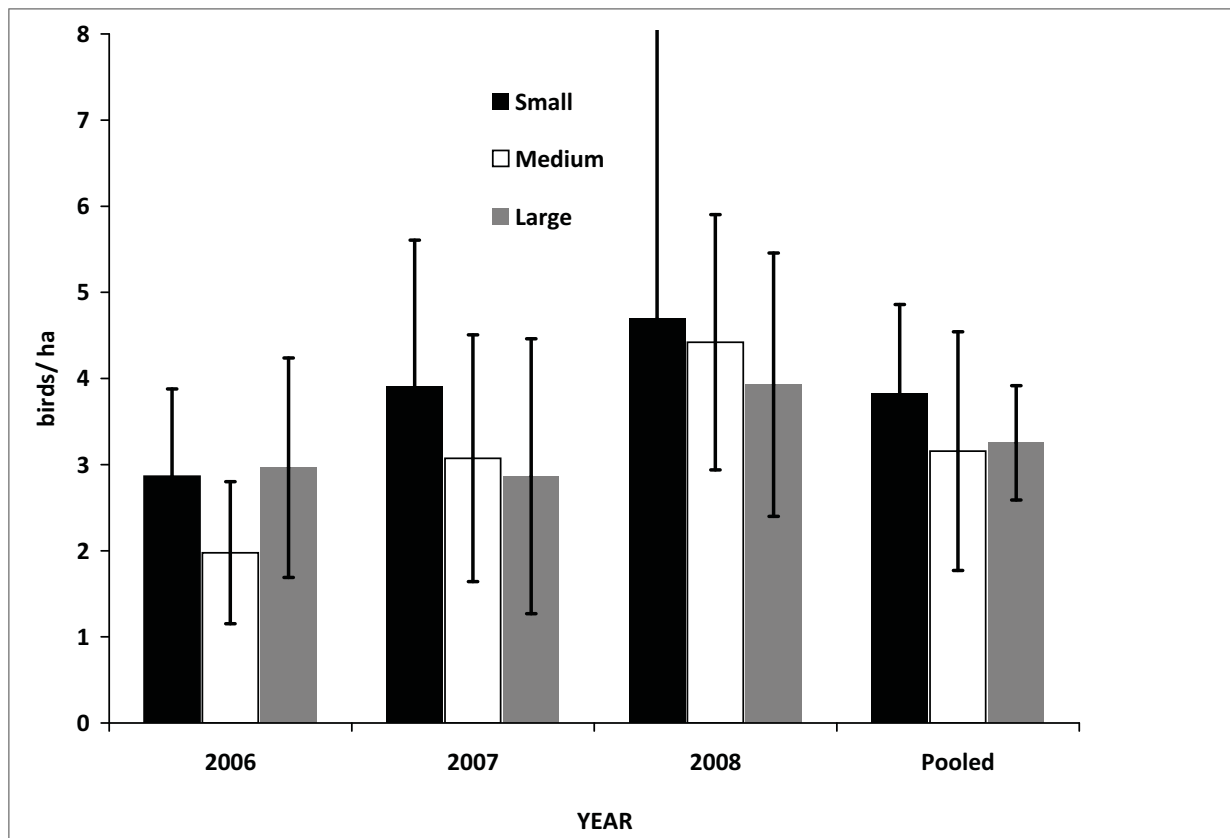


Figure 3.6: Density estimates (Birds/ha) northern bobwhites under three different fire size treatments observed on a private ranch in south Florida, US, 2006-2008. Red line indicates the initiation of treatments, and pooled estimates only include years post initiation of treatments.

## CHAPTER 4

### NEST HABITAT SELECTION BY NORTHERN BOBWHITES ON SOUTH FLORIDA RANGELANDS AT TWO SPATIAL SCALES<sup>3</sup>

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<sup>3</sup>Martin, J.A., W. E. Palmer, J. P. Carroll. To be submitted to: *Journal of Wildlife Management* as a note.

#### 4.1 INTRODUCTION

Northern bobwhites (hereafter, bobwhites; *Colinus virginianus*) are one the most studied animal species in the world. However, the published literature is scant on information regarding bobwhite nest site selection, especially in the eastern portion of the population range (however, see Parnell 2002, Puckett et al. 1995, White et al. 2005). In the Midwest and Southwest, several authors have described the importance of numerous fine scale habitat features for nest site selection (Lusk et al. 2006, Rader et al. 2007, Taylor et al. 1999, Townsend et al. 2001). However it is likely that differences exist between the ecological drivers for selection between subtropical or temperate areas of the Southeast versus more arid ecosystems of the Southwest. Nest selection in subtropical systems is likely driven by fine scale habitat characteristics, climatic conditions, coarser scale habitat conditions, habitat management, and interactions among those drivers (White et al. 2005). Under most circumstances, eastern subtropical habitats do not lack sufficient cover for nesting bobwhites but may lack the quality of cover they potentially seek. In the Southwest, it is believed that > 600 nest sites/ha is a minimum amount of nesting cover (Hernandez et al. 2003) this threshold can be met on a majority of old-field or native ground cover settings in the Southeast.

Bobwhites may select nest sites based on fine scale vegetation cues, but it is possible that selection decisions are made at coarser scales within the bird's operating landscape (White et al. 2005). Previous studies have shown with other ground nesting species that spatial arrangement and composition may determine nest site selection (Staller et al. 2002, Stephens et al. 2005, White et al. 2005). We measured bobwhite nest selection at two spatial scales to determine the cues used by bobwhites to select areas for reproduction in subtropical rangelands of Florida.

## 4.2 METHODS

### 4.2.1 STUDY AREA

The climate in south Florida is subtropical and humid with average annual temperatures in the mid-20s C, ranging from about 16 C in mid-winter to about 27 C in summer. Rainfall averages about 137 cm, with 50–60 % of it occurring from June to September (Obeysekera et al. 1999, USFWS 1999).

The study area is managed for bobwhite habitat and hunting. Cattle were excluded from the quail management areas, and had been for approximately 7 years. The predominant habitat type on the ranch is mesic-pine flatwoods, and exotic grass pasture (i.e. improved pasture). The quail management areas have historically been burned on a 2-3 year return interval within the traditional dormant season (January-early March). The flatwoods had an over-story of predominately longleaf pine (*Pinus palustris*) and some pockets of South Florida slash pine (*Pinus elliottii* var. *densa*). The herbaceous vegetation consisted of highly pyrogenic species, such as saw palmetto (*Serenoa repens*), wiregrass (*Aristida* spp.), bluestems (*Andropogon* spp.) and creeping bluestem (*Schizachyrium* spp.).

### 4.2.2 FIELD DATA COLLECTION

We captured bobwhites using standard wire walk-in funnel traps (February - April, 2006 - 2008) baited with grain sorghum (Stoddard 1931). Birds were banded and fitted with 6.4-6.9 g pendant-style radio transmitters and released (American Wildlife Enterprises, Monticello, FL, USA). All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists' Union 651988) and those of the University of Georgia, Institutional Animal Care and Use Committee (IACUC Protocol No. 2001-GB-01). Radio-marked bobwhites were located using homing techniques (White and Garrott 1990) 3 - 5 days per week and approached to within 10 - 25 m. Locations

were taken using a programmable telemetry receiver and a three-element hand-held yagi antenna. We approximated the bobwhite's location using geometric calculations which required a GPS position of the observer, distance to the bird in meters, and compass bearing. We assumed that birds were nesting if in the same location on 2 consecutive days (Burger et al. 1995*b*). Once the nest had been initiated it was flagged. Nests were checked twice daily, once in the morning to detect depredations from the previous night and in the afternoon to detect if bird was on recess. Egg counts were taken when birds were on recess. Nests were monitored until termination (Burger et al. 1995*a*). Upon nest termination, the fate of the nest was determined by visual inspection of the nest bowl and egg fragments. If nests were successful, the number of successful eggs that hatched was recorded. We did not attempt to determine cause specific failure of nest based upon findings by Staller et al. (2005).

#### 4.2.3 MICRO-SITE VEGETATION DATA COLLECTION

We measured vegetation characteristics at all known nest sites and random locations. A random site was determined by a random azimuth and predetermined distance from nest (20 meters). We quantified visual obstruction, and canopy cover of numerous vegetation functional groups (i.e., grass, forb, woody, saw palmetto, litter, vine, and bare ground) at each location. We measured visual obstruction from the mean of four observations from the four cardinal directions using a Robel pole (Robel et al. 1970) placed at the center of the nest bowl or at a random location. Observations were taken at a distance of 3 m and height of 1 m. The mean obstruction value was used for each location. We estimated percent canopy cover at each nest and random site using a modified 1 m Daubenmire frame (Daubenmire 1959). The disc of vulnerability [adapted from (Kopp et al. 1998)] for each location was determined by placing a tennis ball within the nest bowl or random location and taking the maximum distance the ball could still be seen from the four cardinal directions. The mean of the four values was used to calculate the area of a circle (i.e. disc),

this value can be interpreted as an index for nest concealment. Furthermore, the distance to nearest human created edge (e.g. road, tractor trail, or fenceline) was determined by pacing from each location. However, using an Geographic Information System and the *Near* tool these distances were also to test the accuracy and validity of the observers values (ESRI 2009).

#### 4.2.4 LARGE-SCALE LANDSCAPE METRICS

We used a different set of random points to calculate nest selection at the larger scale. The random points were constrained to fall within the known area traversed by bobwhites in this study determined by telemetry locations. We selected four landscape metrics (Table 4.1) that may explain variation in nest selection at a larger scale. We constructed a 450 m buffer around each nest to calculate landscape configuration metrics. This buffer was chosen based on homerange and movement data specific to this study area (J. A. Martin, unpublished data). The metrics were selected from those possible within Fragstats (McGarigal et al. 2002) based on our understanding of bobwhite ecology and how landscape structure may hypothetically affect nest site selection. Furthermore, we explored how landscape composition within the buffer would affect selection.

#### 4.3 DATA ANALYSIS

Prior to modeling, a Pearson Correlation procedure was run for each pair of predictor variables (see Table 4.1 for variable descriptions). Variables that were deemed correlated if  $r > 0.30$  were eliminated from the analysis to avoid multicollinearity. We also plotted scatter plots and box plots of each variable to expect the data's distribution and relationships with other variables (see 4.1). If variables were correlated or depicted a noticeable relationship from the scatter plots, those variables were not included in the same models.

#### 4.3.1 NEST HABITAT SELECTION

We used logistic regression to model the probability a bobwhite would construct a nest under various habitat characteristics and landscape configuration. The response variable was a binary value, 1 for nest or 0 for random location, and the vegetation characteristics and landscape metrics were used as covariates. The generic logistic model would be:

$$y = 1/(1 + \exp^{-(\beta_0 + \beta k)}) \quad (4.1)$$

where  $k$  is a vector of covariates included in the model.

#### MODEL SELECTION

Nest selection models were assessed on how well they fit the data using Akaike's Information Criterion [AIC; (Burnham and Anderson 2002)]. The relative fit of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002), which can take a value from 0 to 1, with the best-fitting candidate model having the greatest Akaike weight. We then calculated  $AIC_c$  (AIC corrected for small sample sizes) values,  $AIC_c$  weights, model-averaged parameter estimates and unconditional standard errors for each effect and overall survival (Burnham and Anderson 2002).

#### 4.4 RESULTS

We observed 139 northern bobwhite nests throughout the three years of study. However because of logistical constraints and the implementation of prescribed fires we were only able to collect vegetation data (Table 4.2 and Figure 4.2) on 88 nests (2006,  $n = 28$ ; 2007,  $n = 25$ ; 2008,  $n = 35$ ). At the 450 m spatial scale we used all 139 nests and 137 random points to make predictions.

The top ranking model garnered much of the AIC wt. ( $w_i = 0.92$ ;  $r^2 = 0.20$ ; Table 4.3); this model contained percent grass cover (GRASS), disc of vulnerability (DOV), total vegetation canopy cover (CANCOV), and the amount of litter (LITT). The next best model

was 27 times less likely than the top ranking model ( $w_i = 0.03$ ;  $r^2 = 0.18$ ). The remaining models received very little support based on AIC. However, the global model explained 20 % of the variation in selection based on the  $r^2$  value.

At the 450 m scale, the top model received the majority of the weight ( $w_i = 0.88$ ;  $r^2 = 0.14$ ) and included the % PAST variable. It was 5 times more likely than the second best model ( $w_i = 0.17$ ;  $r^2 = 0.15$ ). Based on the  $r^2$  values, the models at the nest scale were better at explaining variation than at the 450 m scale. The global model at the nest-site scale explained 21% of the variation compared to the 15% for the larger scale models.

Unconditional parameter estimates indicated a multitude of effects on nest site selection (see Table 4.4). Most parameter estimates confidence intervals overlapped zero or had a null effect. However, some variables suggested biological significance, including: GRASS, DOV, LITT, CANCOV, and % PAST. This is in concordance with the top ranking models at both scales that included all of these variables. The scaled odds ratio for GRASS ( $1.2 \times 2$  Daubenmire values; which is equivalent to an increase of ca. 12 % in grass cover) indicates selection to be 2.24 times more likely. Conversely, a 2 m<sup>2</sup> increase in the area a nest can be seen decreases the likelihood of selection by a factor of 2.94. A biologically meaningful increase (10%) in litter and total canopy coverage increased the odds of selection by a factor of 2.14 and 2.57, respectively. At the 450 m scale, only the % pasture within the buffer had biological meaning. The scaled odds ratio for % PAST indicated that for every 10% increase in pastureland bobwhites were 9.45 times less likely to select those areas for nesting; conversely, a similar increase in native flatwoods will increase the odds by 10-fold.

#### 4.5 DISCUSSION

Based on our findings, general conclusions can be drawn on how bobwhites select sites for nesting: (1) bobwhites prefer areas with higher amounts of native grasses, (2) nest sites were more likely in areas of high concealment, less than 2.5 m<sup>2</sup> of viewing area, and (3) are

found in an areas with less pasture at the local landscape scale. Bobwhites are selecting sites for nesting at both scales we investigated. Bobwhites likely are seeking micro-site vegetation characteristics to assure survival of the clutch (see Chapter 2). Nest site choices at larger habitat scales may be a function of the perceived gains in fitness (i.e. increased survival of young). Bobwhites have precocial young with limited movement capabilities the first 14 days of life (Taylor and Guthery 1994); therefore, daily biological requirements are needed within a close proximity to the hatch site. In our study, bobwhites favored areas with lesser amounts of exotic grass pasture. Exotic pasture has been described previously being negative for chick movement and survival (Barnes et al. 1995, Burkhart 2004). The avoidance of pasture at larger scales is likely a function of increasing the likelihood of offspring survival post-hatch. Bobwhites expend a large amount of time and energy investment in hatched broods relative to other families of birds; therefore, they tradeoff their individual survival for fecundity (Martin 1995).

Previous research indicated that landscape configuration was important for explaining nest selection for bobwhites (White et al. 2005). We did not find this to be the case in our study. The landscape configuration metrics were not selected in the models or had biologically meaningful effect sizes. We contribute the lack of landscape configuration effects to be a function of 2 things: an artifact of the landscape scale measured and the differences in our landscape compared to those in the Southeast (Donovan et al. 1997, Guthery 1999). Our landscape was more intact and was less affected by fragmentation than those investigated by White et al. (2005). Within the extent of our study area fragmentation is quite minimal relative to larger extents.

Our results concur with the literature regarding nest concealment for bobwhites (Arredondo et al. 2007). Arredondo et al. (2007) found nests detected at no greater than 4 m<sup>2</sup> while random sites were detectable greater than 5 m<sup>2</sup> away. These results were corroborated in Kansas and Oklahoma (Taylor et al. 1999, Townsend et al. 2001), where bobwhite nests were found in vegetation more conducive to concealment. Martin (Chapter

1) reported bobwhite survival to be higher for nests with lower viewing areas (i.e. more concealed). These findings collaboratively establish that bobwhites seek nest sites with greater concealment.

Concordant with previous research, nest sites had higher amounts of grass cover compared to random sites (Lusk et al. 2006, Taylor et al. 1999). The dominant grasses used for nesting cover and substrate on our study area were wiregrass and creeping bluestem. These grasses form small colonies larger than average clump grasses and allow bobwhites to conceal their nests. Creeping bluestem has decreased in prevalence throughout most of south Florida because of over-grazing and improper fire management (L.L. Yarlett and Roush 1970, White and Terry 1979). On our study area, creeping bluestem was the dominant grass species and was most abundant on patches burned after April 1st. Unlike the arid Southwest, we believe grass clumps for nesting are not limiting on this study area (Guthery 1986, Hernandez et al. 2003, Lehmann 1984); however, the data suggests bobwhites select sites with higher amounts of grass cover relative to those available.

#### 4.6 MANAGEMENT IMPLICATIONS

Bobwhites make decisions on where to nest based on the likelihood of success of the nest itself and the subsequent offspring, these decisions are affected by habitat at multiple scales. Our study illustrates the similarities between nest site selection among bobwhites in different ecoregions of the US. The objective for the habitat manager is to manage succession through space and time such that optimal nest sites are available (Guthery 1997). We suggest habitat managers in the Southeast create vegetative conditions that create high nest concealment composed of mostly herbaceous plants, moderate amounts of litter, and maintain substantial amount of native flatwoods on the landscape. Landscape configuration was irrelevant in this landscape, but these results will likely vary on the landscape in question (Donovan et al. 1997). Researchers and managers in more complex

landscapes should not ignore landscape configuration as a potential driver for bobwhite nest selection.

#### 4.7 ACKNOWLEDGMENTS

We would like to thank our private donors for supporting this research through funding and land access. We would also like to thank the USDA-Bobwhite Restoration Project, Tall Timbers Research Station and Land Conservancy, Inc., and the Graduate School University of Georgia and Warnell School of Forestry and Natural Resources for funding. We thank the many technicians and interns that braved the elements in the pursuit of this data. We thank the helpful comments of peers that improved this draft.

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Table 4.1: Explanatory variable descriptions and possible relationship with northern bobwhite nest habitat selection at two spatial scales. Data take from a private ranch, FL. USA, 2006-2008.

Explanatory Variable	Description
DOV	Disc of vulnerability : an index of nest concealment; as this value increases the nest can be seen from ground level at a farther distance
BARE	Bare ground: the amount of bare ground around the nest bowl; more bare ground likely indicates less nest concealment
DISTEDGE	Distance to human created edge;
MPI	Mean Proximity Index; a measure of the degree of isolation and fragmentation of a patch, an increase in this value indicates more fragmentation; more fragmentation likely indicates more predation
IJI	Interspersion Juxtaposition Index; as the number increases patches of habitat are more adjacent;
PRD	Patch richness density; number of patch types in 450 m buffer;
FORB	Forb cover; the amount of forbs around nest bowl
SAW	Saw palmetto ( <i>Serenoa repens</i> ) ; the amount of saw palmetto around the nest bowl
GRASS	Grass cover; the amount of grass cover around the nest bowl
WOOD	Woody cover; the additional amount of woody cover around the nest bowl excluding saw palmetto

Table 4.1 – Continued

Explanatory Variable	Description
LITT	Litter; the amount of litter surrounding the nest bowl
CANCOV	Canopy cover; the amount of total canopy coverage by all plants species surrounding the nest bowl
ROBEL	Robel pole value; a measurement of visual obstruction
DISTWETLD	Distance to wetland; the distance (m) from the nest site to the nearest wetland
% PAST	The percentage of pastureland surrounding the nest site within the 450 m buffer
% NATIVE	The percentage of native groundcover surrounding the nest site within the 450 m buffer
% WETLDS	The percentage of wetlands surrounding the nest site within the 450 m buffer

Table 4.2: Mean and SE for explanatory variables included in nest habitat selection models for northern bobwhites in south Florida, US, 2006-2008.

Explanatory Variable	Actual		Random	
	$\bar{X}$	SE	$\bar{X}$	SE
<b>Nest site scale</b>				
FORB <sup>1</sup>	4.24	0.25	4.65	0.27
GRASS <sup>1</sup>	7.93	0.22	7.22	0.21
WOOD <sup>1</sup>	2.88	0.27	3.34	0.30
SAW <sup>1</sup>	3.65	0.32	3.47	0.28
CANCOV <sup>1</sup>	3.75	0.41	1.29	0.20
LITT <sup>1</sup>	7.06	0.30	6.88	0.26
BARE <sup>1</sup>	3.57	0.26	4.76	0.28
DISEGE <sup>2</sup>	21.59	2.44	24.78	2.32
ROBEL <sup>1</sup>	3.39	0.14	3.12	0.12
DOV <sup>3</sup>	2.03	0.15	3.30	0.23
DISWET <sup>2</sup>	265.89	196.12	89.77	5.31
<b>450 m Scale</b>				
MPI	28.51	1.06	22.17	1.07
IJI	62.09	0.64	65.41	0.71
PRD	11.02	0.11	11.25	0.1
% PAST	0.06	0.01	0.16	0.02
% NATIVE	0.49	0.01	0.43	0.01

<sup>1</sup>Daubenmire value

<sup>2</sup>meters

<sup>3</sup>m<sup>2</sup>

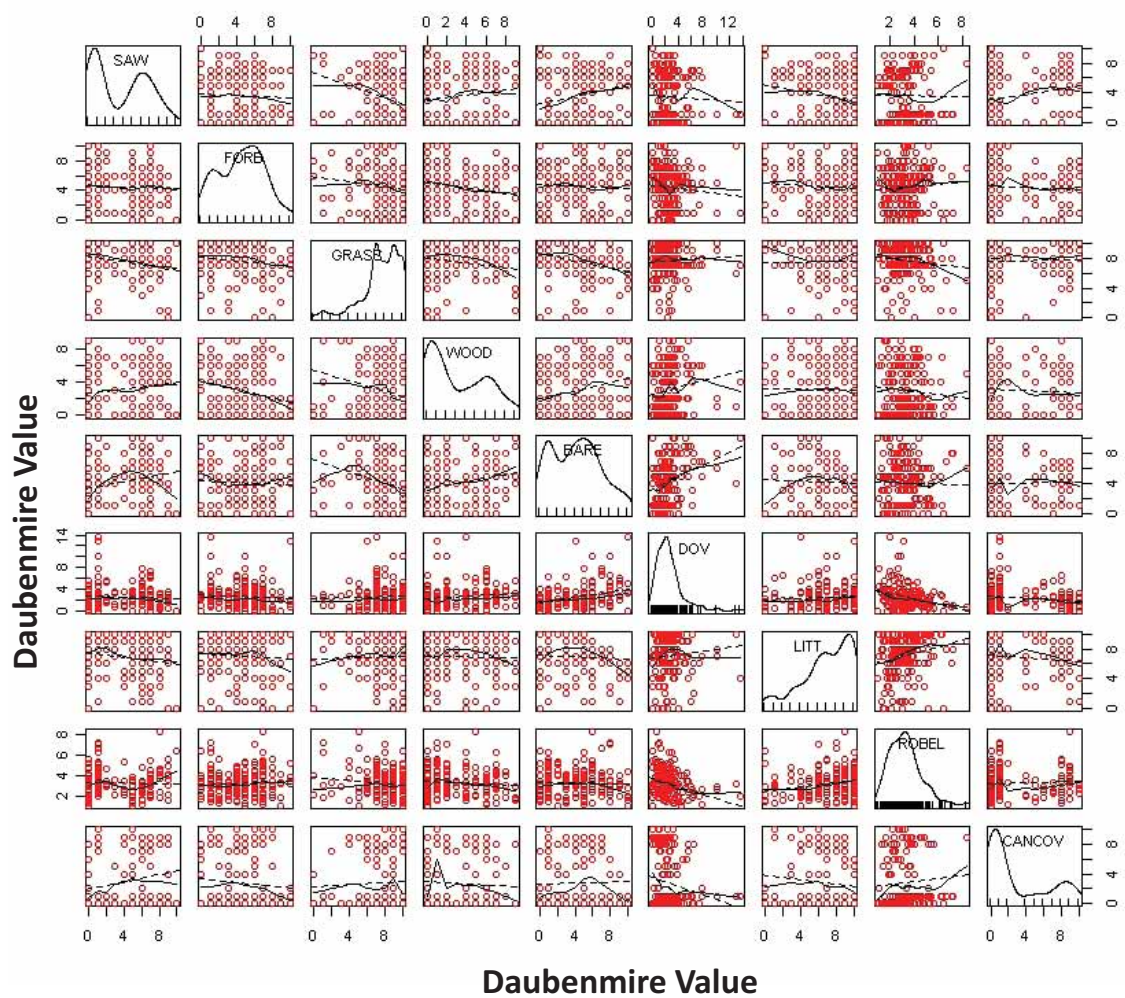


Figure 4.1: Scatter-plot of each of the variable's values, relationships between variable pairs, and the data distribution of each variable (the right diagonal). In each cell, the broken line represents the linear relationship with the paired variable and the solid line is a non-parametric spline to fit the data.

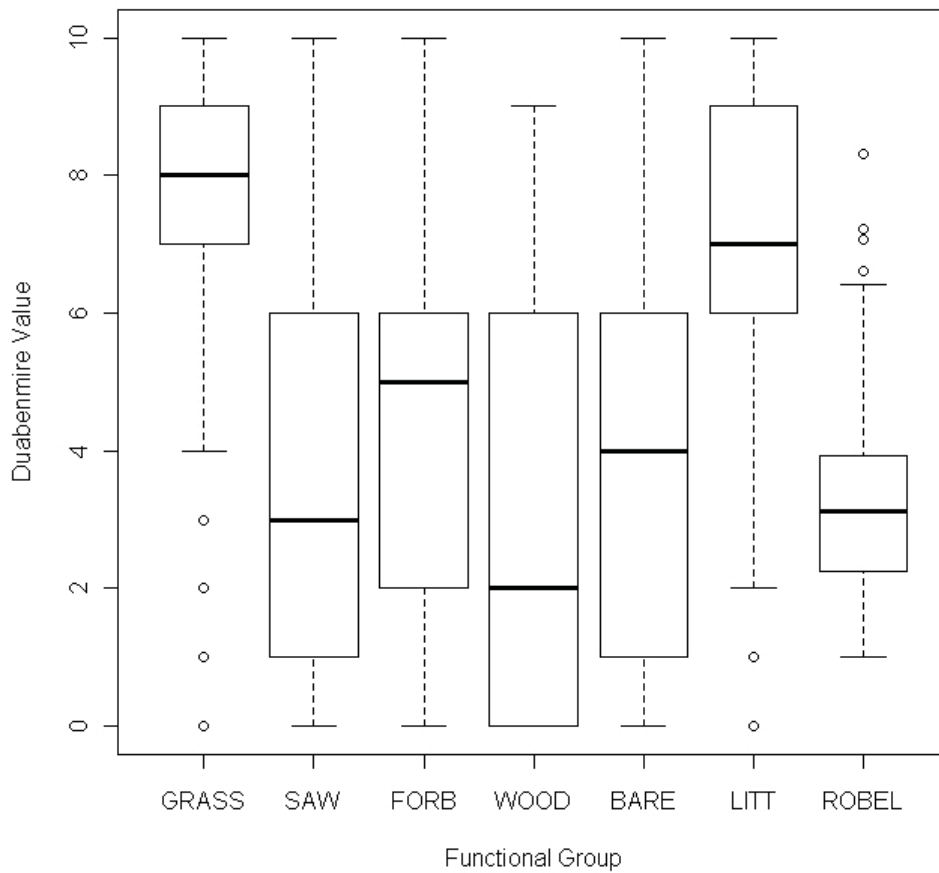


Figure 4.2: Box-plot (Solid line = median; box encompasses 2.5 and 97.5 % quantiles; limits represent minimum and maximum; and dots are outliers) diagram of vegetation variables used to describe habitat selection by northern bobwhites. Plants within functional groups are similar plants based on physiological and structural characteristics.

Table 4.3: Models describing variation in nest habitat selection for northern bobwhites in Florida, USA, 2006-2008. Models are ranked by differences in  $\Delta AIC_c$  values.

Model	K	AIC	Deviance	$\Delta AIC$	$w_i$	$r^2$
GRASS+DOV+CANCOV+LITT	4	314.34	304.34	0	0.92	0.20
BARE+DOV+ROBEL+CANCOV	4	320.95	310.95	6.61	0.03	0.18
GLOBAL	10	322.14	302.14	7.8	0.02	0.21
BARE+DOV+ROBEL+CANCOV+EDGE	5	322.59	310.59	8.25	0.01	0.18
BARE+DOV+ROBEL+CANCOV+DISWATER	5	322.93	310.93	8.59	0.01	0.18
GRASS	1	377.43	373.43	63.09	0.00	0.02
GRASS+FORB	2	379.24	373.24	64.9	0.00	0.02
SAW+FORB+GRASS+WOOD	4	381.1	371.1	66.76	0.00	0.03
ROBEL	1	383.04	379.04	68.7	0.00	0.01
WOODY	1	383.11	379.11	68.77	0.00	0.00
FORB	1	384.32	380.32	69.98	0.00	0.00
SAW+WOOD	2	384.89	378.89	70.55	0.00	0.01
SAW	1	384.89	380.89	70.55	0.00	0.00
<b>450 m Scale Models</b>						
% PAST	1	330.71	326.71	0	0.83	0.14
MPI+JI++PRD+% PAST	4	333.93	321.93	3.22	0.17	0.15
MPI+JI++PRD+% NATIVE	4	358.1	346.1	27.39	0.00	0.09
MPI+JI++PRD+% WETLDS	4	364.52	352.52	33.81	0.00	0.07
% NATIVE	1	374.43	370.43	43.72	0.00	0.02

Table 4.4: Unconditional model-averaged parameter estimates and Odds Ratio for explanatory variables included in northern bobwhite habitat selection models on a private ranch, Florida, US, 2006-2008.

Variable	Parameter Estimate	SE	Odds Ratio	95 % CL
Intercept	-1.146	0.797	—	—
FORB	-0.003	0.050	0.997	(0.90,1.10)
SAW	0.005	0.050	1.005	(0.91,1.11)
GRASS	0.190	0.060	1.209	(1.07,1.36)
WOOD	0.020	0.050	1.020	(0.92,1.13)
BARE	-0.100	0.364	0.905	(0.44,1.85)
DOV	-0.385	0.083	0.680	(0.57,0.80)
LITT	0.066	0.047	1.068	(0.97,1.17)
CANCOV	0.251	0.050	1.285	(1.16,1.42)
ROBEL	-0.048	0.085	0.953	(0.80,1.13)
DISTEDGE	-0.003	0.005	0.997	(0.99,1.01)
DISTWETLD	0.0003	0.0002	1.000	(0.99,1.00)
<b>450 m Scale</b>				
Intercept	-0.152	1.054	—	—
MPI	0.001	0.001	1.001	(0.99,1.00)
IJI	-0.015	0.020	0.985	(0.95,1.02)
PRD	-0.120	0.140	0.887	(0.67,1.17)
% PAST	-0.057	0.012	0.945	(0.92,0.97)
% NATIVE	0.020	0.010	1.020	(1.00,1.04)

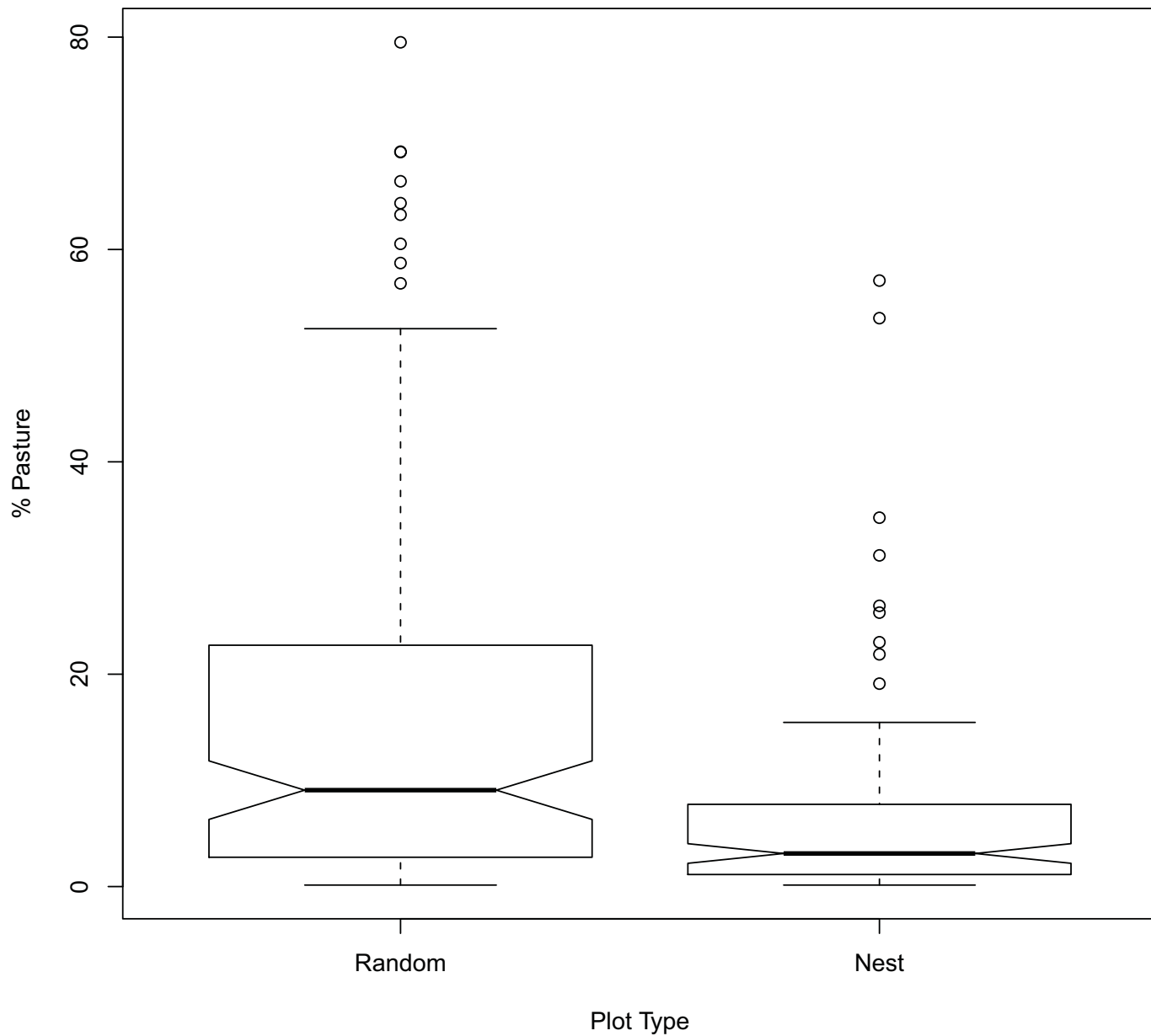


Figure 4.3: Box plot diagram (Solid line = median; box encompasses 2.5 and 97.5 % quantiles; limits represent minimum and maximum; and dots are outliers) comparing % Pasture for actual and random northern bobwhite nest sites in south Florida, US, 2006-2008. Notches that do not overlap are considered significantly different.

CHAPTER 5

ASPECTS OF NORTHERN BOBWHITE ECOLOGY ON SOUTH FLORIDA PASTURELAND<sup>4</sup>

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<sup>4</sup>J.A. Martin, W. E. Palmer, and J. P. Carroll. To be submitted to: *Journal of Range Management*.

## 5.1 INTRODUCTION

Historically, northern bobwhites (*Colinus virginianus*) were abundant residents of fire-maintained prairie habitats in peninsular Florida (Frye 1954). However, over the past 40 years bobwhite populations have declined at an annual rate of 4.3 % (Hines 2007), likely due to: degradation of native prairie habitats resulting from incompatible fire management and grazing practices, and conversion of native prairie habitats to pastureland dominated by exotic forages, principally bahia grass (*Paspalum notatum*) and Bermuda grass (*Cynodon dactylon*) (Dimmick et al. 2002, Hines 2007). Exotic pasturelands now occupy 1.2 million ha of what was once suitable bobwhite habitat.

Bobwhite habitat use and demographic parameters are well documented in most agro-ecosystems, but information is lacking for subtropical pasturelands in the Southeastern United States. However, Flanders et al. (2006) and Kuvlesky et al. (2002) described the negative impacts of exotic grasses on bobwhites in the Southwest. In Texas, Flanders et al. (2006) reported bobwhite density was 2.72 (bird/ha) on native pastures (>50% relative dominance); conversely, on exotic pastures (<50% relative dominance) densities averaged 1.42 (bird/ha). Habitat-based studies relative to bobwhite suitability have been conducted on tall fescue (*Festuca arundinacea*) pastures in the Southeast (Barnes et al. 1995, Burger et al. 1990, Washburn et al. 2000). Although these areas differ from the vast bahia pastures of south Florida, these authors concluded that fescue pasture did not meet the biological requirements for bobwhites.

Understanding bobwhite ecology in altered habitats is important for determining habitat opportunities on working pasturelands. Considering the spatial extent and economic importance of pastureland it is important to identify ways to improve these areas for bobwhite conservation. It is also important to quantify the value of remaining native prairie habitats to bobwhites.

We could not experimentally test the effects of pastureland compared to more native habitats on bobwhite demographics simultaneously because the study area was predomi-

nately exotic pasture. Therefore, this study establishes baseline information for bobwhites in a landscape dominated by exotic pasture, but some remnant native habitats. Our objectives were to estimate habitat use and selection of bobwhites in a peninsular Florida pastureland agro-system, compare population parameters to those of bobwhites in other habitats, and determine density of bobwhites in this habitat type. We also provide evidence that habitat management can affect bobwhite populations in a landscape dominated by exotic pastureland. This information can be used by conservation planners charged with modeling landscapes for bobwhite habitat suitability. Also, the Northern Bobwhite Conservation Initiative is keenly interested in manipulating pastureland habitats to make them more suitable for bobwhite populations (Dimmick et al. 2002, Palmer and Terhune 2010).

## 5.2 MATERIALS AND METHODS

### 5.2.1 STUDY AREA

This study was conducted on a 2,300 ha private ranch approximately 6 km south of Arcadia, FL, USA. The ranch has been grazed under a deferred rotation grazing system since 1978 similar to that described by Merrill (1954). The ranch separated cattle into multiple herds (depending on season) that were rotated on regular intervals, rarely grazing >50% of the herbage in a given paddock. The objective of the grazing systems was to reduce stress on the native grass species and legumes within pastures, reduce the probability of invasive exotic species occupation [e.g. cogongrass (*Imperata cylindrica*) and tropical soda apple (*Solanum viarum*)], and limit fertilizer inputs (Capece et al. 2007). Annually a moderate amount of bahia grass sod was removed for commercial sale. Also, the ranch maintained ca. 260 ha of citrus groves for commercial sale. The ranch habitat composition was: 59 % pasture, 10 % woody, 7 % semi-improved pasture, 7 % fallow, 6 % seasonal wetlands, 3% unimproved pasture, 3 % young citrus grove, and < 2 % other.

Climate in south Florida is subtropical and humid with average annual temperatures in the mid-20s C, ranging from ca. 16 C in midwinter to ca. 27 C in summer. Rainfall averages about 137 cm, with 50–60 % of it occurring during June–September (Obeysekera et al. 1999, USFWS 1999).

### 5.2.2 HABITAT MANIPULATIONS

During 2004, we manipulated approximately 7 % of the study area (ca. 400 acres) using several habitat management techniques that we believed would create a positive population response. These manipulations included: prescribed fire, seasonal disking, and mechanical brush control. This was not done in an experimental approach because of the spatial arrangement of the study area and the areas occupied by bobwhites. However, manipulations should be viewed as quasi-experimental; therefore, any response (positive or negative) should be considered correlative.

### 5.2.3 DATA COLLECTION

We captured bobwhites using standard wire walk-in funnel traps (February–April, 2004–2005) baited with grain sorghum (Stoddard 1931). Birds were banded and fitted with 6.4–6.9 g pendant-style radio transmitters and released at the site of capture (American Wildlife Enterprises, Monticello, FL, USA). All trapping, handling, and marking procedures were consistent with guidelines in the American Ornithologists' Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists' Union 651988) and those of the University of Georgia, Institutional Animal Care and Use Committee (IACUC Protocol No. 2001-GB-01).

Radio-marked bobwhites were located using homing techniques (White and Garrott 1990) 3 - 5 days per week and approached to within 10–25 m. Locations were taken using a programmable telemetry receiver and a three-element hand-held yagi antenna. We approximated the bobwhite's location using geometric calculations which required a GPS

position of the observer, distance to the bird in meters, and compass bearing. We assumed that birds were nesting if they were recored in the same location on 2 consecutive days following Burger et al. (1995c). Once the nest had been initiated it was flagged. Nests were checked twice daily, once in the morning to detect depredations from the previous night and in the afternoon to detect if bird was on recess. Egg counts were taken when birds were on recess. Nests were monitored until termination to determine fate (Burger et al. 1995c). A land cover map was created using 2004 digital-ortho-quarter-quads (DOQQs) and global positioning systems. The smallest mapping unit was approximately 1 ha. A total of eight macro-habitat types were delineated on the study area. Approximated bobwhite locations were overlaid on the GIS map using the Animal Movement Extension (Hooge and Eichenlaub 1997). Habitat type was spatially joined to each telemetry location. Home range sizes were plotted on a scatter plot diagram to distinguish the minimum number of locations needed to include a bobwhite in the analysis. The minimum was set at 12 at which point home range size began to become asymptotic. All locations from 15 Mar – 18 Oct were used in home range estimations.

#### 5.2.4 DATA ANALYSIS

##### HOME RANGE AND HABITAT ANALYSIS

The Animal Movement extension (Hooge and Eichenlaub 1997) was used to create 100% minimum convex polygons (MCP) for bobwhite home ranges. The ranch boundary was used to delineate the availability of habitats. We used PROC GLM in an ANOVA setting using SAS (SAS Institute 2003) to compare home range sizes between the two years, between sexes, and between two age classes (juvenile and adult). We also tested for interactions between all groups.

We described habitat use during the breeding season (Mar–Oct) at two spatial scales, corresponding to Johnson (1980) 2nd and 3rd order selection using compositional analysis (Aebischer et al. 1993). Habitat composition of the ranch and within each bird's home

range was defined by intersecting the polygons of the ranch and home ranges in GIS. We compared proportions of each habitat type in the study area (availability) with proportions found in each individual's home range (use) to determine 2nd order habitat selection (Aebischer et al. 1993, Johnson 1980). We then compared proportions of habitats in each home range (availability) with radio locations of each individual (use) to determine 3rd order selection (Aebischer et al. 1993, Johnson 1980). Multivariate analysis of variance (MANOVA) was used to test the null hypothesis that bobwhite habitat use was random. The *adehabitat* package (Calenge 2006) for R was used to conduct the analysis according to Aebischer et al. (1993). Prior to analysis, we replaced zero values for use with the value 0.001 which was one order of magnitude less than the smallest recorded non-zero proportion (Aebischer et al. 1993). When a habitat was not available for use, we replaced missing values in each log-ratio with the mean of all non-missing values for the respective log-ratio (Aebischer et al. 1993).

### 5.2.5 REPRODUCTION

Fecundity is the number of young successfully raised during a defined interval, generally one year or breeding season (Gill 2000); annual fecundity reflects the number of nesting attempts and the success of each attempt, clutch size, and the experience of the breeding individual (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 ( $\pi$ ) multiplied by mean brood size ( $\gamma$ ) and mean number of nests produced per year ( $\psi$ ). Thus, the estimator for  $F$  is:

$$\hat{F} = (\pi) * \left(\frac{\gamma}{2}\right) * (\psi) \quad (5.1)$$

where  $\hat{F}$  is the number of juvenile females hatched;  $\pi$  is the estimated probability that a breeding female successfully hatches a clutch (i.e. nest success rate);  $\gamma$  is the estimated mean brood size (see equation 5.6); and  $\psi$  is the mean number of nests built. The

above estimator assumes an equal gender 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, Williams et al. 2002):

$$\hat{var} = \left( var(\hat{\pi}) * (\hat{\gamma}\hat{\psi})^2 \right) + \left( var(\hat{\gamma}) * (\hat{\pi}\hat{\psi})^2 \right) + \left( var(\hat{\psi}) * (\hat{\pi}\hat{\gamma})^2 \right) \quad (5.2)$$

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

$$\hat{P} = \hat{H} * \bar{x} \quad (5.3)$$

where  $\hat{H}$  is the probability that a breeding female produces a successful clutch and  $\bar{x}$  is the mean clutch size. Because equation 5.3 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:

$$\hat{P} = \hat{h}_1\hat{b}_1 + \hat{h}_2\hat{b}_2 + \hat{h}_3\hat{b}_3 \quad (5.4)$$

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:

$$\hat{b} = \frac{1}{y_i} \sum_{j=1}^{y_i} b_{ij} \quad (5.5)$$

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

$$b = \hat{C}S * \hat{H}R \quad (5.6)$$

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, Williams et al. 2002).

#### SURVIVAL ANALYSIS

We based breeding season survival rates on a 273 day interval (15 Mar – 18 Oct). These dates correspond to known breeding activity from our telemetry records. Survival parameters were estimated using Program MARK (White and Burnham 1999) which allows flexibility in modeling survival parameters and estimates. Data structure followed a live-dead (LDLD) format and was read into MARK as a known fates model (Williams et al. 2002). The known fates model works similar to Kaplan-Meier estimation method (Pollock et al. 1989). However, known fates modeling within program MARK allows for the integration of covariates, groups, and selection between models (White and Burnham 1999). We modeled survival with four groups: YEAR (2004 and 2005), and GENDER (male or female). We believed that survival would vary by the year of study and the gender. We also used individual covariates that included the percentage of fallow habitats and improved pasture within each bird's home range.

#### MODEL SELECTION

Survival models were assessed on how well they fit the data using Akaike's Information Criterion [AIC; (Burnham and Anderson 2002)]. The relative fit of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002), which can take a value from 0 to 1, with the best-fitting candidate model having the greatest Akaike weight. We then calculated  $AIC_c$  (AIC corrected for small sample sizes) values,  $AIC_c$  weights, model-averaged parameter estimates and unconditional standard errors for each effect and overall survival (Burnham and Anderson 2002).

## POPULATION ESTIMATION

We estimated bobwhite density using autumn covey-call point-transects, a type of distance sampling (Buckland et al. 2001, Thomas et al. 2009, Wellendorf and Palmer 2005). Observers in our study were trained minimum of two mornings prior to collecting data. At each point observers recorded distance and time of first call for each unique bobwhite covey (Wellendorf et al. 2004). To account for detection differences by distance, we estimated a detection function using program DISTANCE (Thomas et al. 2009, Wellendorf and Palmer 2005). We developed a global detection probability curve from a larger dataset and post-stratified the density estimates to obtain a density estimate for this study area. The type of distance function was selected with information theoretic procedures (AIC values; see above for AIC explanation), and model fit was assessed with  $\chi^2$  model-fit statistics.

We adjusted the density of bobwhite coveys by incorporating the availability of bobwhite coveys to be detected (Diefenbach et al. 2007, 2003). Wellendorf et al. (2004) developed a logistic regression equation to predict the probability of a bobwhite covey to call. The probability is influenced by several weather variables and the number of adjacent coveys that call (i.e. a density dependence response). Lastly, to convert the density of bobwhite coveys to density of bobwhites we used a year specific covey size estimate, observed from intentionally flushed coveys, to derive density of individuals.

We used descriptive statistics to present the bobwhite density results because of our low numbers of covey call surveys for each year. Each survey plot during each year was considered the experimental unit. Variance among these data was used to compute the 95 % confidence interval.

### 5.3 RESULTS

We radio-tagged 41 bobwhites in 2004 (26 female and 15 males) and 40 in 2005 (22 females and 18 males). Because of a limited sample for some individuals (i.e. < 12 locations), we

used 53 individuals for home range estimation of which 31 were females and 22 were males. Twenty five hens were alive on April 15 in 2004 and they produced twelve nests. In 2005, 22 hens were alive on April 15 and they produced 24 nests. Five covey call surveys were conducted twice each year for each year of study, which produced 50 bobwhite detections.

### 5.3.1 HOME RANGE

Mean summer home range size pooled for both years, genders, and age classes was 43.1 ha ( $\pm 5.8$  SE). The global model testing the difference in home range size for all parameters was not significant ( $F=1.21$ , 1,1 df,  $P=0.31$ ). Home range size did not differ between years ( $F=1.03$ , 1,1 df,  $P=0.31$ ), or genders ( $F=1.95$ , 1,1 df,  $P=0.17$ ) nor by age ( $F=1.51$ , 1,1 df,  $P=0.23$ ).

Home ranges of bobwhites were not distributed among habitats on the study site randomly (2nd order:  $\Lambda = 0.198$ ; 7,54 df;  $P < 0.0001$ ). In addition, bobwhites did not use the habitats within their home range at random (3rd order:  $\Lambda = 0.44$ , 5,50 df;  $P < 0.0001$ ). At the 2nd order level bobwhites preferred fallow (FALL) habitats followed in order by un-improved pasture (UNIMP) and seasonally wet areas (WET).

At the 3rd order level, bobwhites preferred fallow habitats followed by young citrus grove, un-improved pasture, semi-improved pasture (SEMIMP), pasture and seasonally wet areas. For the 3rd order analysis two habitat categories were dropped because they were unavailable to bobwhites within their home ranges: other and woody.

### 5.3.2 SURVIVAL

Predation was the leading cause of mortality (98%,  $n=80$ ); one bobwhite died from decapitation by a mowing machine while incubating a nest. Estimated survival for the weekly periods during our study interval was 0.97 (95% CI: 0.92–1.01). The composite model for

survival is:

$$\phi = 3.295 + 0.257 * \beta_{YEAR} - 0.092 * \beta_{GENDER} + 0.16 * \beta_{PAST} - 0.08 * \beta_{FALL} \quad (5.7)$$

The best-approximating model indicated that bobwhite survival was dependent on the weekly survival period ( $w_{S(t)} = 0.39$ ; Table 5.1). The null model had a relatively high weight indicating that the main independent variables explained little variation in survival ( $w_{null} = 0.10$ ; Table 5.1). Seasonal survival was (S) =0.33 in 2005 and 0.24 in 2004. Males had a higher weekly survival than females. The percentage of improved pasture had a small positive effect on survival ( $w_{PAST}=0.16$ ; SE = 0.176), and percentage of fallow habitat had a small negative effect on survival ( $w_{FALL}=-0.08$ ; SE = 0.155); however, their confidence limits overlapped zero (Table 5.1).

### 5.3.3 REPRODUCTIVE PARAMETERS

Predation was the leading cause of nest failure (n=3), one nest was abandoned for an unknown cause, and one nest was flooded and then abandoned. In 2005 predation was the leading cause of nest failure (n = 4), and three nests were abandoned for unknown causes. One nest failed because the incubating male was killed by farm machinery. All measured nesting parameters were higher in 2005 than 2004 (Table 5.6).

In 2004, only one bobwhite had multiple nests; however, in 2005 5 bobwhites had multiple nests. Nest success was higher in 2005 than 2004 ( $0.67 \pm .03$  vs.  $0.58 \pm .07$ ). Furthermore, the other reproduction metrics were higher in 2005 than 2004, resulting in greater estimates of fecundity and productivity (Table 5.6).

### 5.3.4 BOBWHITE ABUNDANCE

We used 115 covey detections to construct the global detection function, including the 50 detections from this study. The best detection model was a uniform with hermite polynomial adjustments (AIC=155.44;  $\chi^2 = 0.1214$ ,  $P = 0.94$ ). A mean covey size of 10 and 12 was used for 2004 and 2005, respectively. Bobwhite density in 2004 was  $0.52 \pm 0.54$  95% CI (birds/ha) and  $0.75 \pm 0.51$  95% CI (birds/ha) for 2005.

## 5.4 DISCUSSION

### 5.4.1 HOME RANGE

Home range sizes of the bobwhites in our study are relatively large compared to those reported in ecosystems of the southeastern US. The most similar home range size estimates found in the literature were from a study conducted near the Flint Hills of Kansas (Taylor et al. 1999b). Their home range estimates in the rangeland habitats averaged near 103 ha for males and 54 ha for females. In south Texas, reported female bobwhite home ranges are less than 28 ha in grazed pastures (Whiting and Sloan 1993); however, unlike this study their pastures consisted of mostly native plant species. In North Carolina, estimates of home range size in a row crop ecosystem were similar to that of Whiting and Sloan (1993), 32 ha (Puckett et al. 2000). In the well-managed quail plantations of south Georgia and north Florida, Sisson et al. (2000) and Wellendorf and Palmer (2009) found home ranges to be less than 5 ha. It has been postulated that home range size is correlated, if not casually related, to the quality of habitat (Odum and Kuenzler 1955), which suggests that the habitat in this study area is of poorer quality than other areas studied.

There were no statistical differences in home range sizes among years, genders, or age classes; this is likely because of low sample sizes and high variation within groups. However, ecologically bobwhites, regardless of age or gender, had to transverse much of the same conditions on the study site. Both genders participate in reproduction, reducing

the chance of gender specific home range estimates. Also, only breeding season home ranges were measured; therefore, juveniles had several months from the previous breeding season to adapt and familiarize themselves to the area. Quantity of usable habitat space changed very little between the years making it plausible that home range sizes were not different.

#### 5.4.2 HABITAT USE

Breeding season habitat use in this study is consistent with previous studies of bobwhite ecology (Cook 2004, Parnell 2002, Puckett et al. 2000, Taylor and Burger 2000, Williams et al. 2000). The fallow habitat type was the most preferred. Fallow areas mostly consisted of native grasses and shrubs that have been reported as preferred micro-habitat (Kopp et al. 1998, Taylor et al. 1999a). Many of the fallow areas were on the fringe of pastures suggesting they received less grazing pressure from cattle. The un-improved pasture was very similar to the fallow areas and was also highly preferred. This habitat type contained very little exotic forage grass such as bahia. Bobwhites could transverse these areas freely (Burkhart 2004). The remaining pasture types, semi-improved and improved pasture received the least amount of use. These types consisted of mostly exotic forage grasses known to be detrimental to birds (Flanders et al. 2006, Kuvlesky et al. 2002).

Bobwhites avoided woody habitats at both spatial scales. Unlike some other studies, the woody habitat types of this study area are closed canopy oak hammocks and planted citrus groves. These cover types provide little understory vegetation and are likely a refugia for predators (Seckinger et al. 2008). Also, mast production in these areas is very limited compared to other oak forests in the Southeast.

#### 5.4.3 SURVIVAL

The survival rates extrapolated to an annual estimate ( $0.97^{52} = 0.20$ ) derived from this study are lower estimates by from those in in a high quality habitat (Palmer and Wellendorf 2007,

Terhune et al. 2007), but higher than those reported by in areas of limited habitat (Burger et al. 1995a, Corteville 1998).

The analysis showed weak relationships between bobwhite breeding season survival and the explanatory variables—the confidence intervals included zero for the parameter estimates. The top ranking model suggests that variation in survival is dependent on the bi-weekly time period. Weekly weather influences can change dramatically in south Florida during the breeding season. During the study time period, weeks with abundant rainfall greater than 25 cm occurred causing a significant area of the landscape to become flooded—a natural hydrological process in the region (Obeysekera et al. 1999). Modeling these affects on survival is difficult, especially given the sample size. Furthermore, the weather variables are correlated with time making it difficult to separate the influences of weather versus random variation in time. The time varying model likely ranked high because it acts as a surrogate for time correlated weather patterns.

The parameter estimates suggest that survival was higher in the second year of our study—one year after implementing habitat management and may suggest that bobwhites may have been responded to the alterations. However, annual fluctuations in survival are also common for bobwhite populations (Burger et al. 1995b, Cox et al. 2004, Palmer and Wellendorf 2007, Terhune et al. 2007).

Bobwhite survival was only slightly affected by the habitat variables in our analysis. As modeled, the percentage of the habitats were used; however, a more appropriate metric may have been the configuration of habitats or landscape context of bobwhite home ranges. Seckinger et al. (2008) found that the amount of unusable space (closed canopy forest) for bobwhites had a negative effect on survival. Conversely, the pasture was used by bobwhites, because of the open nature and connectivity of the landscape. Furthermore, the vast acreage of pasture are not as conducive to predators as is closed canopy forest. Pastureland may be neutral in regards to survival, but limits bobwhite populations by their ability to occupy the entire landscape.

We assumed the estimates of survival obtained from the sampled population is reflective of the true population rate. Guthery and Lusk (2004) questioned telemetry-based estimates of survival, and suggested the survival estimates derived from most telemetry studies are biased low. However, Palmer and Wellendorf (2007) and Terhune et al. (2007) provided evidence to the contrary for their populations of interest. The stabilizing age ratio (R) for the survival estimate reported herein is 4 (juveniles/adults), less than the 7 used as a benchmark to determine the validity of survival estimates by Guthery and Lusk (2004) suggesting the estimates are valid and recruitment only has to be moderate to maintain a low density population with adequate survival.

#### 5.4.4 NESTING

Nest success was relatively high compared to other bobwhite studies (Burger et al. 1995c). The open pastureland has a limited amount of edge and human-induced travel corridors for predators (Gates and Gysel 1978, Martin 1995). In England, Potts (1986) found that partridge nests were relegated to nest near field edges because of insufficient cover in agriculture fields. He found these nest were mostly unsuccessful because of predator movements along edges. Similarly in North Carolina, bobwhite nest success was low in the narrow strips of habitat around row crop fields (Puckett et al. 1995). In our study area, nests were not directly tied to human-induced edges that may act as travel corridors for predators (Martin 1995) likely reducing predation pressure on nesting bobwhites. The expansive pastureland system is likely negative for meso-mammal predators, reducing habitat space, and decreasing their abundance. For example, the study area provides little mammalian predator refugia (e.g. oak hammocks and citrus groves; <5%), essentially reducing the usable space for mammalian predators. Nest success may be limited in its application to capture changes in bobwhite demographics (Sandercock et al. 2008), other reproductive rates help explain the amount of reproduction occurring within the population. The flexible mating strategies for bobwhites allow them to re-nest and have

multiple clutches (Burger et al. 1995c), reducing the effect of a failed nest on overall reproduction.

The productivity and fecundity estimates suggest that bobwhites were producing chicks at an adequate rate for viability. These estimates were much higher in the second year of study, while the estimates of the first year would not have likely been able to maintain the population. Although, the estimates of fecundity may suggest that reproduction was occurring at levels to sustain the population, we have no data on chick recruitment. Bobwhite chick survival remains an enigma (DeMaso et al. 1997), little data exists on the stage of the bobwhite life cycle. Therefore, we make the assumption that chick survival and recruitment was above the threshold to maintain  $\lambda > 1$ .

#### 5.4.5 BOBWHITE DENSITY

Bobwhite density data does suggest that bobwhite density was positively associated with habitat manipulations. This would be plausible considering higher survival and higher productivity during the second year of study. The increase in covey size between the years was a major factor in the density increase. Ellis et al. (1969) suggested that smaller increases in abundance were experienced in covey size whereas large increases were caused by formation of new coveys of bobwhites.

Reported densities of bobwhites are sparse because techniques that incorporate detection rates have not been used readily in the past. Most studies report relative abundance (coveys/point) or an index value that is assumed to relate to the underlying abundance (Johnson 2008, *sensu*). Leif and Smith (1993) estimated density of bobwhites to be between 0.43 and 0.60 birds/ha using line-transect distance sampling on rangeland habitat in Texas. Smith and Burger (2009) found densities of bobwhites to be less than 0.36 birds/ha in an intensive agriculture landscape. Terhune et al. (2009) demonstrated a 75% (0.86 to 1.48 birds/ha) in bobwhite density following habitat restoration of an agricultural land-

scape. These reported densities are comparable to those obtained in this study providing support that the estimates are plausible.

The demographic parameters reported herein are relatively low compared to those reported for other agro-ecosystems, but not at levels that warrant the disregard of pastureland as a functional bobwhite habitat. Veech (2006) reported that more populations were increasing in pastureland landscapes than decreasing, further suggesting its potential value for management. Conversely, Guthery et al. (2001) suggests that bobwhite abundance is negatively associated with "tame pasture" throughout the Southwest. Management of pasturelands and type of grazing system employed on the pasturelands will likely be the deciding factor on the utility of pastures for bobwhite conservation (Hammerquist-Wilson and Crawford 1981). Our study area was surrounded by large areas of open habitats; either pastureland, native rangeland, or agriculture, which likely bolstered populations on the study area. Pasturelands in areas surrounded by forest would likely produce different results because of increased predation pressure and lack of immigration.

#### 5.4.6 MANAGEMENT IMPLICATIONS

The Northern Bobwhite Conservation Initiative (NBCI) plan's goal is to identify and prioritize areas of suitable or potentially suitable habitat throughout the range of the bobwhite (Dimmick et al. 2002). The plan identifies pastureland as a habitat type in need of conversion to a more suitable land cover type for bobwhites. The costs associated with restoration of pastureland to native rangeland are not conducive under most economic scenarios. The conservation of bobwhites across large landscapes may be better served if pastureland is considered a habitat that is in need of management instead of restoration (i.e. conversion). We suggest the development of objective-based strategies to manage pastureland similar to the approach taken with intensive row crop agriculture landscapes (Burger 2006). However, the challenges will be greater in exotic grass pastures because of

the constant encroachment of exotic grasses into the "native areas" and the disturbances created by cattle.

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Table 5.1: Models predicting breeding season survival for northern bobwhites in Florida, USA. Models are ranked by differences in  $\Delta AIC_c$  values.

Model	K	$AIC_c$	$\Delta AIC_c$	$W_i$	Deviance
$S^{(t)}$	22	396.49	0	0.39	351.69
$B_{YEAR}$	2	398.42	1.93	0.15	394.41
$S^{(i)}$	1	399.19	2.7	0.1	397.19
$B_{YEAR} + B_{PAST}$	3	399.34	2.85	0.09	393.32
$B_{YEAR} + B_{GENDER}$	3	400.17	3.68	0.06	394.15
$B_{YEAR} + B_{FALL}$	3	400.19	3.7	0.06	394.17
$B_{PAST}$	2	400.64	4.15	0.05	396.64
$B_{GENDER}$	2	400.67	4.18	0.05	396.66
$B_{FALL}$	2	400.91	4.42	0.04	396.9

Table 5.2: ANOVA results for comparing homerange sizes among gender, age, and year groups for northern bobwhites on south Florida pastureland.  $\alpha = 0.05$ .

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
GENDER	1	3334.21	3334.21	1.87	0.1780
AGE	1	4407.11	4407.11	2.48	0.1226
YEAR	1	907.91	907.91	0.51	0.4788
GENDER:AGE	1	88.11	88.11	0.05	0.8250
GENDER:YEAR	1	2241.42	2241.42	1.26	0.2678
GENDER:YEAR	1	276.23	276.23	0.16	0.6955
GENDER:AGE:YEAR	1	3210.84	3210.84	1.80	0.1860
Residuals	45	80115.94	1780.35		

Table 5.3: Model averaged parameter estimates for the models describing northern bob-white survival on south Florida pastureland.

Model Parameter	Coefficient	SE	95% CI	
			Lower	Upper
Intercept	1.270	0.350	0.580	1.960
Year	0.660	0.040	0.570	0.740
% PAST	-0.240	0.030	-0.300	-0.180
GENDER	-0.360	0.100	-0.570	-0.160
% FALL	-0.080	0.155	0.222	0.382

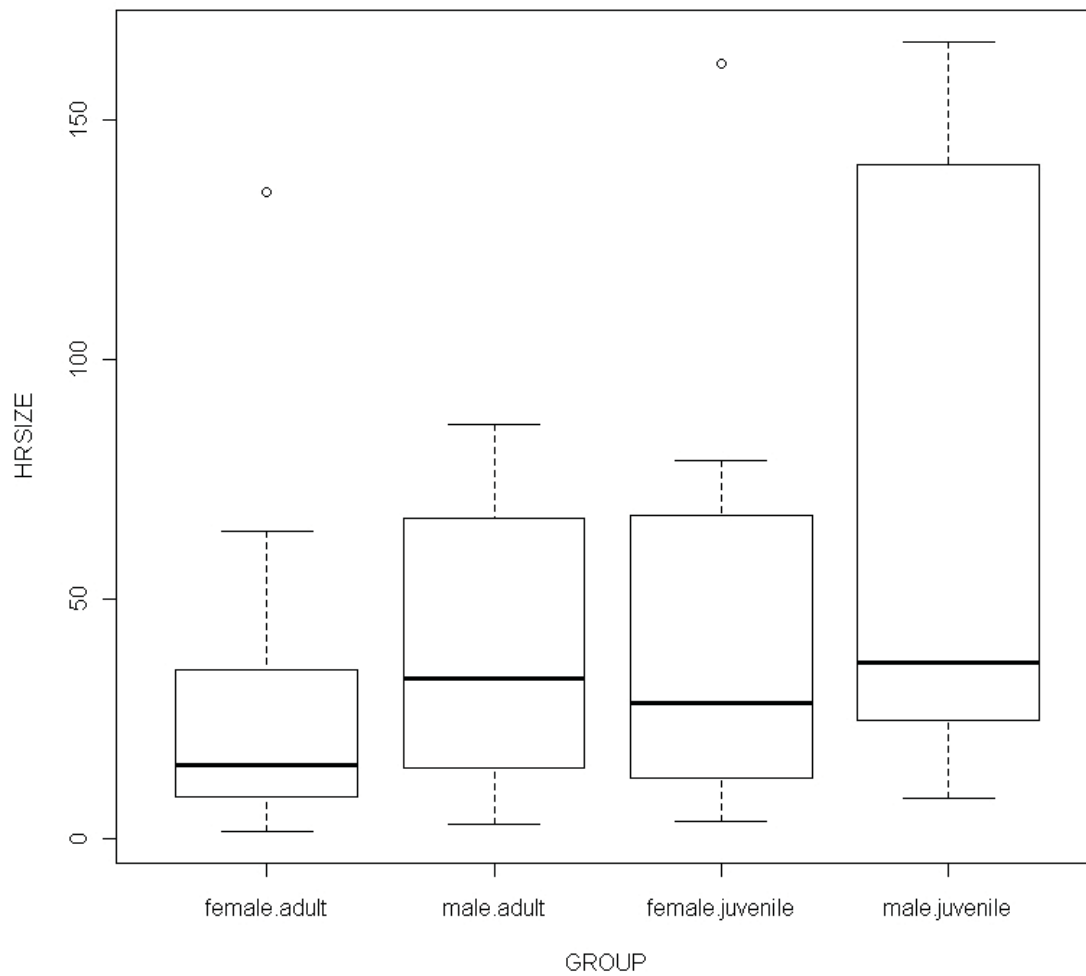


Figure 5.1: Box plots for home range size (ha) ( $n = 53$ ) for four groups of northern bobwhites on south Florida, US pastureland as estimated by 100% MCP home range estimator, 2004–2005.

Table 5.4: Results of compositional analysis based on 100% minimum convex polygon (MCP) home ranges (2nd order). Within the matrix, (+) signifies that the row habitat is preferred over the column habitat, whereas a (-) signifies the opposite. Significant difference between habitats ( $P < 0.05$ ) is indicated by (+++) or (---).

	FALL	PAST	OTHER	SEMIMP	UNIMP	WET	WOOD	YGROVE
FALL	0	+++	+++	+++	+++	+++	+++	+++
PAST	---	0	---	-	---	---	+++	-
OTHER	---	+++	0	+	---	---	+++	+++
SEMIMP	---	+	-	0	---	---	+++	+
UNIMP	---	+++	+++	+++	0	+	+++	+++
WET	---	+++	+++	+++	-	0	+++	+++
WOOD	---	---	---	---	---	---	0	---
YGROVE	---	+	---	-	---	---	+++	0

Table 5.5: Results of compositional analysis based on radio locations within a bird's home-range (3rd order). Within the matrix, (+) signifies that the row habitat is preferred over the column habitat, whereas a (-) signifies the opposite. Significant difference between habitats ( $P < 0.05$ ) is indicated by (+++) or (---).

	FALL	PAST	SEMIMP	UNIMP	WET	YGROVE
FALL	0	+++	+++	+++	+++	+++
PAST	---	0	-	-	+++	---
SEMIMP	---	+	0	-	+++	---
UNIMP	---	+	+	0	+++	-
WET	---	---	---	---	0	---
YGROVE	---	+++	+++	+	+++	0

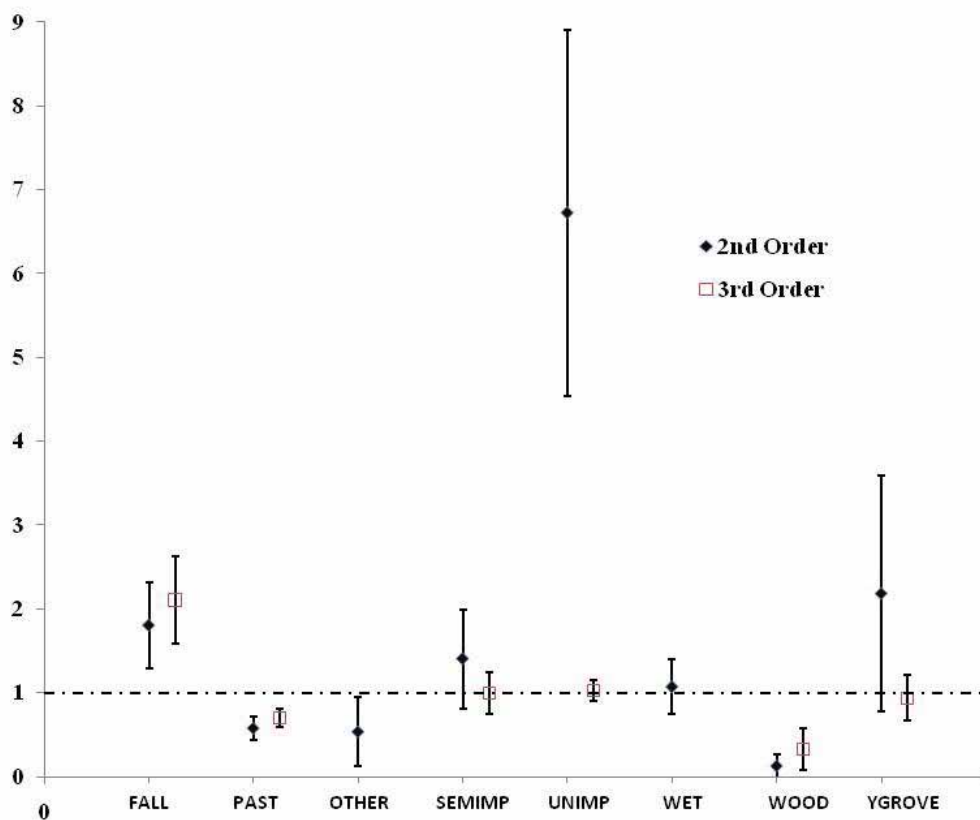


Figure 5.2: Manly's resource selection ratios for northern bobwhites on pastureland in south Florida, USA, 2004-2005. Values above 1 indicate selection and those below 1 indicate avoidance.

Table 5.6: Reproductive parameters for northern bobwhites on pastureland in Florida, USA, 2004–2005.

Parameter	Year	n	$\bar{x}$	90 % CI
<b>Clutch Size</b>				
	2004	12	10.9	2.53
	2005	24	11.72	1.58
	Pooled	36	11.36	1.13
<b>Nest success</b>				
	2004	12	0.58	0.07
	2005	24	0.667	0.03
	Pooled	36	0.639	0.02
<b>Broods per hen</b>				
	2004	25	0.28	0.05
	2005	22	0.728	0.06
	Pooled	47	0.489	0.02
<b>Productivity Index</b>				
	2004	25	2.4	1.34
	2005	22	5.9	1.36
	Pooled	47	4	0.98
<b>Fecundity</b>				
	2004	25	1.199	0.42
	2005	22	4.26	1.07
	Pooled	47	2.52	0.5

## CHAPTER 6

### SUMMARY AND CONCLUSIONS

Deep-ecology critics, especially, will quickly point out that fire predates people, that lightning and locally, volcanoes kindle fire, that there is no reason to compromise a natural process with a human presence. Fire is natural, and people can only pervert fire's planetary purposes. But that argument misses the point precisely. One creature does possess the power to start and stop fires. If that power resided in a species of Lepidoptera or in a marsupial, and particularly if that creature set fires on an order 10:1 to lightning, no one would question the nearly total biological basis for fire. We do so only because we are that creature.

–Pyne (2006).

The opinion of fire by the wildlife community has mostly been positive throughout the last 100 years. However, the opinion of how fire should be used has ebbed and flowed with the changing perceptions on how or if we are suppose to manipulate the environment to meet objectives. Or should we not have objectives? Our answers to these questions dictate our view of fire management. Do we mimic natural processes to bring back pristine conditions of previous times, often arbitrarily set, or manage to meet our needs for today. The answer likely falls somewhere in the gray middle.

My research suggest that managers should include fire size into the equation when predicting species response to fire. Under south Florida rangeland conditions, bobwhites consistently performed better under the small fire regime compared to the larger fire

sizes. Ironically, the fire sizes represented here are magnitudes smaller than those often used by public land managers on areas managed for grassland birds species—oftentimes with bobwhite management a primary objective. Public land managers are under the torch, so to speak, to get X amount of acres burned to meet their annual management goals. They valiantly achieve these goals (most of the time) and pronounce success in their management program. But really what has been accomplished? One could argue that large fire sizes are natural and once swept unchecked across the landscape. But we know Native Americans burned plenty and often (Abrams and Nowacki 2008, Nowacki and Abrams 2008), and if this true, fires would meet patches lacking fuel from the last fire or the intensity of fires were likely much different than ours today—something had to give. Even if large fires were the norm, we cannot expect organisms to respond the same today with a much different surrounding landscape. In this research, I did not have a fire size large enough to meet a threshold that once reached bobwhites would no longer persist. Research and empirical models are needed for bobwhites and other disturbance dependent species like that of Armstrong (1988) and Miller (1982).

I provide evidence that season of fire can affect bobwhite demography. Nest survival rates were highest in patches burned during the dormant season. Also, hazard rates were higher for those birds using mostly growing season burns. However, the interpretation of fire season in this context should be carefully stated and interpreted. I continue to advocate growing season fire but not exclusively. Bobwhites are likely better served by the mosaic of vegetation created by varying fire season. Furthermore, from a management perspective having flexibility in fire season allows smaller areas to be burned while keeping fire return intervals shorter. Our study site was in need of some restoration of the ground cover and growing season fires allowed this to be accomplished with fewer mechanical treatments. I recommend a step-down process for restoring a landscape by fire for bobwhite management (assuming timber density is within limits compatible for bobwhites): (1) initiate burning at the proper frequency given the site productivity—typically

18 months–36 months, (2) conduct burns during the season(s) that enhance or restore vegetation to a desired outcome—a grass/forb community with scattered shrub patches, and (3) once vegetation conditions are near desirable levels begin to manage area with fires at the lowest size logistically feasible. We realize these are very broad recommendations and allow for slack in habitat through time (Guthery 1999), but no matter how much science we conduct there will always be art involved in wildlife management (Leopold 1933) because knowledge will be lacking or uncertainty will be great.

I do not pretend the results in this dissertation are static. Someone in a different landscape, at a different time, under different conditions may find much different results. Land managers always face uncertainty and have to make decisions in spite of it. I encourage an adaptive management approach to large management areas that can manage and monitor species response to varying fire size. In the future, I hope to uncover the possible mechanisms for decreased fitness in larger fires.

## LITERATURE CITED

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APPENDIX A

DAUBENMIRE

Table A.1: Daubenmire values used for vegetation analysis.

<u>Value</u>	<u>% Cover</u>
1	trace
2	0.5
3	1.5
4	3.5
5	7.5
6	17.5
7	38.5
8	62.5
9	85
10	97.5

## APPENDIX B

### NEST SURVIVAL FUNCTION

```
#####Custom link function for logistic exposure model for Nest Survival
logexp <- function(days = 1)
{
  linkfun <- function(mu) qlogis(mu^(1/days))
  linkinv <- function(eta) plogis(eta)^days
  mu.eta <- function(eta) days * plogis(eta)^(days-1) *
    .Call("logit_mu_eta", eta, PACKAGE = "stats")
  valideta <- function(eta) TRUE
  link <- paste("logexp(", days, ")", sep="")
  structure(list(linkfun = linkfun, linkinv = linkinv,
                mu.eta = mu.eta, valideta = valideta, name = link),
            class = "link-glm")
}
```

## APPENDIX C

### BIOGRAPHY

*James Alan Martin was raised in Roxboro, North Carolina as a member of the Sappony Indian tribe. He spent much of his youth working on the tobacco farm of a neighbor and family friend, or hunting with his Grandfather. These undertakings helped to foster within him a deep appreciation for the land and its resources. Late one afternoon, nearing the completion of his undergraduate degree in Environmental Studies from the University of North Carolina at Asheville, James found himself watching a covey of quail feed along the edge of a harvested corn field. Their behavior intrigued him; he wondered why they fed as they did, what made them choose that particular location, and what could be done to restore their populations to abundance. It was at that moment that James realized that it was his life's calling to work toward the conservation of wildlife. This led him to pursue a Master of Science degree at the University of Georgia and Tall Timbers Research Station. His MS coursework was to focus on the economic ramifications of Northern Bobwhite restoration on a working cattle ranch in southern Florida, but midway through his MS coursework, James was offered the opportunity to take on additional responsibilities for an opportunity to earn a Doctorate of Philosophy. That work eventually became this dissertation. While at the University of Georgia, James was honored with numerous awards, including the UGA Outstanding Teaching Assistant Award in 2006, and the Warnell School of Forestry and Natural Resources most prestigious honor for graduate students, the E.L. Cheatum Memorial Award, during 2009. During November 2008, James married Nevena Crawford, a fellow graduate of UGA's Warnell School of Forestry and Natural Resources, and a kindred spirit who shared James' love of wild things and wild places. In his spare time James enjoys training field-bred English Cocker Spaniels, writing non-fiction essays,*

*and various outdoor pursuits, the most notable of which includes hunting upland game birds and fly fishing.*

—Written by A.B. Butler