

Factors Related to Nest Survival and Over-winter Survival of a Northern Bobwhite
(*Colinus virginianus*) Population in Southwest Florida

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DEDICATION

This work is dedicated to the memory of my grandparents William and Virginia Hamilton and Hayden and Ernestine Phebus. Growing up and spending time with them on their farms initiated my love of nature. I would also like to dedicate this work to the memory of my friend George R. Mayfield, who taught me most everything I know about the wondrous world of birds.

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ABSTRACT

The northern bobwhite (*Colinus virginianus*) is a gallinaceous upland game bird dependent on early successional grassland habitat for reproduction and survival. Bobwhite populations have been declining range-wide for nearly a half century. The habitat of Babcock-Webb Wildlife Management Area (BWWMA) in southwest Florida is mostly virgin, early successional grassland and pine flatwoods. Although BWWMA is located in the far southern end of the bobwhite range, the area is a popular public land for bobwhite hunting. The BWWMA bobwhite population has declined evidenced by a dramatic decrease in harvest over the last 20 years. The two objectives of my research were to (1) describe nest habitat selection and daily nest survival of the bobwhite population on BWWMA, and (2) evaluate factors related to over-winter (1 October – 30 March) survival of the BWWMA bobwhite population. Specifically, I evaluated nest-site habitat selection and modeled daily nest survival as a function of biologically meaningful spatial, temporal, climatic, and habitat related covariates (Part II). I tested the hypothesis that bobwhites selected nesting habitat at the landscape level. There was no evidence that bobwhites selected specific habitats for nesting, but basin marsh and wet flatwoods cover types were used for nesting slightly more than they were available. The incubation period nest survival rate was 0.477 (SE = 0.027). Daily nest survival rates did not differ among years, the hunting zone in which the nest was located, or between genders of the incubating bird. Nest survival was positively related to the percent of basin marsh habitat within a 1000-m radius of the nest. Daily nest survival declined over the nesting period. I modeled the over-winter survival rates of bobwhites as a function of hunting pressure and other spatial, temporal, climatic and habitat covariates (Part III). The average over-winter survival rate was 0.402 (SE = 0.023). Year, time, and hunting zone were important factors influencing over-winter survival. Hunting pressure was the factor most related to over-winter survival. I evaluated management oriented questions related to over-winter survival of bobwhites on BWWMA. Food strip management and prescribed fire did not appear to be related to over-winter survival. Harvest rates were greater than others reported from studies in the Southeast and results suggested that, to some extent, harvest was additive to natural mortality. If the goal of management is to increase the

BWWMA bobwhite population, reduction in harvest rate is one likely effective management strategy for achieving that goal.

TABLE OF CONTENTS

PART I: INTRODUCTION.....	1
LITERATURE CITED	5
PART II: NEST HABITAT SELECTION AND FACTORS INFLUENCING NEST SURVIVAL OF NORTHERN BOBWHITE (<i>Colinus virginianus</i>) IN SOUTHWEST FLORIDA	8
ABSTRACT.....	9
INTRODUCTION	9
STUDY AREA	12
METHODS	14
Field Methods	14
Trapping	14
Handling and Marking	16
Radio Telemetry	16
Nest Location and Monitoring	17
Data Analyses	17
Nest Habitat Selection	18
Daily Nest Survival	19
RESULTS	27
Nest Habitat Selection	29
Daily Nest Survival.....	31
DISCUSSION	37
Nest Habitat Selection	38
Daily Nest Survival.....	42
CONCLUSIONS.....	49
LITERATURE CITED	51

PART III: OVER-WINTER SURVIVAL OF A NORTHERN BOBWHITE (<i>Colinus virginianus</i>) POPULATION IN SOUTHWEST FLORIDA	57
ABSTRACT.....	58
INTRODUCTION	58
STUDY AREA	61
METHODS	63
Field Methods	63
Trapping	63
Handling and Marking	64
Radio Telemetry.....	65
Harvest Data Collection	65
Data Analyses	66
Over-winter Survival.....	66
Management Questions	73
RESULTS	76
Over-winter Survival	76
Management Questions	90
DISCUSSION	97
MANAGEMENT IMPLICATIONS	103
LITERATURE CITED	106
PART IV: CONCLUSIONS.....	109
LITERATURE CITED	112
VITA	113

LIST OF TABLES

PART II

Table 2.1: Descriptions and abbreviations for the 12 habitat categories on BWWMA in southwest Florida, 2003 – 2009.	21
Table 2.2: Description of the three preliminary model suites for daily nest survival rate and the corresponding model notation used in later results tables....	25
Table 2.3: Estimates of yearly nesting parameters of northern bobwhites in southwest Florida, 2003 – 2009.	28
Table 2.4: Total area and proportions of each habitat category available to and used by nesting northern bobwhites in southwest Florida, 2003 – 2009.	30
Table 2.5: Selection of nest habitats by northern bobwhites in southwest Florida, 2003 – 2009.	30
Table 2.6: Number of nests monitored and nesting periods of bobwhites in southwest Florida, 2003 – 2009.	32
Table 2.7: Summary of model-selection results from the first preliminary model suite for nest survival of northern bobwhites in southwest Florida, 2003 – 2009.	34
Table 2.8: Summary of model-selection results from the second preliminary model suite for nest survival of northern bobwhites in southwest Florida, 2003 – 2009.	34
Table 2.9: Summary of model-selection results from the third preliminary model suite for nest survival of northern bobwhites in southwest Florida, 2003 – 2009.	34
Table 2.10: Summary of model-selection results from the fourth model suite for nest survival of northern bobwhites in southwest Florida, 2003 – 2009.	35
Table 2.11: Summary of model-selection results from the fifth model suite for nest survival of northern bobwhites in southwest Florida, 2003 – 2009, including final additive models.	35
Table 2.12: Beta estimates and 95% confidence intervals (CI) for parameters in the seven best models for nest survival of northern bobwhites in southwest Florida, 2003 – 2009.	36
Table 2.13: Average nesting parameter estimates of northern bobwhites in southwest Florida, 2003 – 2009, and other bobwhite populations	39

Table 2.14: General site-level nest-site habitat description for bobwhite nests in southwest Florida, 2003 – 2009.....	41
--	----

PART III

Table 3.1: Description of the model notation in the four preliminary model suites for the over-winter survival analysis of northern bobwhites in southwest Florida, 2003 – 2009.....	69
--	----

Table 3.2: Encounter period dates, lengths, and hunting for each over-winter period of the southwest Florida bobwhite study, 2003 – 2009.....	77
---	----

Table 3.3: Summary of model-selection results from the first model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009...78	
--	--

Table 3.4: Parameter estimates and 95% confidence intervals for covariates in the S(year+t+Sex+Age) model in the first model suite for bobwhite over-winter survival in southwest Florida, 2003 – 2009.....	79
---	----

Table 3.5: Summary of model-selection results from the second model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009.....	80
---	----

Table 3.6: Parameter estimates and 95% confidence intervals for the top three models in the second model suite for over-winter survival of bobwhites in southwest Florida, 2003 – 2009.....	81
---	----

Table 3.7: Summary of model-selection results from the third model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009...82	
--	--

Table 3.8: Parameter estimates and 95% confidence intervals for the best model in the third model suite for over-winter survival of bobwhites in southwest Florida, 2003 – 2009.....	83
--	----

Table 3.9: Hunting zone over-winter survival estimates and 95% confidence intervals for northern bobwhites in southwest Florida, 2003 – 2009.	83
--	----

Table 3.10: Summary of model-selection results from the fourth model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009.....	84
--	----

Table 3.11: Parameter estimates and 95% confidence intervals for the three best models in the fourth model suite for over-winter survival of bobwhites in southwest Florida, 2003 – 2009.....	84
---	----

Table 3.12: Summary of model-selection results from the fifth model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009...	85
Table 3.13: Summary of model-selection results from the sixth model for over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009...	87
Table 3.14: Parameter estimates and 95% confidence intervals for covariates in the best model of the sixth model suite for bobwhite over-winter survival in southwest Florida, 2003 – 2009.....	88
Table 3.15: Questions and answers for the six management related analyses for northern bobwhites in southwest Florida, 2003 - 2009.....	91
Table 3.16: Summary of model-selection results from management Question 1 relating food strips to over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009.	91
Table 3.17: Parameter estimates and 95% confidence intervals for the models evaluated for Question 1 relating food strips to over-winter survival of bobwhites in southwest Florida, 2003 – 2009.	92
Table 3.18: Summary of model-selection results from management Question 2 relating burning to over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009.	92
Table 3.19: Parameter estimates and 95% confidence intervals for the model evaluated for Question 2 relating burning to over-winter survival of bobwhites in southwest Florida, 2003 – 2009.....	92
Table 3.20: Summary of model-selection results from management Question 3 relating hunting pressure to survival of bobwhites during the regular hunting season on BWWMA in southwest Florida, 2003 – 2009.....	93
Table 3.21: Parameter estimates and 95% confidence intervals for the model evaluated for Question 3 relating hunting pressure to survival of bobwhites during the regular hunting season on BWWMA in southwest Florida, 2003 – 2009.....	93
Table 3.22: Estimated harvest rates of northern bobwhites during the regular hunting season on BWWMA in southwest Florida, 2003 – 2009.	95
Table 3.23: Estimated harvest rates of northern bobwhites during the zone F hunting season on BWWMA in southwest Florida, 2003 – 2009.	95
Table 3.24: Summary of model-selection results from management Question 5 about the effects of harvest rates on over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009.....	96

Table 3.25: Parameter estimates and 95% confidence intervals for the model evaluated for Question 5 on the effects of harvest rates on over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009.....	96
Table 3.26: Summary of model-selection results from management Question 6 about the relationship between over-winter survival and pre-hunt density the following year of northern bobwhites in southwest Florida, 2003 – 2009.	97
Table 3.27: Parameter estimates and 95% confidence intervals for the model evaluated for Question 6 on the relationship between over-winter survival and pre-hunt density the following year of northern bobwhites in southwest Florida, 2003 - 2009	97
Table 3.28: Pre-hunt density estimates for bobwhites in each hunting zone on BWWMA in southwest Florida, 2003 – 2009.	102
Table 3.29: Harvest rates and associated hunting pressures for bobwhite hunting on BWWMA in southwest Florida.	105

LIST OF FIGURES

PART II

Figure 2.1: Babcock-Webb Wildlife Management Area in southwest Florida with five hunt management zones, 2002 – 2009.....	14
Figure 2.2: Habitat cover layer for Babcock-Webb WMA in southwest Florida depicting habitat categories available on the management area, 2002 – 2009.	23
Figure 2.3: Proportions of available and used cover types for nesting northern bobwhites in southwest Florida, 2003 – 2009.	31
Figure 2.4: Daily nest survival rate trend and 95% confidence interval for the 203 interval nesting period of northern bobwhites in southwest Florida, 2003 – 2009, estimated from model averaging.....	37
Figure 2.5: Typical nesting habitat of bobwhite nests on BWWMA in southwest Florida, 2003 – 2009	42
Figure 2.6: Nesting incubation activity by week for the 204-day nesting period of northern bobwhites in southwest Florida, 2003 – 2009.....	46
Figure 2.7: Graphical depiction of the relationship between the BM1000 covariate and daily nest survival rate for bobwhites in southwest Florida, 2003 – 2009.....	47

PART III

Figure 3.1: Babcock-Webb Wildlife Management Area with five hunt management zones.	62
Figure 3.2: Habitat cover layer for Babcock-Webb WMA in southwest Florida depicting habitat categories during the northern bobwhite study, 2002 – 2009.	72
Figure 3.3: Babcock-Webb Wildlife Management Area in southwest Florida with food strips in red and five hunt management zones, 2002 – 2009.....	73
Figure 3.4: Encounter period survival rate estimates and 95% confidence intervals for each year of the northern bobwhite study in southwest Florida, 2003 – 2009.....	89
Figure 3.5: Over-winter survival rate estimates and 95% confidence intervals for each year of the northern bobwhite study in southwest Florida, 2003 – 2009.....	90

Figure 3.6: Relationship between total hunting pressure and harvest rate of northern bobwhites in southwest Florida, 2003 – 2009.....	94
Figure 3.7: Relationship between harvest rate and over-winter survival of northern bobwhites in southwest Florida, 2003 – 2009.....	96
Figure 3.8: Predicted harvest rates in relation to observed hunting pressures and associated harvest rates during the northern bobwhite study in southwest Florida, 2003 – 2009.	103

PART I

INTRODUCTION

North American native, grassland ecosystems have diminished by an estimated 80% since the mid-1800's (Knopf 1994, Noss et al. 1995). As a result, many grassland bird populations have been declining for almost a half century (Brennan et al. 2005). Only 5% of eastern grassland bird species exhibited significant population increases from 1966 – 2008 (Ziolkowski et al. 2010). The decline in populations has been attributed to loss of habitat through afforestation, fragmentation, and deterioration (Brennan et al. 2005). Afforestation is viewed as the leading factor related to grassland habitat loss and grassland species population declines in the eastern United States (Askins 2000). However, urban development, monoculture farming, pasture improvement, invasive herbaceous exotics, and fire exclusion are other major factors contributing to native grassland deterioration and fragmentation in the eastern United States (Exum et al. 1982, Brennan 1991, Askins 2000, Brennan et al. 2005, Perkins and Vickery 2007, Flanders et al. 2009).

Northern bobwhite (*Colinus virginianus*) is a grassland bird species that has been declining for at least the past 45 years (North American Breeding Bird Survey, Sauer et al. 2011). Range-wide, northern bobwhite (hereafter “bobwhite”) populations declined by 3.7% per year from 1966 to 2008 and an alarming 7.3% decrease between 2007 and 2008 (Ziolkowski et al. 2010). Significant local declines have also been reported. In Florida, the bobwhite population declined 4.1% per year from 1980 to 2007, and a decline of 4.9% per year has been reported in the coastal flatwoods region during the same time period (Sauer et al. 2008). The magnitude and persistence of this decline requires research from biologists to understand the nature and consequences of the dwindling bobwhite population. Knowledge gained from research will aide in education of managers, landowners, and the general public, all of whom play a vital role in the challenge of reversing the bobwhite population decline.

Bobwhites have received considerable research attention for the past 80 years (Hernández et al. 2002). As a popular upland gamebird, bobwhites have long been a focus of interest for hunters. Historically, bobwhites were found in scattered patches throughout their geographic range (Klimstra 1982, Burger 2001). Forests dominated the landscape and bobwhites existed in openings created by natural disturbances or by

disturbances created by Native Americans. From the mid-1800's to the early 1900's, European settlers cleared the land for various purposes, and bobwhite populations expanded throughout the Southeast (Burger 2001). Generally, bobwhite habitat consists of early successional plant communities (Burger 2001). Early settlers created and maintained farms by opening up small patches within large tracts of forest and provided excellent early successional habitat renewed with each annual farming cycle.

The dominant factor in the decline of bobwhite populations seen today is the loss of quality habitat (Brennan 1991). In the coastal plain region, extensive logging after European settlement was followed by fire exclusion. As a result, longleaf pine (*Pinus palustris*) woodlands became one of the most critically endangered ecosystems in North America (Askins 2000). Much of the land cleared of timber was left idle with fire excluded. This resulted in dense forests of fire-sensitive species unusable by grassland bird species such as the bobwhite (Askins 2000). Other cleared land was converted to farmland. Until the early 1900's, farmers burned native pastures for cattle and maintained the pine savanna ecosystem (Askins 2000). However, an increase in monoculture farming reduced diversity on the landscape (Exum et al. 1982). Farms and farm fields ever increasing in size have reduced the overgrown fence rows and small fields important for bobwhite nesting and brood cover (Klimstra 1982).

Whereas habitat degradation and fragmentation have resulted in bobwhite population declines, there are still large tracts of land with quality habitat. Although the habitat quality may be suitable in these places, other factors are continuing to depress bobwhite numbers. Bobwhite hunting is a component of over-winter mortality that may contribute to population decline (Roseberry and Klimstra 1984, Brennan 1991, Williams et al. 2004). Survival during the over-winter period has been identified as a key factor related to bobwhite population change (Folk et al. 2007, Sandercock et al. 2009). Bobwhite populations may be stable or increase only if harvest stays below a critical threshold (Landers and Mueller 1986, Williams et al. 2004). There is also a relationship between bobwhite population parameters (i.e., nest survival) and climatic and biological variables (Stoddard 1931, Frye 1954, Taylor et al. 1999a, Taylor et al. 1999b, Lusk et al. 2001, Lusk et al. 2002, Staller et al. 2002, Cooper et al. 2009, Hernández et al. 2009). If

managers can understand the relationships between these factors and bobwhite population parameters, more effective management may reverse local and regional population declines.

This research was initiated to gain an understanding of factors limiting bobwhite populations toward the southern extreme of the bobwhite's geographic range. Specifically, the objectives of my study on the Babcock-Webb Wildlife Management Area were to (1) determine the factors related to nest survival of bobwhites (Part II); and (2) determine the factors related to over-winter survival of bobwhites (Part III). I present overall conclusions gathered from my research and analyses in Part IV. Individual Parts II and III are written as stand-alone manuscripts for future publication.

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PART II

NEST HABITAT SELECTION AND FACTORS RELATED TO NEST SURVIVAL OF NORTHERN BOBWHITE (*Colinus virginianus*) IN SOUTHWEST FLORIDA

ABSTRACT

I evaluated nest-habitat selection and factors related to daily nest survival of a northern bobwhite population in southwest Florida, USA during 2003 to 2009. Of the birds alive and radio-tagged on 1 April each nesting season ($n = 327$ females, $n = 369$ males), 58% of females and 17% of males incubated ≥ 1 nest, and 39% of females and 9% of males successfully hatched ≥ 1 nest. Of the birds that incubated a nest, females averaged 1.23 (SE = 0.03) nests per bird and males averaged 1.02 (SE = 0.02) nests per bird. Nest success was 59% for females and 52% for males. Mean clutch size was 12.37 eggs (SD = 2.96). I evaluated nest-habitat selection by radio-tagged female bobwhites monitored during the breeding season. I modeled effects of temporal, climatic, and biotic factors on daily survival rates for bobwhite nests ($n = 400$) using Program MARK. Nine broad habitat categories were used to analyze nest-habitat selection. Based on a resource selection probability function analysis, bobwhites did not select nest-sites based on cover type ($P = 0.279$); although there was limited support for preferential use relative to availability of basin marsh and wet flatwoods habitats. The proportion of basin marsh and wet flatwoods habitat at two spatial scales around nests were included as covariates in models related to daily nest survival. The best-supported models indicated that daily nest survival had a negative linear relationship with time during the nesting season and a positive relationship with the proportion of basin marsh within a 1000-m radius of the nest. Daily nest survival did not differ by year, hunting zone, or sex, nor by rainfall and temperature. Daily nest survival for the 204-day nesting period ranged from 0.992 (SE = 0.006) on 9 March to 0.949 (SE = 0.016) on 7 September. The nest survival rate for the 23-day incubation period estimated from the constant survival model was 0.477 (SE = 0.027). The results of this study suggested that bobwhite nest-habitat selection was random at the resolution I investigated. Daily nest survival declined over time and was affected by habitat surrounding the nest.

INTRODUCTION

Grassland bird species have been experiencing population declines across the United States for decades (Brennan et al. 2005). Northern bobwhite (hereafter

“bobwhite”) populations have declined rangewide at 3.7% per year from 1966 to 2008 (Ziolkowski et al. 2010). The factors most frequently attributed to bobwhite population declines were habitat loss and fragmentation (Brennan 1991, Dimmick et al. 2002). The National Bobwhite Conservation Initiative (NBCI) developed habitat management objectives for distinct regions within the bobwhite range with a goal of restoring bobwhite populations to 1980 levels (Dimmick et al. 2002). To support implementation of the plan, information is needed on habitat requirements and demographics of separate populations so that contemporary management strategies can be developed.

The NBCI stated that “a lack of nesting and brood rearing cover was the major limiting factor over much of the range of the northern bobwhite” (Dimmick et al. 2002:3). To manage nesting cover properly, it is important to understand nesting habitat selection and requirements specific to local bobwhite populations. Many studies have documented site-level nest habitat selection and the relationship of nest-site habitat characteristics to nest success (Taylor et al. 1999a, Taylor and Burger 2000, Townsend et al. 2001, Lusk et al. 2006, Rader et al. 2007, Collins et al. 2009). Taylor et al. (1999a) found that nest-sites in Kansas had taller vegetation and more visual obstruction and litter than random sites and that successful nests were surrounded by taller grass, less shrub coverage, and less litter than depredated nests. Lusk et al. (2006) reported similar results in northern Texas with regard to nest-site selection and nest success, but unlike in Kansas, they found a positive relationship between shrub coverage and nest success. Nest-site selection was similar in southern Texas to that in northern Texas, but nest success was related to climatic factors rather than any particular nest-site characteristics (Rader et al. 2007). Taylor and Burger (2000) reported that nest sites were not selected based on vegetation characteristics but that successful nests had more bare ground and less litter coverage than unsuccessful nests in Mississippi. In New Jersey, greater visual obscurity and litter cover were qualities of selected nest sites, but no site characteristics evaluated were related to nest success (Collins et al. 2009). It is clear that some common factors exist in nesting habitat selection (e.g., selection for native grasses), but also that there are differences among populations in how habitat factors are related to nest success.

At a macro scale, Rader et al. (2007) investigated the influence of percent woody coverage on the landscape on bobwhite nest survival in southern Texas and found no relationship. In Kansas, successful bobwhite nests were observed to have greater coverage of native grass hayfields around them at intermediate scales and less coverage of native rangeland at small scales (Taylor et al. 1999b). Staller et al. (2002) studied macro-habitat influence on nest survival in south Georgia and north Florida. They reported that bobwhites typically selected nest-sites with less surrounding hardwood drain habitat and that nest success may have been greater at sites with less surrounding hardwood drain habitat.

Other factors may influence nest survival for bobwhites. Generally, bobwhites depend on rain at crucial times during the year to assure an adequate food supply and enough moisture to perpetuate chick development during nest incubation. Most research has focused on the lack of rain and its effects on bobwhite populations (Lusk et al. 2001, Lusk et al. 2002, Cooper et al. 2009, Hernández et al. 2009). In the semi-arid region of Texas, above average rainfall during the growing season enhanced vegetation growth resulting in increased food and cover (Cooper et al. 2009). The timing and amount of rain in this region caused the populations to exhibit a “boom and bust” phenomenon with a positive population response (or “boom”) in times of above average rainfall and a negative response (“bust”) when rain amounts were below average (Hernández et al. 2009).

In mesic regions, productivity tends to have a negative relationship with increased rainfall (Cooper et al. 2009). Southern Florida has a hot-humid climate with a rainy season between May and November, a period during which it receives 70% of its annual rainfall (Black 1993). Tropical moisture and heat produce regular afternoon thunderstorms that can produce substantial rainfall within relatively short periods of time. Frye (1954) found an inverse relationship between summer rainfall and the percentage of juvenile bobwhites in the fall population in southwest Florida. Excessive summer rainfall in some habitats, therefore, may reduce bobwhite abundance through reduced nest success and/or recruitment. However, Frye (1954) could not find a definitive relationship between total bobwhite abundance in autumn and summer rainfall. More recently, Miley

and Lichtler (2006) found no negative effect of summer rainfall on bobwhite demographic parameters in south-central Florida, but good drainage on that study site may have contributed to the lack of response.

Temperature has also been shown to directly affect bobwhite nest survival (Roseberry and Klimstra 1984, Rader et al. 2007). Roseberry and Klimstra (1984) attributed a small portion of nest failures in southern Illinois to extreme temperatures. Conversely, daily nest survival increased with increasing mean maximum daily temperatures in southern Texas (Rader et al. 2007). Temperature may also produce indirect effects on bobwhite nest success. For example, Frye (1954) observed that cooler spring temperatures in southwest Florida delayed pair formation and nest initiations. Such a setback could push peak nesting periods to coincide with peak predator density or activity periods.

I estimated nesting rate, bird success, nests per nesting adult, nest success, and average clutch size for cohorts of bobwhites alive and radio-tagged on 1 April, as well as nest habitat selection and factors influencing daily nest survival of a northern bobwhite population in southwest Florida from 2003 to 2009. Objectives of my study were to: (1) determine if bobwhites preferred certain cover types for nesting among those available, and (2) evaluate relationships between daily nest survival rates and year, time, sex, hunt zone, climate (particularly rainfall), and habitat composition covariates.

STUDY AREA

The study was conducted on the Fred C. Babcock-Cecil M. Webb Wildlife Management Area (hereafter “BWWMA”). BWWMA is a 26,302-ha state-owned wildlife management area managed by the Florida Fish and Wildlife Conservation Commission, located about 8 km east of Punta Gorda, Charlotte County, Florida. The habitat is southern pine flatwoods with south Florida slash pine (*Pinus elliottii* var. *densa*) dominating the overstory. Other tree species included cabbage palm (*Sabal palmetto*), live oak (*Q. virginiana*), and laurel oak (*Q. laurifolia*). The understory was dominated by saw palmetto (*Serenoa repens*) intermixed with other woody shrub species such as southern waxmyrtle (*Myrica cerifera*), gallberry (*Illex glabra*), and dwarf live

oak (*Q. minima*). Herbaceous vegetation in the understory included broomsedge (*Andropogon* spp.), wiregrass (*Aristida stricta*), and slough grass (*Scleria muhlenbergii*). *Sesbania* (*Sesbania* sp.) food strips were planted each spring to provide food and cover for bobwhites and other species throughout the fall and winter months. Seasonal and perennial ponds and wetlands of various sizes were dispersed throughout the landscape. Frye (1954) described BWWMA's vegetation, geology, soils, and land uses in detail. Prior to the initiation of the bobwhite study, BWWMA was divided into five hunt zones used as treatment areas for various hunting regulations. Zones were labeled A, B, C, D, and F and ranged from 3,132 ha to 6,258 ha (Figure 2.1). In most cases, zone boundaries were delineated by barbed wire fences. Zones A – D were the largest in size. Bobwhite hunting was allowed on those zones throughout the regular BWWMA quail hunting season from mid-November through the end of December. Zone F was the smallest zone. Bobwhite hunting was allowed only on two consecutive days in late January each year.

Wildlife management on BWWMA included cattle grazing, prescribed fire, and roller chopping to maintain early successional habitat. Grazing was permitted in various sections of zones A, B, C, and D at various times of year throughout the study. Each year, prescribed fires were implemented from December to March. The majority of the BWWMA (i.e., 50 – 100%) was prescribe-burned each year. Summer burns were added to the burn plan to promote seed production of wiregrass. Roller chopping occurred year round to reduce saw palmetto coverage, set back overall habitat succession and promote vegetation growth.

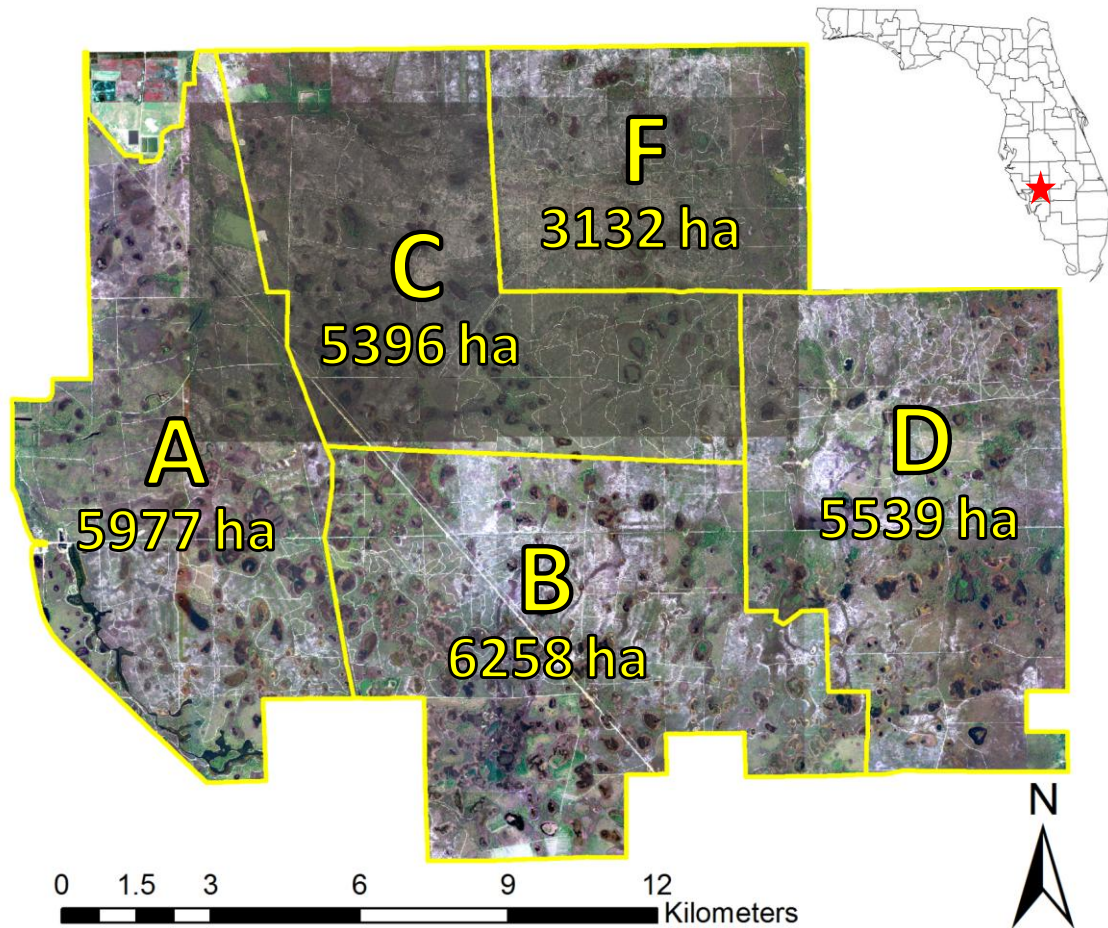


Figure 2.1: Babcock-Webb Wildlife Management Area in southwest Florida with five hunt management zones, 2002 - 2009.

METHODS

Field Methods

Trapping: I began trapping bobwhites on the study area in October 2002 and continued year round until 31 March 2009. Trapping ceased for six weeks in zones A-D each year during the regular BWWMA quail hunting season and for two days in zone F during the quail quota hunt each January. I used six trapping methods throughout the study: baited funnel trap, funnel live decoy trap, night mist netting using radio telemetry, night cast netting using radio telemetry, diurnal cast netting using radio telemetry, and diurnal cast netting using bird dogs.

I utilized baited funnel traps year round for the entire duration of the study. Traps were constructed of 2.54 x 5.08 cm welded wire and were 76.20 x 76.20 cm and about 25.40 cm tall, resembling the Stoddard (1931) trap. Two funnels constructed of the same welded wire were placed on opposite sides of each trap offset from each other. Initially, I placed traps at varying intervals along roads and fire breaks and baited the traps with milo (*Sorghum* spp.). Because wild hogs regularly disrupted or destroyed baited traps, I changed the bait to wild bird seed, which included only a small amount of milo and cracked corn (*Zea mays*) to reduce the attraction to hogs. I also modified trap locations and placed them where I observed bobwhites. After setting, I covered the trap with cut palmetto or cabbage palm fronds for camouflage and to resemble escape cover. I checked traps twice daily, in early morning and late evening. The traps were typically left set until they were moved.

I used pen-reared female bobwhites as live decoys in funnel traps during the breeding season (April to October). I constructed holding cubes to contain the live females inside the traps. The cubes were built using the same welded wire that was used for the funnel traps, 20.32 cm wide by 20.32 cm deep by 15.24 cm tall, with one side hinged allowing opening to insert and remove the female bobwhite decoys. The floor of the cube was solid and made of white corrugated plastic. I placed traps where males had been observed, and I did not restrict the traps to roads and firebreaks. I placed wild game callers (Western Rivers, Lewisburg, TN) broadcasting female bobwhite calls at many of the trap sites to attract males and to entice the female decoys to call. I incorporated bait with this method in August to October to further entice birds into the live decoy traps.

I tried night mist netting during fall and winter 2003 to 2004. Using radio telemetry, I located coveys at night and set two mist nets in a “V” shape adjacent to the roosting covey. Once set, I attempted to flush the birds into the nets. This procedure was done at night because it was discovered that the coveys were less likely to run or flush before the nets could be set. The greatest success with this method was on the darkest, coldest nights.

In January 2003, I first attempted to throw a cast net over a covey pointed by bird dogs. I tried various net sizes and weights over the years, but the most success was with

2.74-m radius nets with about 1.48 kg of lead weight per meter. The small, light nets were easier to throw and open. Extra weight did not seem to be necessary to keep birds under the net in most cases. This turned out to be an important addition to my trapping strategy for radio-tagging birds in “new” coveys (coveys that previously had no radioed quail). I used cast nets with dogs mostly in the fall and winter when the bobwhites were in coveys.

I began using cast nets to capture additional bobwhites in coveys with at least one radioed bird shortly after I discovered the use of cast nets with bird dogs. I located bobwhites by radio telemetry and, depending on the number of workers at the site, threw 1 to 3 cast nets onto the covey. I used this method in the fall and winter when the bobwhites were in coveys.

Handling and Marking: After capture, birds were held in cloth bags until they could be processed, typically immediately after capture. Processing of each bird included recording age, sex, and mass (g). I determined age and sex by plumage (Rosene 1969). I placed bobwhites in a short shear stocking for containment to determine mass with a 300-g spring scale. Every captured bird was tagged with a uniquely numbered aluminum leg band. I also fitted birds of both sexes and age classes weighing >130 g with a 6 – 7-g neck loop radio transmitter (American Wildlife Enterprises, Monticello, FL). After a bird was processed, I released it at its point of capture. Total processing time averaged 10 minutes.

Radio telemetry: I attempted to locate radio-tagged birds once every 4 days. Because of limited manpower, equipment malfunction, and inclement weather, some bobwhites were located at greater time intervals. I located radioed bobwhites using R4000 telemetry receivers and 3-element yagi antennas (Advanced Telemetry Systems, Isanti, MN). To estimate radio locations, I approached within 20 m of each radio-tagged bird. I marked each bird’s location using Trimble Geoexplorer 3 GPS receivers (Trimble Navigation Limited, Sunnyvale, CA) by entering an azimuth and distance to the bird’s actual location into the GPS unit. If the bird was seen running or flushed, I determined the exact location of the bird. Other information recorded in the GPS unit at the time of marking a location was the date, time, and hunt zone.

Nest location and monitoring: I used radio telemetry to locate all nests of monitored birds from mid-March through mid-October. To keep from unnecessarily flushing the bobwhites, I noted the location of individual birds from week to week. A bobwhite observed in the same location two times consecutively was checked to determine if a nest was present. Once I located a nest, I marked the location with GPS, photographed the nest site and surrounding habitat, and placed flags in the area so that the nest could be easily relocated. I attempted to check each nest at least every third day from the time it was located until its fate was determined. If the adult was off the nest during a nest check, I recorded the number of eggs. Eventually, I assigned each nest to one of three fates: hatched, destroyed, or abandoned. A hatched nest was a nest with ≥ 1 egg hatched. A nest was classified as destroyed when it was obvious that the nest did not hatch and the nest structure and/or eggs were damaged. Abandoned nests were left intact but were no longer incubated by an adult. I considered a nest successful if it hatched and failed if it was destroyed or abandoned.

Data Analysis

I estimated various nesting parameters for each sex in a cohort of birds alive and radio-tagged on 1 April each year. Typically, nests were not located prior to the incubation stage. Consequently, my estimates for nesting rate and average nesting attempts likely are lesser and my nest success estimate greater than the true parameter. I defined nesting rate as the proportion of the cohort attempting to incubate ≥ 1 nest (Burger et al. 1995). Bird success rate was the proportion of the cohort that successfully hatched ≥ 1 nest (Burger et al. 1995). Because of radio failure or loss, contact was lost with 44 females and 82 males originally included in the 1 April cohort. These birds were excluded from estimates of nesting rate and bird success (Burger et al. 1995). I defined average nesting attempts as the nests per nesting adult (i.e., the average number of nests incubated by individuals that incubated ≥ 1 nest). Nest success rate was the proportion of all nests that were successful (i.e., hatched ≥ 1 egg) (Burger et al. 1995). I estimated mean clutch size from nests with successful egg counts incubated by the 1 April cohorts of birds.

Nest Habitat Selection: I evaluated 3rd order habitat selection of nesting bobwhites (Johnson 1980) with the resource selection probability function (RSPF) described by Arthur et al. (1996). This method uses the technique of maximum likelihood estimation and allows availability to change among animals. A measure of the proportion of each cover type available to the animal and one location of habitat use (i.e., only one cover type is used) is required. I used the proportion of each cover type within each female's home range as available habitat and the cover type where the nest was found as the measure of habitat use.

I calculated the home range of female bobwhites with ≥ 10 radio locations using locations from 1 January up to and including the nest location for each breeding season of the study. The locations for each female were plotted using ArcGIS version 9.3 (ESRI, Redlands, California). The home range was determined by 100% minimum convex polygon using the ABODE extension (Laver 2005). If a female had < 10 locations prior to nesting or a male bobwhite was incubating the nest, the available home range for that nest was determined by creating a circular buffer around the nest location equal in area to the average area of all the estimated home ranges.

Both female and male bobwhites contribute to nest construction (Stoddard 1931, Rosene 1969), suggesting that males have some influence on nest-site selection. However, in south Florida, I observed male bobwhites regularly traveling up to 1 km to reach females calling in decoy traps during the breeding season. Therefore, only female home ranges prior to nesting were used to determine the extent of habitat availability and mean home range size.

Twelve cover types were described on the BWWMA study area (Table 2.1). Ruderal habitat was classified more in terms of location than vegetation. Because the purpose of this analysis was to determine if certain cover types defined by vegetation characteristics were used more than would be expected by availability, I excluded the ruderal cover type from the analysis. I calculated the proportion of cover types available to nesting bobwhites using a habitat cover type layer of BWWMA developed by the Florida Fish and Wildlife Conservation Commission in 2005 – 2006 (Figure 2.2). Home ranges or nest buffers were used as outlines in ArcGIS to clip the habitat cover layer and

determine the proportion of each cover type within the range. I assigned used nest habitat as the cover type within which the nest was located. I observed that bobwhites seemed to prefer nesting among palmettos. Therefore, I hypothesized that bobwhites would show selection for mesic flatwoods and/or dry prairie cover types for nest locations because of (1) their relatively dry nature, and (2) more palmettos relative to other cover types.

Daily Nest Survival: I used Program MARK nest survival models to calculate the daily survival rate (DSR) of bobwhite nests (White and Burnham 1999, Dinsmore et al. 2002). Program MARK nest survival models utilize the Mayfield method (Mayfield 1961) for calculating the DSR of nests from exposure days while allowing the inclusion of covariates for explaining variation in DSR. I modeled the relationship between DSR and several covariates selected from *a priori* hypotheses about factors influencing bobwhite nest DSR. I used a hierarchical modeling approach with three preliminary model suites, a fourth model suite comparing top models from the preliminary suites and a fifth model suite with all possible combinations of the most supported models from the fourth suite. I chose this hierarchical approach to avoid combinations of models which lacked biological plausibility (Anderson 2008). I added an interaction between basin marsh and wet flatwoods habitats to models in the fifth suite to determine if there was a strong difference in effects of the two habitat variables on DSR. I used Akaike's information criterion (AIC_c) for model selection (Burnham and Anderson 2002). Within each preliminary model suite, I used evidence ratios to determine levels of support. Evidence ratios (hereafter "ER") are calculated within a model suite as

$$ER = w_{min} / w_i$$

where w_{min} is the Akaike weight (w) for the best model in the suite and w_i is the individual w for all the models in the suite ($i = 1, 2, \dots, i$) (Anderson 2008). Following this ratio, the best model will have $ER = 1$. All other models will have $ER > 1$ with less support as the ER gets larger. ER are likened to odds ratios with raffle tickets, where an evidence ratio of 100 for model w_i is equivalent to model w_i having 1 raffle ticket compared to model w_{min} having 100 raffle tickets in a drawing to determine which model

is most likely given the data (Anderson 2008). Anderson (2008) suggested that an arbitrary cutoff for model selection (i.e., $\Delta AIC_c \leq 2$) should not be used. I considered all models within each preliminary suite, and decided which models to include in the fourth suite based on the range and relative difference of ER.

Table 2.1: General descriptions and abbreviations for the twelve habitat categories on BWWMA in southwest Florida 2002 - 2009.

Habitat Category	Abbreviation	Description
Basin Marsh	BM	Large, irregularly shaped wetlands maintained by fire occurring every 1 -10 years. Vegetation is herb-dominated, but varies in species content from the deepest centers to the progressively shallower edges.
Depression Marsh	DM	Small rounded wetlands maintained by fire every 1 - 10 years. Vegetation is herb dominated, but species content changes from the deep center to the shallow edges. Typically dry out in periods lacking rain.
Dry Prairie	DP	Nearly treeless flatlands dominated by a variety of herbs and low shrubs. Maintained by fire every 1 - 4 years. Distinction from wet prairie by presence and abundance of saw palmetto.
Hydric Hammock	HH	Forested wetlands dominated by hardwood species. Fire is rare because of saturated soils.
Mesic Flatwoods	MF	Open pine canopy forests with a diverse understory of shrubs and herbs. Maintained by fire every 2 - 5 years. Distinction from wet flatwoods by presence and abundance of saw palmetto.
Mesic Hammock	MH	Closed canopy forests of hardwood species. Fire is rare. Occur along edges and as islands within basin marsh habitat.

Table 2.1: (continued).

Habitat Category	Abbreviation	Description
Improved Pasture	PI	Unnatural community dominated by exotic grasses suitable for cattle grazing.
Semi-improved Pasture	PS	Unnatural community prepared for cattle grazing, but still resembles a natural community.
Pine Plantation	PP	Silvicultural operations with a dense monoculture of pine trees.
Ruderal	R	A variety of habitat types that have been altered by human activity but may still resemble the natural community. Located in the vicinity of buildings and roads.
Wet Flatwoods	WF	Open pine canopy forests with an understory of hydrophytic shrubs and herbs. Maintained by fire every 2 - 5 years. Distinction from mesic flatwoods by near absence of saw palmetto.
Wet Prairie	WP	Nearly treeless flatlands dominated by a variety of hydrophytic herbs and shrubs. Maintained by fire every 2 - 5 years. Distinction from dry prairie by near absence of saw palmetto.

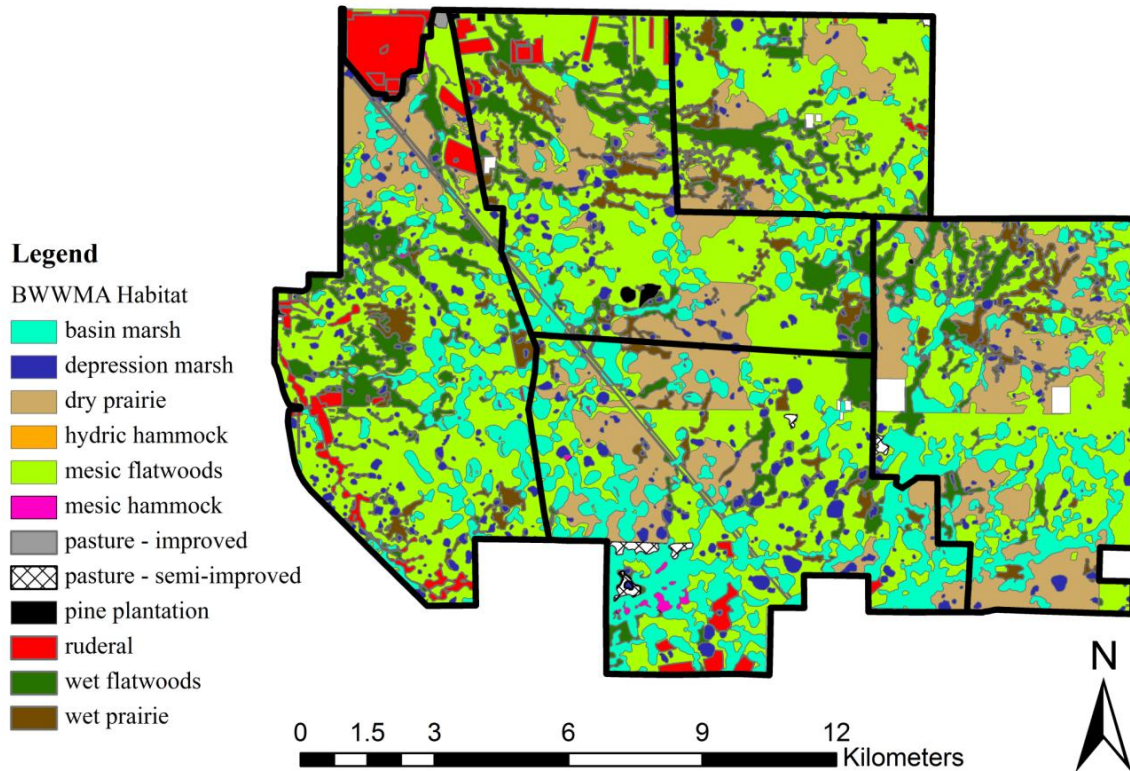


Figure 2.2: Habitat cover layer for Babcock-Webb WMA in southwest Florida depicting habitat categories available on the management area during the northern bobwhite study, 2002 - 2009. Hunting zones are labeled in figure 2.1.

In the first model suite, I evaluated models with the grouping variables of year, sex, hunting zone and within-season temporal variables (Table 2.2). I expected annual variation in DSR because of changes in predator population densities and fluctuations in broad scale weather patterns (Dinsmore et al. 2002). Whereas the hunting zones consisted of generally the same cover types, there was variation in overall size, shape, and juxtaposition of cover types among zones (Figure 2.2). Therefore, I considered differences in DSR among hunting zones to be plausible. Females typically incubate more nests than males (Stoddard 1931). Some studies have shown that the gender of the incubating bird had no effect on nest success (Roseberry and Klimstra 1984, Burger et al. 1995). Nevertheless, I tested that hypothesis on my study population. Variation in DSR within the nesting season is also expected because of changing weather (i.e., increasing

temperatures and fluctuating precipitation) and also fluctuations in predator activity. Researchers of avian grassland species found support for models evaluating linear and quadratic relationships between nest DSR and time (Grant et al. 2005, Davis et al. 2006). I hypothesized that DSR would either decrease linearly over the nesting season because of increasing predator activity and increasing severity in temperature and rainfall, or have a curvilinear (quadratic) relationship with time over the nesting season because of fluctuations in the aforementioned factors.

In the second suite of models, I evaluated environmental variables associated with each nest (Table 2.2). Daily rainfall data were available from a Southwest Florida Water Management District data collection station on the west side of BWWMA. I used these data to calculate rainfall covariates associated with each nest. The time intervals for the total rainfall covariates were chosen as divisions of the incubation period of bobwhites. The total incubation period of bobwhites is 23 days $\pm$ 1 day (Rosene 1969, Brennan 1999). Researchers in south Florida have determined that nest flooding of avian grassland species could be a significant cause of nest mortality (Pranty 2000, Perkins and Vickery 2005). Therefore, I hypothesized that there was a negative relationship between the amount of rainfall and DSR. My analysis was exploratory beyond this hypothesis to determine at what point the relationship with rainfall was negative. The covariates I included were the total rainfall (cm) 3, 12, and 23 days prior to the fate of the nest, respectively. By including these three covariates in the daily nest survival models, I determined first if there was a relationship between rainfall and DSR, and second, at what time scale and/or quantity of rain the relationship occurred.

Table 2.2: Description of the three preliminary model suites for daily nest survival rate and the corresponding model notation used in later results tables. A constant survival model (S(.)) containing only the intercept was included in each suite, but is not included in this table.

Model Suite	Model	Notation
I. Group and Time Models	Year	S(year)
	Linear Time	S(T)
	Quadratic Time	S(T+TT)
	Zone	S(zone)
	Sex	S(sex)
	Year by Linear Time Interaction	S(year*T)
	Year by Quadratic Time Interaction	S(year*(T+TT))
II. Climate Models	Total rainfall 3 days prior to nest fate	S(TR3D)
	Total rainfall 12 days prior to nest fate	S(TR12D)
	Total rainfall 23 days prior to nest fate	S(TR23D)
	7.62 cm event 3 days prior to nest fate?	S(3in3)
	# 7.62 cm rain events 12 days prior to nest fate	S(3in12)
	Average temperature (°C) 12 days prior to fate	S(AvgT12D)
	Quadratic TR23D	S(23*23)
III. Habitat Models	Quadratic AvgT12D	S(T12*T12)
	% Basin Marsh within 100 m radius of nest	S(BM100)
	% Basin Marsh within 1000 m radius of nest	S(BM1000)
	% Wet Flatwoods within 100 m radius of nest	S(WF100)
	% Wet Flatwoods within 1000 m radius of nest	S(WF1000)
	Burn status of nest site	S(burn)
	BM100 + WF100	S(BM100+WF100)
	BM1000 + WF1000	S(BM1000+WF1000)

I included two other variables associated with rainfall. I hypothesized that rain events (a short-term continuous amount of rain) may affect the DSR by flooding the nesting area. These rain events may impact the DSR (1) directly by inundating the nest causing failure, (2) indirectly by concentrating predators on the high ground where the nests are located, or (3) by intensifying the scent of the nest and/or incubating adult resulting in easier location by predators. Frye (1954) used 7.62 cm of rain as a basis for examining differences in nest success and juvenile recruitment among years of his study on the BWWMA. Pranty (2000) found Florida grasshopper sparrow (*Ammodramus* *savannarum floridanus*) nests flooded after rain events less than 6.84 cm. I included covariates of whether the nest experienced a continuous rain event of ≥ 7.62 cm three days prior to its fate and the number of rain events ≥ 7.62 cm twelve days prior to its fate.

Temperature shifts throughout the breeding season could increase activity of snakes and other nest predators. Extreme temperature has also been shown to negatively affect bobwhite nesting in Texas through stress on the adult and eggs causing nest abandonment or failure (Guthery et al. 2001, Guthery et al. 2005). For that reason, I included the average daily temperature ($^{\circ}\text{C}$) for the twelve days prior to the fate of the nest as a climatic variable and hypothesized that DSR would decrease with increasing average temperature.

In the third model suite, I evaluated models with covariates related to habitat characteristics (Table 2.2). Burn status was a categorical variable grouping nests by whether vegetation at the actual nest location had been burned the previous non-breeding season. Dimmick (1971) suggested that burn status of a nest site could have an indirect effect on nest success because nests in fields burned the previous fall were initiated later in the season than nests in unburned fields. He also observed that more bobwhites nested in unburned fields than fields burned the previous non-breeding season (Dimmick 1971). I hypothesized that nests in vegetation burned the previous non-breeding season would have lower DSR than nests in previously unburned vegetation. The other variables included in this model suite were the proportion of basin marsh cover type within 100-m and 1000-m radii of the nest, and the proportion of wet flatwoods cover type within 100-m and 1000-m radii of the nest. These cover types were based upon the

results of the nest-site habitat selection analysis. I hypothesized *a priori* that the proportion of the most favored cover types around each nest location would positively influence DSR. I chose the radial distances of 100 m and 1000 m to capture local and landscape habitat scales, respectively, because habitat cover types and their associations are important to bobwhites at a wide range within landscapes (White et al. 2009).

In the fourth model suite, I compared the most supported models from the first three suites. I calculated ER for all of the models in the fourth suite and used the ER to determine the models I included in the fifth model suite. I considered the range and relative difference of ER for selection of models to include in the fifth suite. In the fifth model suite, I modeled all combinations of the most supported models from the fourth model suite. I assumed that the models with enough support to be included in the fifth suite had justification to be combined because of my conservative hierarchical approach and model selection methods. I also added an interaction term between habitat variables to models in the fifth suite to determine support for models allowing cover type proportions to vary differently. I considered a covariate within a model to be an important factor if the 95% confidence interval for the beta estimate did not overlap zero.

I used weighted model averaging to average the DSR estimates across all models in the fifth model suite. I calculated the probability of a nest surviving a given 23-day incubation period as the product of 23 consecutive daily survival rates starting on day one of the period. I used a 23-day incubation period because it is a rangewide average bobwhite incubation period (Rosene 1969, Brennan 1999). I also estimated a constant breeding season DSR from the constant survival model. The constant 23-day incubation period survival rate estimate was calculated as the constant DSR to the 23rd power. The standard error for the constant 23-day incubation period survival rate was calculated using the delta method (Powell 2007).

RESULTS

I caught 711 bobwhites (393 males and 318 females) using the baited funnel trap method, and 755 bobwhites (658 males and 97 females) using the decoy funnel trap method over the duration of the study. Forty-four bobwhites (24 males and 20 females)

were caught using the night cast net method. I caught 459 (225 males and 234 females) bobwhites using the dog cast net method, and 54 (27 males and 27 females) and 202 (93 males and 109 females) bobwhites by using the night telemetry cast net and diurnal telemetry cast net methods, respectively.

Bobwhites of both sexes in the 1 April cohort incubated 234 (females) and 64 (males) nests respectively from 2003 to 2009. Nesting rates were consistently greater for females than males and were variable among years for females and more so for males. The pooled nesting rates over the seven nesting seasons of the study were 58% for females and 17% for males (Table 2.3). Yearly bird success rates were also greater for females than males. Pooled estimates were 39% and 9% for females and males, respectively. Females averaged 1.23 (SE = 0.03) nests per nesting adult; the average nesting attempts per male was 1.02 (SE = 0.02; Table 2.3). Nest success rates were similar for both sexes in most years and the pooled success rates were 59% for females and 52% for males. The overall mean clutch size (n = 212 nests) was 12.37 (SD = 2.96; Table 2.3).

Table 2.3: Estimates of yearly nesting parameters of northern bobwhites in southwest Florida, 2002 - 2009. Parameter estimates are derived from a cohort of bobwhites alive and radio-tagged on 1 April each year.

Year	# alive and radioed 4/1		Nesting Rate ^a		Bird Success ^b		Nests/Nesting Adult ^c				Nest Success ^d		Clutch Size					
	Male	Female	Male	Female	Male	Female	Male	SE	Female	SE	Male	Female	Male	SD	Female	SD	Overall	SD
2003	10	7	10	100	0	57	1.00	0.00	1.14	0.14	0	50	16.00	0.00	12.86	2.12	13.25	2.25
2004	39	31	13	61	10	42	1.00	0.00	1.00	0.00	80	68	15.00	4.73	14.00	2.97	14.10	3.13
2005	73	73	36	62	16	40	1.00	0.00	1.33	0.08	46	58	11.94	3.10	12.62	2.23	12.42	2.51
2006	52	48	17	60	15	42	1.11	0.11	1.24	0.08	80	56	13.43	1.27	11.59	2.85	11.97	2.69
2007	63	70	6	46	3	30	1.00	0.00	1.44	0.11	50	52	9.50	5.67	11.06	3.18	10.86	3.49
2008	62	44	16	57	8	45	1.00	0.00	1.20	0.08	50	67	12.25	2.22	12.85	2.44	12.71	2.34
2009	70	54	11	61	3	41	1.00	0.00	1.06	0.04	25	63	11.86	2.73	13.10	3.09	13.06	3.08
Pooled	369	327	17	58	9	39	1.02	0.02	1.23	0.03	52	59	12.25	3.23	12.40	2.89	12.37	2.96

^a Percent of adults in cohort that attempted to incubate a nest.

^b Percent of adults in cohort that successfully incubated a nest (i.e., hatched a nest)

^c Average number of nests per nesting adult.

^d Percent of nests that successfully hatched.

Nest Habitat Selection: I calculated the home range of 168 female bobwhites. Average home range size was 33.37 ha. A circular buffer (radius = 326 m) was created around 174 nest locations to estimate habitat availability for incubating females with <10 locations prior to nesting or females constructing nests incubated by males. Of the eleven habitat types considered for the nest habitat selection analysis, nine were available to nesting bobwhites by being present in at least one home range or nest buffer boundary. Therefore, the nest habitat selection analysis considered these nine cover types. Six of these cover types contained at least one bobwhite nest during the study (Table 2.4).

I analyzed nest habitat selection for 336 out of 400 bobwhite nests. To allow equal weight within each year among individuals for the analysis, 58 nests were excluded because they were re-nests of individual bobwhites within breeding seasons. Six additional nests were excluded from the analysis because they were within the ruderal cover type.

No overall difference occurred between observed habitat use and what would be expected by chance ($F = 9.80$, $df = 8$, $P = 0.279$; Table 2.4). Mesic hammock, semi-improved pasture, and pine plantation were never used for nesting (Table 2.4). Basin marsh and wet flatwoods were the only two types used at a greater proportion than they were available (Figure 2.3). These categories also had the greatest RSPF's of 0.210 and 0.214, respectively (Table 2.5). The other cover types were used proportionally less than they were available to nesting bobwhites (Figure 2.3).

Table 2.4: Total area and proportions of area of each habitat category available to and used by nesting northern bobwhites in southwest Florida, 2003 - 2009. Habitat categories are described in Table 2.3.

	Habitat Category												Total
	BM	DM	DP	HH	MF	MH	PI	PS	PP	R*	WF	WP	
Total Available in Study Area (ha)	4534.2	1132.5	4024.1	2.0	11405.5	54.3	14.5	91.6	44.7	1114.0	2741.8	1232.1	26391.1
Total Available to Nesting Bobwhites (ha)	1449.7	510.0	1889.7	0.0	5314.8	3.1	0.0	0.4	19.1	151.1	1249.5	799.1	11386.5
Total Bobwhite Nests	53	13	47	0	150	0	0	0	0	6	50	23	342
Proportion Available in Study Area (%)	17.2	4.3	15.2	0.0	43.2	0.2	0.1	0.3	0.2	4.2	10.4	4.7	100.0
Proportion Available to Nesting Bobwhites (%)	12.7	4.5	16.6	0.0	46.7	0.0	0.0	0.0	0.2	1.3	11.0	7.0	100.0
Proportion of Bobwhite Nests (%)	15.5	3.8	13.7	0.0	43.9	0.0	0.0	0.0	0.0	1.8	14.6	6.7	100.0

* The ruderal habitat type was excluded from the nest resource selection analysis because of its relation to location rather than vegetation. The total nests used in the analysis was 336 which reflects the exclusion of the 6 nests in ruderal habitat.

Table 2.5: Nest habitat selection analysis results of northern bobwhites in southwest Florida, 2003 - 2009. Habitat category abbreviations are described in Table 2.3.

Model	Habitat RSPF									Likelihood	Deviance	df	P
	BM	DM	DP	MF	MH	PS	PP	WF	WP				
No Selection ^a	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111	3.6×10^{-122}	559.26888	0	
Selection ^b	0.210	0.139	0.142	0.141	0.000	0.000	0.000	0.214	0.153	4.8×10^{-120}	549.46943	8	
Difference, Null Model vs Selection/Pooled Data											9.79945	8	0.279

^a The no selection model tests the likelihood of equal RSPF's for each habitat given the data.

^b The selection model shows RSPF's for each habitat type given the data and calculated through iteration.

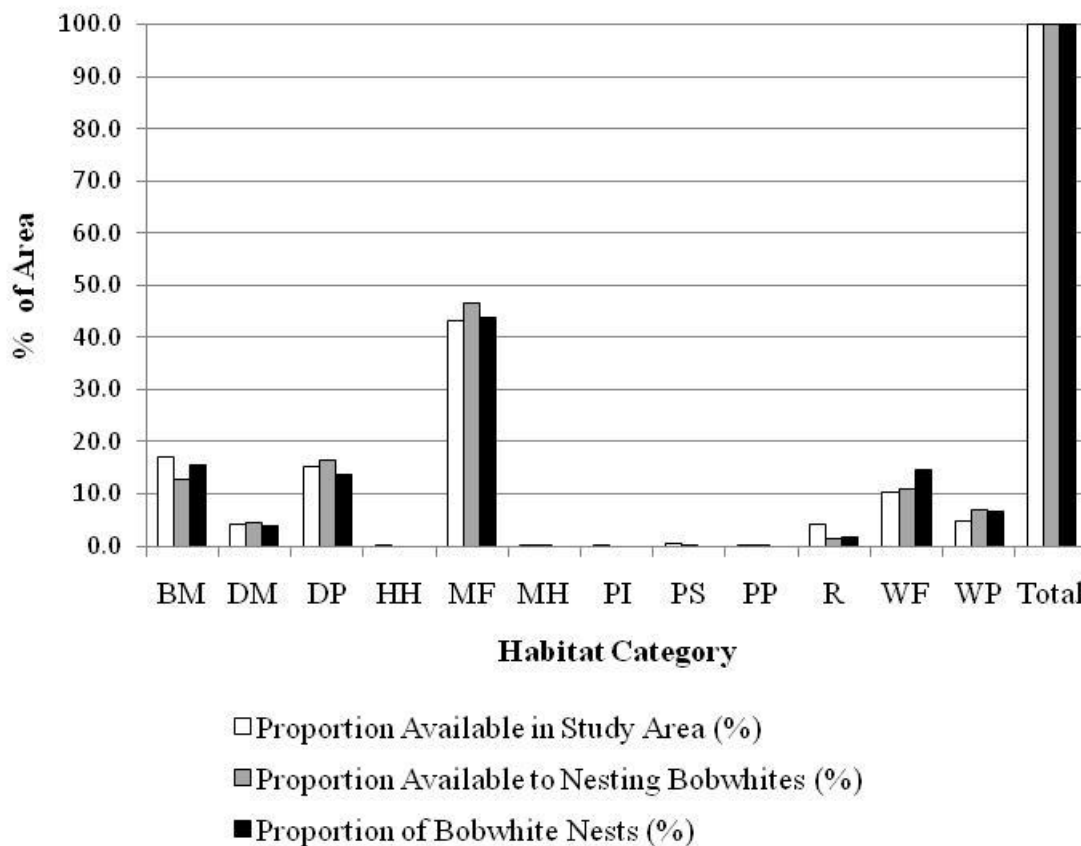


Figure 2.3: Available and used habitat category proportions for nesting northern bobwhites in southwest Florida, 2003 - 2009. Habitat categories are described in Table 2.3.

Daily Nest Survival: I determined daily nest survival using the nest histories of 400 nests over the seven breeding seasons of the study from 2003 to 2009. Over the seven breeding seasons of the study, bobwhite nests were active from 9 March (first nest located) through 28 September (last checked date for last nest), for a 204-day nesting period. However, among years, the nesting periods were highly variable (Table 2.6).

In the first model suite, only linear and quadratic time had strong support with ER of 3.4 and 1.0 respectively (Table 2.7). Models with the grouping variables of year, zone, and sex had little support (ER >100 for all). Although the constant survival model lacked

support (ER = 114.2), I calculated the constant survival model DSR (0.9683; SE = 0.0024) for comparative purposes. Two other models testing for a year by time interaction were not supported because year differences were not a factor.

Table 2.6: Yearly number of nests monitored (n) and nesting periods of northern bobwhites in southwest Florida, 2002 - 2009.

Year	n	Nesting Period				Days ^d
		Start Date ^a	(Day of Period) ^b	End Date ^c	(Day of Period)	
2003	18	5/7/2003	(60)	8/10/2003	(155)	96
2004	27	4/28/2004	(51)	6/23/2004	(107)	57
2005	107	4/13/2005	(36)	9/5/2005	(181)	146
2006	57	3/9/2006	(1)	9/1/2006	(177)	177
2007	73	4/25/2007	(48)	9/28/2007	(204)	157
2008	75	4/14/2008	(37)	9/19/2008	(195)	159
2009	43	4/15/2009	(38)	6/30/2009	(114)	77

^a Date the first nest was found.

^b Numeric location of the date within the 204 day nesting period for the entire study.

^c Date of the last day the last nest was checked.

^d Total length of nesting period.

In the second suite of models, none of the climatic covariates I evaluated explained variation in DSR. The constant survival model was the most parsimonious (ER = 1.0; Table 2.8).

In the third suite, the model S(BM1000) was the most parsimonious model (Table 2.9). With an ER = 16.8, the S(WF1000) model was also included in the fourth suite. All other models, including the constant survival model, lacked support with ER >100 for all.

In the fourth model suite, I compared 13 models, 2 from the first suite, 9 from the second suite, and 2 from the third suite. Four models had support in this fourth suite with ER <17 (Table 2.10). The model of DSR as a function of the BM1000 covariate was the

most parsimonious with $ER = 1$. The relationship between DSR and BM1000 was positive and important: the beta estimate for BM1000 was 2.82. The DSR as a function of quadratic time model had support with $ER = 1.4$. The beta estimates for linear time (-0.03) and quadratic time (0.0001) were important indicating a decline in DSR over the nesting period with the slope approaching zero near the end of the nesting period. The model of DSR as a function of linear time only had support with $ER = 4.76$ and the beta for linear time (-0.006) was important. The final model with support from the fourth suite was the WF1000 model with $ER = 16.83$. This model involved a negative relationship between DSR and the WF1000 covariate, and the beta for WF1000 (-1.89) was important.

In the fifth model suite, I evaluated ten additional models with combinations of the additive effects of the four top models from the fourth suite. Seven of the additive models were supported in the model suite with $ER < 37$ (Table 2.11). All of the top seven models included the effect of linear time. In these models, the relationship between linear time and DSR was consistently negative and important (Table 2.11). Six of the top models included the basin marsh covariate effect. For all of these models the parameter estimates for the BM1000 variable were positive and important (Table 2.12). All other variable beta estimates in the top seven models had confidence intervals that included zero the majority of the time, suggesting weak relationships (Table 2.12).

DSR estimated from averaging models in the fifth suite ranged from 0.9486 to 0.9916 and exhibited a clear negative linear trend over time with a possible quadratic effect (Figure 2.4). For a 23-day incubation period, the nest survival rate ranged from 0.2978 for a nest that initiated incubation on day 173 (28 August) to 0.7912 for a nest that initiated incubation on day 1 (9 March). The overall DSR estimated from the constant survival model was 0.9683 ($SE = 0.0024$), and the overall 23-day incubation period survival rate was 0.4766 ($SE = 0.0269$).

Table 2.7: Summary of model-selection results from the first preliminary model suite for nest survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 2.1.

Model	<i>K</i>	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(T+TT)	3	1024.2877	0	0.75706	1.0000	1018.2830
S(T)	2	1026.7326	2.4449	0.22296	3.3955	1022.7303
S(zone)	5	1033.6154	9.3277	0.00714	106.0308	1023.6037
S(.)	1	1033.7643	9.4766	0.00663	114.1870	1031.7635
S(sex)	2	1034.2464	9.9587	0.00521	145.3090	1030.2441
S(year)	7	1038.0331	13.7454	0.00078	970.5897	1024.0112
S(year*TT)	15	1041.4263	17.1386	0.00014	5407.5714	1011.3322
S(year*T)	14	1042.6907	18.403	0.00008	9463.2500	1014.6084

Table 2.8: Summary of model-selection results from the second preliminary model suite for nest survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 2.1.

Model	<i>K</i>	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(.)	1	1033.7643	0	0.18535	1.0000	1031.7635
S(TR23D)	2	1034.1564	0.3921	0.15235	1.2166	1030.1541
S(3in12)	2	1034.5994	0.8351	0.12208	1.5183	1030.5971
S(AvgT12D)	2	1034.9132	1.1489	0.10435	1.7762	1030.9109
S(TR3D)	2	1035.0187	1.2544	0.09899	1.8724	1031.0164
S(TR12D)	2	1035.0578	1.2935	0.09707	1.9094	1031.0555
S(3in3)	2	1035.117	1.3527	0.09424	1.9668	1031.1147
S(AvgT12D*AvgT12D)	3	1035.227	1.4627	0.0892	2.0779	1029.2223
S(23*23)	3	1036.1453	2.381	0.05636	3.2887	1030.1406

Table 2.9: Summary of model-selection results from the third preliminary model suite for nest survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 2.1.

Model	<i>K</i>	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(BM1000)	2	1023.6105	0	0.92584	1.0000	1017.5467
S(WF1000)	2	1029.2564	5.6459	0.05502	16.8273	1019.6082
S(WF100)	2	1033.5248	9.9143	0.00651	142.2181	1025.2541
S(.)	1	1033.7643	10.1538	0.00578	160.1799	1029.5225
S(BM100)	2	1034.1837	10.5732	0.00468	197.8291	1031.7635
S(burn)	2	1035.7305	12.12	0.00216	428.6296	1030.1814

Table 2.10: Summary of model-selection results from the fourth and comprehensive model suite for nest survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 2.1.

Model	K	AIC_c	ΔAIC_c	AIC_c Weights	Evidence Ratio	Deviance
S(BM1000)	2	1023.6105	0	0.49609	1.0000	1019.6082
S(T+TT)	3	1024.2877	0.6772	0.35359	1.4030	1018.2830
S(T)	2	1026.7326	3.1221	0.10414	4.7637	1022.7303
S(WF1000)	2	1029.2564	5.6459	0.02948	16.8280	1025.2541
S(.)	1	1033.7643	10.1538	0.0031	160.0290	1031.7635
S(TR23D)	2	1034.1564	10.5459	0.00254	195.3110	1030.1541
S(3in12)	2	1034.5994	10.9889	0.00204	243.1814	1030.5971
S(AvgT12D)	2	1034.9132	11.3027	0.00174	285.1092	1030.9109
S(TR3D)	2	1035.0187	11.4082	0.00165	300.6606	1031.0164
S(TR12D)	2	1035.0578	11.4473	0.00162	306.2284	1031.0555
S(3in3)	2	1035.117	11.5065	0.00157	315.9809	1031.1147
S(AvgT12D*AvgT12D)	3	1035.227	11.6165	0.00149	332.9463	1029.2223
S(23*23)	3	1036.1453	12.5348	0.00094	527.7553	1030.1406

Table 2.11: Summary of model-selection results from the fifth model suite for nest survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 2.1.

Model	K	AIC_c	ΔAIC_c	AIC_c Weights	Evidence Ratio	Deviance
S(T+TT+BM1000+WF1000+BM*WF)	6	1009.2815	0	0.28275	1.0000	997.2650
S(T+TT+BM1000+WF1000)	5	1009.6936	0.4121	0.2301	1.2288	999.6819
S(T+BM1000+WF1000+BM*WF)	5	1010.5688	1.2873	0.14855	1.9034	1000.5571
S(T+BM1000+WF1000)	4	1010.649	1.3675	0.14271	1.9813	1002.6412
S(T+TT+BM1000)	4	1011.2823	2.0008	0.10397	2.7195	1003.2745
S(T+BM1000)	3	1011.7704	2.4889	0.08146	3.4710	1005.7657
S(T+TT+WF1000)	4	1016.4516	7.1701	0.00784	36.0651	1008.4438
S(T+WF1000)	3	1019.4258	10.1443	0.00177	159.7458	1013.4211
S(BM1000+WF1000)	3	1023.5514	14.2699	0.00023	1229.3478	1017.5467
S(BM1000)	2	1023.6105	14.329	0.00022	1285.2273	1019.6082
S(BM1000+WF1000+BM*WF)	4	1023.8788	14.5973	0.00019	1488.1579	1015.871
S(T+TT)	3	1024.2877	15.0062	0.00016	1767.1875	1018.283
S(T)	2	1026.7326	17.4511	0.00005	5655.0000	1022.7303
S(WF1000)	2	1029.2564	19.9749	0.00001	n/a	1025.2541
S(.)	1	1033.7643	24.4828	0	n/a	1031.7635

Table 2.12: Parameter estimates and 95% confidence intervals (CI) for the top seven models in the fifth and final model suite for nest survival of northern bobwhites in southwest Florida, 2003 - 2009. Parameter abbreviations are described in Table 2.1.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(T+TT+BM1000+WF1000+BM*WF)	Intercept	5.1654085	0.7970355	3.6032189	6.7275981
	T	-0.0337773	0.0146208	-0.0624341	-0.0051204
	TT	0.0001138	0.0000652	-0.000014	0.0002416
	BM1000	3.9845132	1.3152067	1.406708	6.5623185
	WF1000	-0.0037641	1.2701846	-2.4933259	2.4857977
	BM1000*WF1000	-13.891186	8.99368	-31.518799	3.7364275
S(T+TT+BM1000+WF1000)	Intercept	5.272582	0.793689	3.7169516	6.8282124
	T	-0.0323409	0.014563	-0.0608844	-0.0037974
	TT	0.0001075	0.0000649	-0.0000196	0.0002346
	BM1000	2.6173084	0.912394	0.8290162	4.4056006
	WF1000	-1.5110086	0.7903635	-3.0601211	0.0381039
S(T+BM1000+WF1000+BM*WF)	Intercept	3.8943631	0.3044528	3.2976357	4.4910906
	T	-0.0085577	0.0021308	-0.0127341	-0.0043813
	BM1000	4.1666505	1.3194909	1.5804483	6.7528527
	WF1000	-0.0172453	1.261678	-2.4901342	2.4556436
	BM1000*WF1000	-12.843491	8.9465973	-30.378822	4.6918398
S(T+BM1000+WF1000)	Intercept	4.0573539	0.2848629	3.4990227	4.6156852
	T	-0.0084916	0.0021447	-0.0126951	-0.004288
	BM1000	2.8663303	0.9033537	1.0957571	4.6369035
	WF1000	-1.4058298	0.7889839	-2.9522383	0.1405787
S(T+TT+BM1000)	Intercept	4.8527075	0.7520166	3.3787549	6.3266601
	T	-0.0297877	0.0143611	-0.0579355	-0.0016399
	TT	0.0000978	0.0000641	-0.0000279	0.0002234
	BM1000	3.1592892	0.8609712	1.4717856	4.8467928
S(T+BM1000)	Intercept	3.7726082	0.2320132	3.3178623	4.2273541
	T	-0.0081667	0.0021435	-0.0123679	-0.0039656
	BM1000	3.3434151	0.8576717	1.6623784	5.0244517
S(T+TT+WF1000)	Intercept	5.9515728	0.7692465	4.4438497	7.4592959
	T	-0.0378577	0.0145061	-0.0662897	-0.0094257
	TT	0.0001364	0.0000641	0.0000107	0.000262
	WF1000	-2.3384679	0.7341551	-3.7774119	-0.8995238

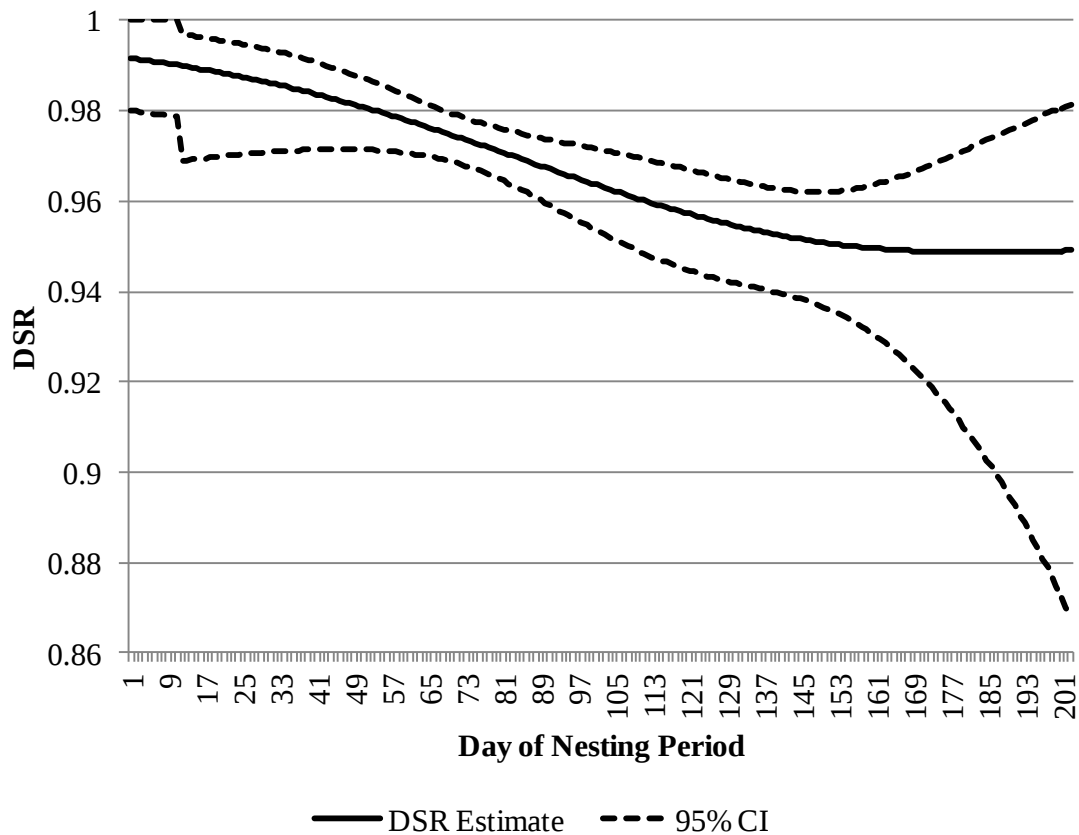


Figure 2.4: Daily nest survival rate trend and 95% confidence interval for the 203 interval nesting period of northern bobwhites in southwest Florida, 2003 - 2009, estimated from model averaging the models in suite five.

DISCUSSION

The estimated nesting rates from my study (58% female, 17% male) were lower than those reported from declining populations in Missouri (66% female, 29% male; Burger et al. 1995) and New Jersey (69% female, 20% male; Collins et al. 2009), higher than Mississippi (38% female, 7% male; Taylor and Burger 1997), and similar to a female nesting rate of 57% for an abundant population in Georgia (Terhune et al. 2006) (Table 2.13). Bird success rate on my study area (42% females, 9% males) was greater than in Mississippi (13% female, 5% male; Taylor and Burger 1997), but similar to

Missouri (40% female, 14% male; Burger et al. 1995) and Georgia (35% female; Terhune et al. 2006).

My estimates of average nesting attempts included birds that incubated a nest and then died before the end of the nesting period. Burger et al. (1995) estimated average nesting attempts only for birds that survived the entire nesting period. Consequently, their results for females (1.8 nests/female) were greater than my estimate (1.23 nests/female). However, their estimate for males (1.0 nests/male) was similar to BWWMA (1.0 nests/male) indicating that incubating males typically incubate only one nest per nesting period. Dimmick (1974) reported a 39% nest success rate in Tennessee. His estimate included nests that were located and failed prior to the incubation stage, and therefore, are not directly comparable to the BWWMA estimate. The overall success rate for nests reaching the incubation stage was greater on my study area (57%) than others reported from telemetry studies in the Southeast (45% - DeVos and Mueller 1993, 34% - Puckett et al. 1995, 49% - Staller et al. 2002, 54% - Terhune et al. 2006). With the exception of Puckett et al. (1995), whose study site was primarily in an agriculture landscape, these southeastern telemetry studies were conducted on areas managed specifically for bobwhites with high bobwhite densities. The average clutch size of 12.37 eggs on BWWMA was within the range of other studies throughout the bobwhite range (range 11.5 - 14.0 eggs; Sandercock et al. 2009).

Nest Habitat Selection: I used an arbitrary minimum number of ten locations per female as the criteria for estimating the average home range size because I was not attempting to describe and report specific conclusions regarding home range size. Ten locations coincide with a conservative minimum tracking time of five weeks (assuming one location every four days) that I believed was sufficient to describe available habitat for a given female.

Table 2.13: Average estimates of nesting parameters of northern bobwhites in southwest Florida, 2003 - 2009, and other studies throughout the bobwhite range.

Study	State	DSR	23-day Incubation	Nesting Rate	Bird Success		Nests/Nesting						Average Clutch Size
			Period Survival	(%)	(%)	Adult		Nest Success (%)					
			(%)	Male	Female	Male	Female	Male	Female	Pooled			
BWWMA	FL	0.9683	0.4766	17	58	9	39	1.02	1.23	52	59	57	12.37
Dimmick 1974	TN	.	.	.	.	.	.	.	.	.	.	39	11.90
Devos and Mueller 1993	FL	.	.	.	.	.	.	.	.	.	.	45	12.80
Burger et al. 1995	MO	0.9661	0.4523*	29	66	14	40	1.00	1.80	47	61	56	13.82
Pucket et al. 1995	NC	.	.	.	.	.	.	.	.	.	.	34	11.70
Taylor and Burger 1997	MS	0.9609	0.4000	7	38	5	13	.	.	.	.	.	11.70
Staller et al. 2002	FL	.	.	.	.	.	.	.	.	.	.	49	.
Terhune et al. 2006	GA	0.9713	0.5118	.	62	.	36	.	.	.	54	.	.
Rader et al. 2007	TX	0.9593	0.3845	.	.	.	.	.	.	.	.	.	.
Collins et al. 2009	NJ	0.9676	0.4688*	20	69	.	.	.	.	.	.	43	14.20

* Estimates converted from a reported 24-day incubation period survival rate to 23-day incubation period survival rate (DSR²³)

Northern bobwhites did not exhibit strong nest-site habitat selection for cover types at the resolution analyzed in my study. They selected habitats for nesting in proportion to what was available. Of the nine habitat categories available to nesting bobwhites and considered in the analysis, only six were used for nesting. Mesic hammock, semi-improved pasture, and pine plantation were likely unsuitable bobwhite nesting habitat, but were available in such low proportions that their avoidance was not detected. All of the other six cover types were used for nesting, but no selection was detected in the RSPF (Table 2.5). The statistically insignificant results of the RSPF may have some biological relevance. Bobwhites on BWWMA may select nesting habitat at the nest-site level, and, therefore, many of the broad cover types used in the analysis may contain suitable nesting cover at the micro-habitat scale.

In other studies, bobwhite nest-site selection occurred at the micro-habitat scale (Taylor et al. 1999a, Townsend et al. 2001, Lusk et al. 2006, Rader et al. 2007, Collins et al. 2009). These researchers all quantified micro-habitat characteristics at the nest-site, and found differences in those characteristics between paired nest-sites and random sites assumed to be available. The absence of statistically significant results in my analysis is likely a result of only assessing habitat at the landscape scale. The criteria used to create the cover type layer excluded any natural community <0.2 ha within a larger community, and did not distinguish it as a separate polygon in the layer. For example, a small patch of mesic flatwoods within a larger area categorized as wet flatwoods was not distinguished from wet flatwoods at the resolution of my habitat information. Therefore, a nest that occurred in the small mesic flatwoods area would have been assigned to the wet flatwoods type. These discrepancies could have contributed to my inability to identify habitat selection.

An assessment of 353 pictures of individual bobwhite nests from my study revealed more information about bobwhite nest-site selection. Eighty-eight percent of the pictured nests were in some way associated with palmettos (Figure 2.5; Table 2.14). Twelve percent of the nests were in open grass. Palmetto is most associated with dry prairie and mesic flatwoods cover types. Only 57.6% of all nests monitored occurred in dry prairie or mesic flatwoods (Table 2.4). The remaining 30% of nests that occurred in

palmetto were either in small patches of dry prairie or mesic flatwoods habitat within larger patches of other habitat, or in palmetto located within the other cover types. Both are likely because dry prairie and mesic flatwoods can occur in patches <0.2 ha and palmetto is not completely restricted to dry prairie and mesic flatwoods habitats. No matter the case, it seems that bobwhites on BWWMA select nest-sites at a much smaller scale than I analyzed. The abundance of suitable palmetto micro-habitat sites throughout the major macro-cover types suggests that a lack of suitable nest sites was not a limiting factor for bobwhite reproduction on BWWMA.

Table 2.14: General site-level nest-site habitat description for northern bobwhites in southwest Florida, 2003 - 2009. Information gathered from photographs taken of the nest-sites.

Year	Nests Pictured		Nest Location Vegetation			
	n	% of All Nests	Grass		Palmetto	
			n	%	n	%
2003	18	100	3	17	15	83
2004	27	100	2	7	25	93
2005	94	88	3	3	91	97
2006	30	53	2	7	28	93
2007	68	93	11	16	57	84
2008	74	99	15	20	59	80
2009	42	98	6	14	36	86
Pooled	353	88	42	12	311	88

Basin marsh and wet flatwoods cover types, although insignificant in terms of availability and use, were the only two types used disproportionately more than they were available (Figure 2.3). The moist nature of both of these cover types may ensure green vegetation throughout the nesting season supporting adequate insect populations. Insects are components of the diets of adult and juvenile bobwhites during the summer months

(Stoddard 1931, Rosene 1969), which may explain the disproportionate use of basin marsh and wet flatwoods.



Figure 2.5: Typical nesting habitat for bobwhite nests on BWWMA in southwest Florida, 2003 – 2009. This nest was located at the base of the palmetto circled in red.

Daily Nest Survival: The annual chronology of nesting varied widely during my study (Table 2.6). Frye (1954) observed the pair formation of bobwhites and broods appearing earlier in years with warm, dry springs. I was unable to find any differences in average spring temperatures and/or rainfall amounts among years, although I did not have the precise data to evaluate those relationships in depth. In 2004, heavy rains fell during mid and late summer and Hurricane Charlie just missed BWWMA on 13 August. The

rain and hurricane that summer could have caused bobwhites to prematurely cease nesting. Also, field work was limited during the latter part of that summer because of inclement weather; it is possible that some nests were missed. Data collection during the 2009 nesting period suffered similar setbacks because of heavy rains and lack of manpower in the latter half of the nesting period.

Bobwhite daily nest survival rates changed over time. Parameter estimates for time generally indicated a negative trend followed by a leveling off at the end of the nesting season (Table 2.12) portraying a quadratic relationship (Figure 2.4). The 95% confidence interval for quadratic time included zero in three of the four top models. The variability can be seen toward the end of the nesting period in the DSR graph (Figure 2.4). Grant et al. (2005) found support for models with linear and quadratic time trends in their study of two grassland bird species in North Dakota. The ability to evaluate daily survival rates at such fine time scales has been made possible by recent advancements in analytical techniques (Dinsmore et al. 2002). Some bobwhite studies have used the Mayfield (1961) method for calculating daily nest survival rates (Burger et al. 1995, Harris 1995, Collins et al. 2009). This method allows for the separate analysis of nesting periods (i.e., egg laying and incubation) but requires daily survival rates to remain constant within periods. Other studies have used analytical techniques allowing for bobwhite daily nest survival rates to vary as a function of time (Rader et al. 2007, Potter et al. 2011). Both Rader et al. (2007) and Potter et al. (2011) tested models allowing survival rates to vary linearly over time, but neither detected a significant relationship. They did not develop a model for quadratic time.

My *a priori* hypothesis of variability in predator population abundance and/or predator behavior may be supported by the negative DSR trend over time. Staller et al. (2005) noted that predation rates by bobwhite nest predators varied among years; however, they did not comment on any changes over the course of a single season. Raccoon (*Procyon lotor*), nine-banded armadillo (*Dasypus novemcinctus*), and Virginia opossum (*Didelphis virginiana*) were identified as important bobwhite nest predators in north Florida and south Georgia (Staller et al. 2005). Reproduction of these predator species occurs in the spring in Florida (Kern 1991, Smith and Schaefer 1991, Schaefer

and Hostetler 1998), which can result in greater abundances of these species in mid to late summer. Young raccoons and opossums can remain with the mothers for some time after weaning (Kern 1991, Smith and Schaefer 1991). During this time, the behavior of the mothers may change, spending less time idle with the young and more time actively teaching the young to procure food.

During my study, only 28 nests (7.0%) were abandoned. Thirteen nests (3.3%) were abandoned by the incubating adult for no apparent reason, 7 in May, 3 in June, and 3 in July. Four nests (1.0%) were abandoned because the incubating adult was depredated off the nest, 2 in May, 1 in July, and 1 in September. Ten nests (2.5%) were abandoned because the nested was flooded, 7 in June and 3 in July. There was no trend toward increased abandonment as the nesting season progressed. Also, increased vulnerability of nests was not apparent. Vegetation provided more cover through growth as the season progressed. Summer prescribed fires, if used at all, were conducted early in the nesting season each year to provide ample time for wiregrass regrowth and seed production. Roller chopping, if used at all, was consistent throughout the nesting season except for during variable extremely wet periods when it was discontinued. My hypothesis that increased predator abundance and/or predator behavior may increase nest failure responsible for the decrease in DSR over time is further supported by these facts.

Another factor could be fluctuations in availability of prey, including nests of other grassland species, that could distribute predation and relieve pressure on bobwhite nests. Stoddard (1931:427) commented on the alternate prey theory suggesting that it may be true in some cases, but in others, more prey may attract more predators increasing the chance of bobwhite nest predation. Other common ground-nesting bird species that nested at BWWMA included mourning dove (*Zenaida macroura*), common ground-dove (*Columbina passerina*), common nighthawk (*Chordeiles minor*), Bachman's sparrow (*Aimophila aestivalis*), and eastern meadowlark (*Sturnella magna*). On several occasions, I observed mourning dove nests and unfledged squabs on the ground on BWWMA. In the Southeast, 80% of mourning dove nests are initiated between 1 April and 26 August (Otis et al. 2008). Common ground-doves nest from early February to early October in Florida, but over half of the total nests in a breeding season were

initiated between 13 April and 10 June (Bowman and Woolfenden 1997). Information on common nighthawk nesting in the Southeast is limited, however common nighthawks nest in June in Texas (Poulin et al. 1996). I observed a common nighthawk nest on BWWMA on 20 April, 2004 and unfledged common nighthawk chicks on 25 May, 2005. Bachman's sparrows in Arkansas nested between 10 April and 26 August with 85% of all eggs laid between May and July (Haggerty 1988). Eastern meadowlarks nest from March to August (Lanyon 1995). I found an eastern meadowlark nest on 14 May, 2004 on BWWMA that was hatched with chicks three days later. Peak bobwhite nesting during my study occurred between weeks 8 and 15 (27 April to 21 June) of the nesting seasons (Figure 2.6). While all these species have long nesting seasons in the South, many put more effort into nesting earlier in the summer than later. This supports my hypothesis that bobwhite nests may experience relief from predation pressure early in the season because of a plethora of alternate prey.

Climatic variables did not explain variation in DSR in my study. Rader et al. (2007) found positive relationships between both temperature and precipitation and bobwhite nest DSR in southern Texas. Other climatic covariates might have more effectively captured the relationship between climate and daily nest survival on my study if one existed. BWWMA is a large study area and climatic variables, particularly rainfall, may have differed across the region because of the sporadic nature of summer thunderstorms. I was unable to collect more site-specific climatic information across the study area, and therefore, these variables may not have been representative of the conditions occurring at every nest. Alternatively, rainfall and temperature during my study period may not have been so extreme as to influence bobwhite nest survival.

Although the estimate was consistently negative, the 95% confidence interval for the WF1000 variable included zero in four of the five top models in which it appeared (Table 2.12). Therefore, the wet flatwoods cover type did not appear to have a strong relationship with DSR on my study area. However, its inclusion in five of the top seven models suggested some level of importance. Wet flatwoods, by description, are wooded and may harbor known nest predators. Virginia opossums, raccoons, and armadillos

inhabit wooded areas (Kern 1991, Smith and Schaefer 1991, Schaefer and Hostetler 1998).

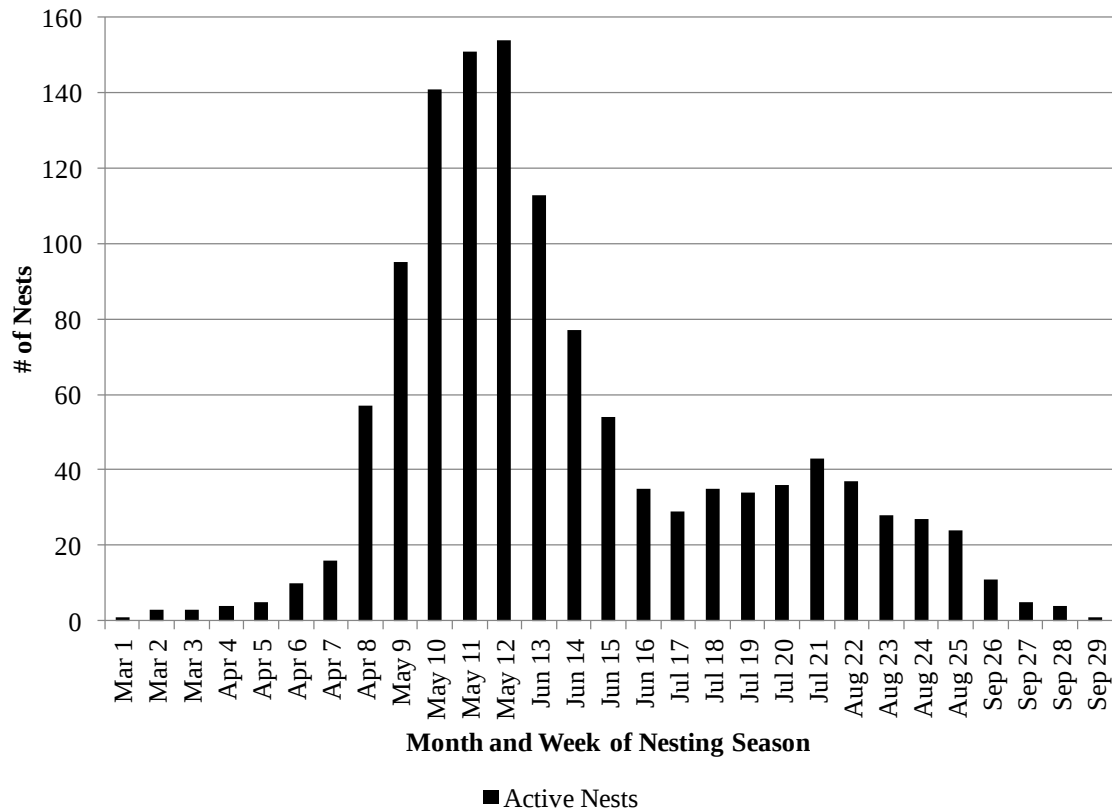


Figure 2.6: Nest incubation activity by week for the 204-day nesting period of northern bobwhites in southwest Florida, 2003 – 2009. Bars represent the number of nests in the incubation stage during each week of the breeding period.

Basin marsh within 1000-m of nests was an important predictor of DSR (Figure 2.7). As nest survival is directly related to fitness and fitness to habitat quality (Van Horne 1983), nest sites in proximity to areas of basin marsh may be considered high-quality nesting habitat. The reason for this may be lesser predation pressure (Staller et al. 2002) and/or shorter distances to food sources for the incubating adults. Insect abundance and diversity have been found to increase as habitat moisture levels increase

(Janzen and Schoener 1968). The moist nature of basin marsh may have supported abundant insect populations that were an important food source for bobwhites during the breeding seasons. Incubating bobwhites will attempt to defend the nest from some nest predators (Staller et al. 2005). Therefore, an incubating adult that had to travel a shorter distance to a food source might have spent more time at the nest defending it from predators. Also, the adult itself may have had a lesser chance of being predated as the travel distance to food, and exposure time to potential predators, decreased.

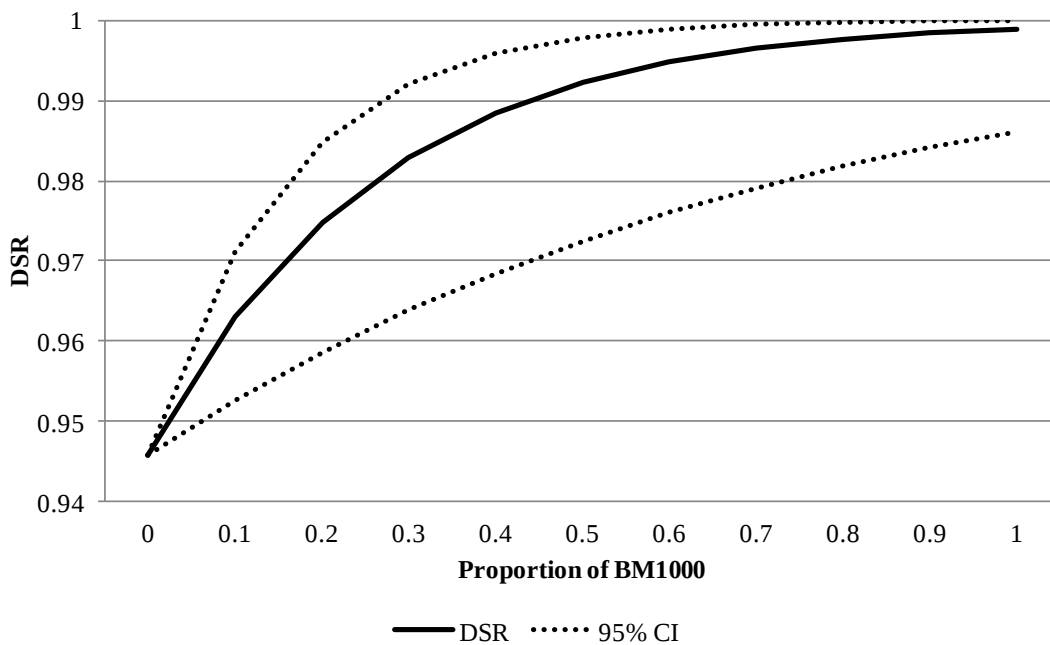


Figure 2.7: Graphical depiction of the relationship between BM1000 and nest DSR for northern bobwhites in southwest Florida, 2003 – 2009. Graph shows beta estimate and 95% confidence interval for the BM1000 covariate in the best model in suite five. Values of other covariates used in the model were 100 for time and 0 for WF1000.

My *a priori* approach to determining which habitat variables to include in my nest DSR analysis was to include only nest buffer compositions of the cover types most

selected for nest sites. However, other cover types were used heavily by nesting bobwhites, and their compositions around nest sites could have been related to nest DSR. Future studies may consider an exploratory approach to determine if other cover types around nest locations have a relationship with nest survival. This may lead to more informative results with regard to bobwhite habitat management.

The estimate of DSR on my study (0.9683; SE = 0.0024) with the constant survival model was similar to the DSR from Texas (0.9593 - Rader et al. 2007) (Table 2.13). Burger et al. (1995) reported that DSR was similar for female first nest (0.9692), renests (0.9458), and male incubated nests (0.9609). Sex was not an important determinant of DSR in my study (Table 2.7), and my DSR estimates for female (0.9701; SE = 0.0027) and male (0.9634; SE = 0.0049) incubated nests were like those reported by Burger et al. (1995) in Missouri. Twenty-three day incubation period nest survival rates of 0.452 in Missouri (Burger et al. 1995) and 0.469 in New Jersey (Collins et al. 2009) were reported from study sites with low or declining bobwhite populations in agricultural settings. They are similar to my 23-day incubation period estimate (0.4766; SE = 0.0269; Table 2.13). Also, comparable to my estimate, Potter et al. (2011) reported a 23-day incubation period nest survival rate of 0.495 on a public area in Iowa that had been undergoing bobwhite management for more than five years. Terhune et al. (2006) reported a slightly greater 23-day incubation period survival rate (0.512) on Georgia study sites intensively managed for bobwhites, including supplemental feeding and predator control. Twenty-three day incubation period survival results from Mississippi (0.40 - Taylor and Burger 1997) were lower than on BWWMA, however, their study site was relatively new to bobwhite habitat management. My results compare well to other bobwhite studies indicating that bobwhites on my study area had similar nest survival rates to other bobwhite populations with various levels of management intensity, and that nest survival rates do not vary tremendously across the bobwhite geographic range.

Other ground nesting grassland bird species including eastern meadowlark [*Sturnella magna* - 0.927], common ground-dove [*Columbina passerine* - 0.944], and common nighthawk [*Chordeiles minor* - 0.932] had lower DSR in one Florida study (Perkins and Vickery 2007) than bobwhites on BWWMA. With the exception of the

common nighthawk, these estimates included a nestling stage of development that could have contributed to the lower DSR. Incubation period survival rates would be more comparable to my results. I used the incubation period for nests of eastern meadowlarks (13 - 14 days; Lanyon 1995), common ground-doves (12 - 14 days; Bowman 2002) and common nighthawks (18 days; Brigham et al. 2011) to calculate incubation period survival rates of 0.359, 0.473, and 0.282 for eastern meadowlarks, common ground-doves, and common nighthawks, respectively. Bobwhite nests on BWWMA appear to survive the incubation stage as well as or better than other Florida ground nesting bird species. Ground nesting passerines likely are vulnerable to a wider array of mammalian nest predators than bobwhites because small mammals can more readily consume passerine eggs whereas most small mammals may not be able to directly consume a bobwhite egg (Ettle et al. 1998).

CONCLUSIONS

Bobwhite nest-site selection in southwest Florida did not differ from available habitat at the plant community scale. However, compositions of certain cover types around the nest at the landscape level were related to DSR. Future south Florida bobwhite research and analyses should test hypotheses of nest-site selection at finer scales and relate those habitat characteristics to nest survival. This information could lead to important nest-site-level structural and compositional vegetation characteristics that have management implications. Furthermore, hypotheses need to be tested as to why certain cover types or characteristics are important to nest survival (i.e., less predators, more food, etc.).

Daily nest survival rate varied as a function of linear time throughout the nesting period, but not by year or as a function of climatic variables. Changes in predator abundance, alternate prey abundance, or climatic variables not tested in this analysis (i.e., site-specific climatic variables) are possible factors related to the decrease in nest survival during the nesting period. Future research should attempt to identify the factors behind the relationship between time and bobwhite nest DSR. Relationships existing between

variables that can be monitored and nest survival may lead to implications for habitat management.

My analysis was intended to be descriptive of the reproductive success of bobwhites in southwest Florida. Two of the results may warrant the attention of managers in this region. First, basin marsh habitat appears to be positively related to bobwhite daily nest survival. Maintaining the integrity of this cover type and managing nesting habitat in and around these communities (i.e., mosaic burns leaving nesting materials and cover) may promote improved nest success. Second, peak nesting occurred between late April and late June, and nest survival rates were lowest at the end of the nesting period (late August to September). Land management conducted during the early nesting period should be carried out in a way that has the least negative impact on bobwhite nesting. For example, roller chopping should be restricted to areas with dense vegetation (i.e., areas least likely to be used for bobwhite nesting). The success of nests during periods of high nesting rates may be important to juvenile recruitment into the fall populations.

The bobwhite nesting parameters estimated in my analysis were equal or better than most other studies from throughout the bobwhite range. Stable and declining populations with various bobwhite densities had similar nest survival rates to BWWMA. Therefore, my results suggest that reproduction in the BWWMA bobwhite population is not clearly responsible for the reported population decline, similar to the conclusions of Sandercock et al. (2009) that nest survival has a minor bearing on bobwhite population change.

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PART III

OVER-WINTER SURVIVAL OF A NORTHERN BOBWHITE (*Colinus Virginianus*) POPULATION IN SOUTHWEST FLORIDA

ABSTRACT

I estimated over-winter survival and addressed six management oriented questions for a hunted northern bobwhite population in southwest Florida over a 6-year study period. I modeled over-winter (1 October to 31 March) survival using Program MARK for six winter periods as a function of temporal, spatial, hunting pressure, climatic, and habitat variables. Model selection results indicated that survival varied over space and time, and that hunting pressure was the single most important factor related to over-winter survival. Other factors related to over-winter survival were pre-hunt bobwhite density and temperature. For the over-winter period across the six years of study, the survival rate averaged 0.402 (SE = 0.023) and the harvest rate averaged 38% during the regular hunting season. Survival decreased as harvest rate increased indicating that some level of harvest was additive to natural mortality during the over-winter period. Management practices of food strip planting and prescribed burning were not directly related to over-winter survival. Lowering harvest rates through reduced hunting pressure may be the single most effective management action to increase bobwhite over-winter survival and potentially stabilize the local bobwhite population.

INTRODUCTION

Northern bobwhite (hereafter “bobwhite”) hunting is a popular sport and is deeply engrained in the heritage of many families throughout the bobwhite’s range. Not only is bobwhite hunting part of a culture, it is important for economic and conservation reasons. In 1991, bobwhite hunters in the Southeast spent about \$95 million on their sport; spent in rural communities with few other sources of income (Burger et al. 1999). The loss or decline of local bobwhite populations could therefore be detrimental to those small communities that rely on bobwhites and the hunters they attract. Also, the management and conservation of bobwhites are funded in part by hunter dollars. Bobwhite constituency groups are largely responsible for public awareness and financial resources that aid in the management of bobwhites and their habitat (Burger et al. 1999). Management for bobwhites also provides suitable habitat for a number of other grassland avian species (Giocomo et al. 2008).

Although, reliable bobwhite survival and abundance estimates can be obtained from well designed studies, factors limiting survival and abundance are difficult to isolate. Weather conditions and fluctuations in predator populations can have tremendous effects on bobwhite populations (Landers and Mueller 1986). Understanding the relationships between bobwhite populations, hunting pressure, and harvest is important because these parameters can be managed. Many studies that focus in part on these relationships have been conducted over the years (Frye 1954, Roseberry and Klimstra 1984, Burger et al. 1995, Guthery et al. 2004, Williams et al. 2009).

In the past, it was thought that harvest had little effect on a bobwhite population's fluctuations and that harvest only affected the composition of a bobwhite population and not its abundance (Frye 1954). Bobwhites may exhibit density dependent responses when hunted such that populations experience greater recruitment (Frye 1954, Roseberry and Klimstra 1984). Yet this is only one factor in a complex combination of limiting factors contributing to the success or failure of local bobwhite populations.

More recently, biologists have concluded that harvest can be additive or compensatory to natural mortality depending on the level or intensity of the harvest. Harvest may stimulate compensation by increasing reproductive effort, although the amount of compensation may be insufficient to offset the impact of harvest in some situations (Roseberry and Klimstra 1984). Williams et al. (2009) found that over-winter survival decreased from 47.9% on non-hunted to 20.9% on hunted study sites and concluded that a harvest rate >60% was additive to natural mortality. Another study found that harvest rates >30% will cause a bobwhite population to decline (Landers and Mueller 1986). It is clear that a better understanding of the impact of harvest is needed and that harvest may affect bobwhite populations differently throughout the geographic range.

Reductions in harvest mortality may be necessary when the focus of management is stabilizing or increasing bobwhite populations (Burger et al. 1995). Various methods have been used to attempt to decrease harvest of bobwhites including reduced bag limits, quotas, and restricted access. All methods reduce the opportunity of individual hunters to hunt. Reducing the bag limit in bobwhite populations with low numbers may affect the

daily harvest of only a small percentage of hunters (Guthery et al. 2004). Since many hunters rarely approach the daily bag limit in these small populations, lowering the bag limit has little effect on the total harvest of populations. Other methods of harvest reduction should be explored and their impacts understood including how much they decrease hunting opportunity.

Climatic factors such as temperature and rainfall have been related to bobwhite abundance (Lusk et al. 2001, Hernández et al. 2009). Robel and Kemp (1997) reported that winter bobwhite mortality increased with extended periods of low temperatures and snow cover in Kansas. In the Deep South, extreme amounts of precipitation and cold temperatures are uncommon. However, cool, moist conditions are thought by hunters to be the most conducive for locating bobwhite coveys. Therefore, temperature and precipitation may be related to harvest, and consequently, to survival during the hunting season.

Habitat characteristics and management have also been related to over-winter survival. Terhune et al. (2007) concluded that habitat suitability and recent habitat manipulations were two likely reasons for site variability in their estimates of over-winter survival of bobwhites in Georgia. Escape cover is a habitat characteristic that is important for bobwhites (Stoddard 1931, Rosene 1969) and has been identified as a limiting factor related to bobwhite population survival (Brennan 1991). Prescribed fire and the establishment of food strips alter the amounts of both escape cover and food available on the landscape. Robel and Kemp (1997) reported that winter survival of bobwhites near food plots was greater than survival of bobwhites far from food plots in Kansas. Other researchers found similar results in Oklahoma with regard to supplemental feeding of bobwhites (Townsend et al. 1999).

I evaluated over-winter (1 October – 31 March) survival of bobwhites in southwestern Florida from 2003 – 2009. The objectives of my study were to (1) model over-winter survival of bobwhites related to hunting pressure and spatial, temporal, biological, and climatic factors, and (2) answer specific management oriented questions related to over-winter survival: (a) what was the relationship between sesbania food strips and over-winter survival?, (b) what was the relationship between prescribed fire the

previous winter and over-winter survival?, (c) what level of hunting pressure during the regular hunt period was related to harvest rates of 15, 20, and 30%?, (d) what were the harvest rates during the regular hunt and zone F hunt each year?, (e) what was the relationship between harvest mortality and over-winter survival?, and (f) was the pre-hunt density the following year related to over-winter survival?

STUDY AREA

The study was conducted on the Fred C. Babcock-Cecil M. Webb Wildlife Management Area (hereafter “BWWMA”). BWWMA is a 26,302-ha state-owned wildlife management area managed by the Florida Fish and Wildlife Conservation Commission, located about 8 km east of Punta Gorda, Charlotte County, Florida. The habitat was southern pine flatwoods with south Florida slash pine (*Pinus elliottii* var. *densa*) dominating the overstory. Other tree species included cabbage palm (*Sabal palmetto*), live oak (*Q. virginiana*), and laurel oak (*Q. laurifolia*). The understory was dominated by saw palmetto (*Serenoa repens*) intermixed with other woody shrub species such as southern waxmyrtle (*Myrica cerifera*), gallberry (*Illex glabra*), and dwarf live oak (*Q. minima*). Herbaceous vegetation in the understory included broomsedge (*Andropogon* spp.), wiregrass (*Aristida stricta*), and slough grass (*Scleria muhlenbergii*). *Sesbania* (*Sesbania* sp.) food strips were planted each spring to provide food and cover for bobwhites and other species throughout the fall and winter months. Seasonal and perennial ponds and wetlands of various sizes were dispersed throughout the landscape. Frye (1954) described BWWMA’s vegetation, geology, soils, and land uses in detail.

Prior to the initiation of the bobwhite study, BWWMA was divided into five hunt zones to be used as treatment areas for various hunting regulations. Zones were labeled A, B, C, D, and F and ranged from 3,132 ha to 6,258 ha (Figure 3.1). In most cases zone boundaries were delineated by barbed wire fences. Zones A – D were the largest in size. Bobwhite hunting was allowed on them four days each week for six weeks throughout the regular BWWMA quail hunting season from mid-November through the end of December. Zone F was the smallest zone. Bobwhite hunting was allowed only on two consecutive days in late January each year.

Wildlife management on BWWMA included cattle grazing, prescribed fire, and roller chopping to maintain early successional habitat. Grazing was permitted in various sections of zones A, B, C, and D at various times of year throughout the study. Each year, prescribed fires were implemented from December to March. The majority of the BWWMA (i.e., 50 – 100%) was prescribe-burned each year. Summer burns were added to the burn plan to promote seed production of wiregrass. Roller chopping occurred year round to reduce saw palmetto coverage, set back overall habitat succession and promote vegetation growth.

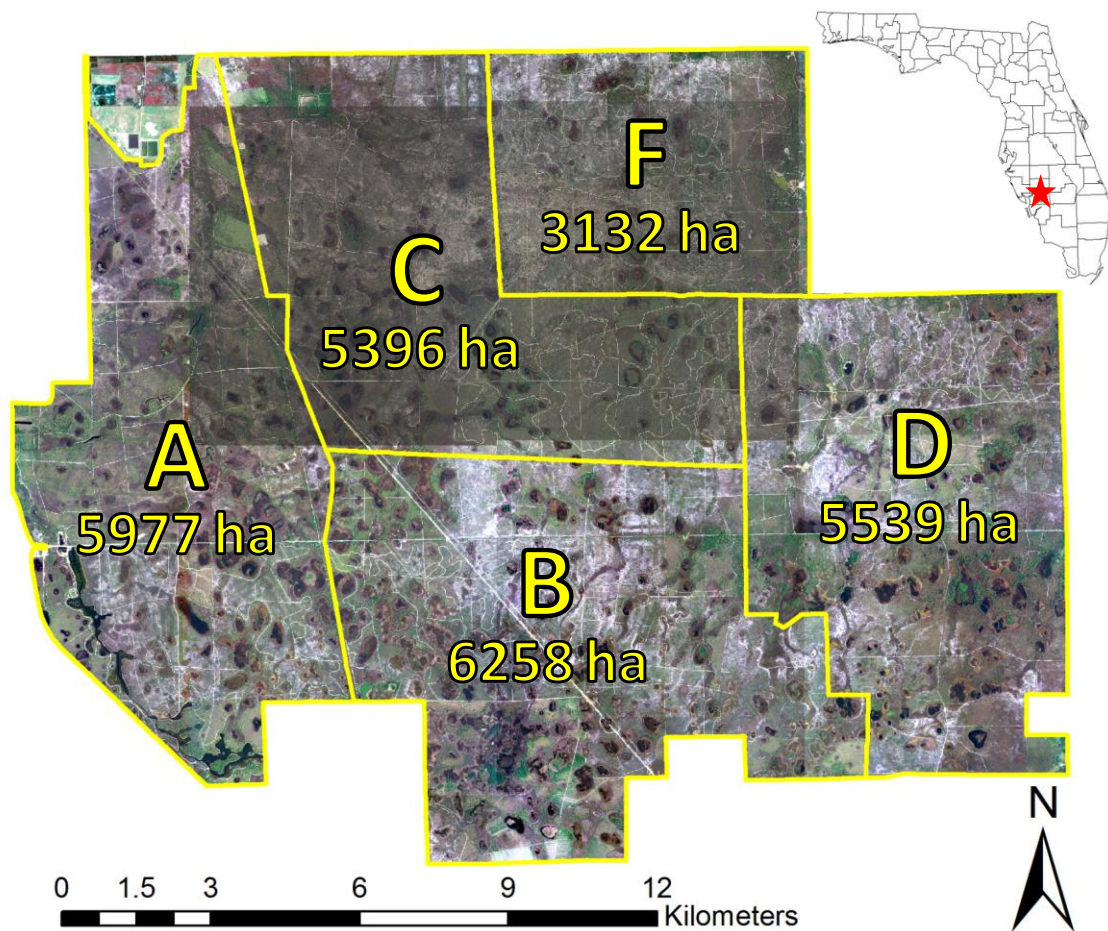


Figure 3.1: Babcock-Webb Wildlife Management Area in southwest Florida with five hunt management zones, 2002 - 2009.

METHODS

Field Methods

Trapping: I began trapping bobwhites on the study area in October 2002 and continued year round until 31 March 2009. Trapping ceased for six weeks in zones A-D each year during the regular BWWMA quail hunting season and for two days in zone F during the quota bobwhite hunt each January. I used six trapping methods throughout the study: baited funnel trap, funnel live decoy trap, night mist netting using radio telemetry, night cast netting using radio telemetry, diurnal cast netting using radio telemetry, and diurnal cast netting using bird dogs.

I utilized baited funnel traps year round for the entire duration of the study. Traps were constructed of 2.54 x 5.08 cm welded wire and were 76.20 x 76.20 cm and about 25.40 cm tall, resembling the Stoddard (1931) trap. Two funnels constructed of the same welded wire were placed on opposite sides of each trap offset from each other. Initially, I placed traps at varying intervals along roads and fire breaks and baited the traps with milo (*Sorghum* spp.). Because wild hogs regularly disrupted or destroyed baited traps, I changed the bait to wild bird seed, which included only a small amount of milo and corn (*Zea mays*) to reduce the attraction to hogs. I also modified trap locations and placed them where I observed bobwhites. After setting, I covered the trap with cut palmetto or cabbage palm fronds for camouflage and to resemble escape cover. I checked traps twice daily, in early morning and late evening. The traps were typically left set until they were moved.

I used pen-reared female bobwhites as live decoys in funnel traps during the breeding season (April to October). I constructed holding cubes to contain the live females inside the traps. The cubes were built using the same welded wire that was used for the funnel traps, 20.32 cm wide by 20.32 cm deep by 15.24 cm tall, with one side hinged allowing opening to insert and remove the female bobwhite decoys. The floor of the cube was solid and made of white corrugated plastic. I placed traps where males had been observed, and I did not restrict the traps to roads and firebreaks. I placed wild game callers (Western Rivers, Lewisburg, TN) broadcasting female bobwhite calls at many of

the trap sites to attract males and to entice the female decoys to call. I incorporated bait with this method in August to October to further entice birds into the live decoy traps.

I tried night mist netting during fall and winter 2003 to 2004. Using radio telemetry, I located coveys at night and set two mist nets in a “V” shape adjacent to the roosting covey. Once set, I attempted to flush the birds into the nets. This procedure was done at night because it was discovered that the coveys were less likely to run or flush before the nets could be set. The greatest success with this method was on the darkest, coldest nights.

In January 2003, I first attempted to throw a cast net over a covey pointed by bird dogs. I tried various net sizes and weights over the years, but the most success was with 2.74-m radius nets with about 1.48 kg of lead weight per meter. The small, light nets were easier to throw and open. Extra weight did not seem to be necessary to keep birds under the net in most cases. This turned out to be an important addition to my trapping strategy for radio-tagging birds in “new” coveys (coveys that previously had no radioed quail). I used cast nets with dogs mostly in the fall and winter when the bobwhites were in coveys.

I began using cast nets to capture additional bobwhites in coveys with at least one radioed bird shortly after I discovered the use of cast nets with bird dogs. I located bobwhites by radio telemetry and, depending on the number of workers at the site, threw 1 to 3 cast nets onto the covey. I used this method in the fall and winter when the bobwhites were in coveys.

Handling and Marking: After capture, birds were held in cloth bags until they could be processed, typically immediately after capture. Processing of each bird included recording age, sex, and mass (g). I determined age and sex by plumage (Rosene 1969). I placed bobwhites in a short shear stocking for containment to determine mass with a 300-g spring scale. Every captured bird was tagged with a uniquely numbered aluminum leg band. I also fitted birds of both sexes and age classes weighing >130 g with a 6 – 7-g neck loop radio transmitter (American Wildlife Enterprises, Monticello, FL). After a bird was processed, I released it at its point of capture. Total processing time averaged 10 minutes.

Radio telemetry: I attempted to locate radio-tagged birds once every 4 days. Because of limited manpower, equipment malfunction, and inclement weather, some bobwhites were located at greater time intervals. I located radioed bobwhites using R4000 telemetry receivers and 3-element yagi antennas (Advanced Telemetry Systems, Isanti, MN). To estimate radio locations, I approached within 20 m of each radio-tagged bird. I marked each bird's location using Trimble Geoexplorer 3 GPS receivers (Trimble Navigation Limited, Sunnyvale, CA) by entering an azimuth and distance to the bird's actual location into the GPS unit. If the bird was seen running or flushed, I determined the exact location of the bird. Other information recorded in the GPS unit at the time of marking a location was the date, time, and hunt zone.

Harvest Data Collection: Harvest records were collected from the bobwhite hunting seasons on BWWMA from 2002 to 2009. All hunters were required to check their harvest at the one and only check station when leaving the area. The hunters showed harvested bobwhites to the check-station attendants and were asked to estimate the number of crippled birds they could not retrieve. All bobwhites were checked by the check station attendants for radio collars and/or leg bands. During the first three days of the hunting season, wings were collected and aged from each checked bird. Records from the check station include the daily and total number of bobwhites harvested per zone by sex, the daily and total number of radio-collared bobwhites harvested per zone by sex, and the daily and total hunter days for each zone.

From 2002 through 2006, harvest regulations were the same for the regular BWWMA quail hunt. These regulations allowed hunting only on Wednesday, Thursday, Saturday, and Sunday for a 6-week period from the middle of November to the end of December. Only 10 hunters were allowed each hunt-day in zones A and B; and zones C and D accommodated the rest of the hunters each day with no limit to the amount of hunter days.

Regulations were altered for the 2007 and 2008 regular hunting seasons. The days of hunting and the maximum (6 week) season length stayed the same, but there was an overall hunter-day quota allotted to the 2007 and 2008 seasons. The average total hunter-days from 2002 – 2006 was 1141. Total hunter-days were reduced to 876 in 2007

and 849 in 2008. In 2007, daily hunter-days were kept as even as possible after each zone received 10 hunters. The hunting season ended for all zones on the day when the overall hunter-day quota was reached. In 2008, regulations were similar to 2007 except that the total allotted hunter-days were divided among the zones. For instance, when zone C reached its quota of 212 hunter days, it was closed to quail hunting for the season and only the other zones could be chosen.

Data Analysis

Over-winter survival: I used Program MARK known-fate models to estimate over-winter survival of 1549 bobwhites on BWWMA in southwest Florida from winters 2003 – 2004 to 2008 – 2009 (White and Burnham 1999). I omitted the 2002 – 2003 data because the sample size was smaller during that over-winter period. I used several covariates to evaluate *a priori* hypotheses about factors influencing over-winter survival. My encounter histories were set up as twelve 2-week periods and one 1-week period totaling 13 periods for each over-winter season. I structured my encounter histories as two-week intervals to meet the assumption of known-fate models that the fate of all marked individuals is known within each encounter period. For each year, I started the two-week period divisions at the beginning of the regular hunting season (i.e., Wednesday each year) and based all other periods on that starting point. I set up the encounter periods this way because I wanted to keep the hunting periods in the same over-winter period each year (i.e., periods 4, 5, and 6 of the 13 over-winter periods contained the main hunt each year). This approach also caused the field trial hunt to be in the same over-winter period each year (period 9) except for the 2008 – 2009 over-winter period when it occurred during period 8.

For the global over-winter survival analysis, I used a hierarchical modeling approach with four preliminary model suites, a fifth model suite comparing the top models from the preliminary suites, and a sixth suite with meaningful combinations of the best models from the fifth suite. I chose this hierarchical approach to avoid the many possible combinations of models including all variables, an approach that could lead to biologically implausible results (Anderson 2008). I used Akaike's information criterion (AIC_c) for model selection (Burnham and Anderson 2002). Within each preliminary

model suite, I used evidence ratios to determine which model(s) had enough support to include in the comprehensive model suite. Evidence ratios (hereafter “ER”) are calculated within a model suite as

$$ER = w_{min} / w_i$$

where w_{min} is the Akaike weight (w) for the best model in the suite and w_i is the individual w for all the models in the suite ($i = 1, 2, \dots, i$) (Anderson 2008). Following this ratio, the best model will have $ER = 1$. All other models will have $ER > 1$ with less support as the ER gets larger. ER are likened to odds ratios with raffle tickets, where an evidence ratio of 100 is for model w_i equivalent to model w_i having 1 raffle ticket compared to model w_{min} having 100 raffle tickets in a drawing to determine which model is most likely given the data (Anderson 2008). Anderson (2008) suggested that an arbitrary cutoff for model selection (i.e., $\Delta AIC_c \leq 2$) should not be used. I considered all models within each preliminary suite, and decided which models to pass to the comprehensive suite based on the range and relative difference of the ER.

In the first model suite, I evaluated models with grouping variables of sex and age as well as models estimating survival with temporal variation (Table 3.1). I modeled sex and age effects on survival because behavior and experience differences could result in gender and age specific survival (Burger et al. 1995, Suchy and Munkel 2000, Taylor et al. 2000). I expected survival to differ each year because of variation in hunting pressure, hunter behavior, regulation changes, weather patterns, and predator abundance. I expected within-year time to be a factor because I hypothesized that survival would be lower during the hunting periods. I evaluated several models allowing survival to vary differently over periods of time to determine which, if any, patterns daily survival exhibited throughout the over-winter period. I added sex and age to the time models with most support in all possible combinations.

In the second model suite, I evaluated the effects of climatic factors on over-winter survival (Table 3.1). I included covariates of the number of days within each encounter period with measureable rainfall, the average rainfall per encounter period, and

the mean temperature for each encounter period. The over-winter period is typically dry and mild in south Florida. Therefore, I wasn't expecting any major influences of these covariates. However, from personal experience and according to hunters, bobwhites are located more readily by bird dogs on cool days and just after or during rain. For this reason, I included these covariates to determine if they influenced over-winter survival, particularly during the hunting seasons. For each of the rainfall and temperature covariates, I evaluated the constant influence on survival. For example, the constant influence of temperature model estimated one beta (i.e., slope) for the relationship between temperature and survival. I also evaluated the climatic covariate influences on survival separately during the no-hunting and hunting periods. For example, the separate influence of temperature model estimated two betas, one for the relationship of temperature to survival during the no-hunting periods, and one for the relationship of temperature to survival during the hunting periods. I did this because I hypothesized that rainfall and temperature do not affect survival during no hunting periods, but may affect survival during the hunting periods. First, I evaluated models with one covariate in each, and then combined the models with the most support in all possible combinations. I did not combine the two rainfall covariate models as I considered these to be redundant.

Table 3.1: Description of the core models and the corresponding model notation in the four preliminary model suites for the over-winter survival analysis of northern bobwhites in southwest Florida, 2003 - 2009. A constant survival model [S(.)] and combinations of the models listed here were evaluated within each model suite.

Model Suite	Model	Notation
I Group and Time Models	Year	S(year)
	Time	S(t)
	Linear Time	S(T)
	Quadratic Time	S(TT)
	Cubic Time	S(TTT)
	Time (Pre-hunt, Hunt, Post hunt, Field trial hunt, Post field trial hunt)	S(PreHuntPostFTHPostFTH)
	Time (Pre-hunt, All hunts, Post hunt)	S(PreHuntPost)
	Time (No hunting, Hunting)	S(NoHunt)
	Sex	S(Sex)
	Age	S(Age)
II Climate Models	Average temperature (°F) during encounter period	S(AvgTemp)
	Days of rainfall during encounter period	S(DayRain)
	Average daily rainfall (cm) during encounter period	S(AvgRain)
	Average temp applied separately to no hunting and hunting periods	S(NHAvgTemp)
	Days of rainfall applied separately to no hunting and hunting periods	S(NHDayRain)
III Habitat Models	Average rainfall applied separately to no hunting and hunting periods	S(NHAvgRain)
	Hunting Zones	S(Zone)
	% Mesic Flatwoods within hunting zone	S(MF)
	% Dry Prairie within hunting zone	S(DP)
	% Food Strips within hunting zone	S(FP)
	% of hunting zone that was burned the previous winter	S(BURN)
	Hunting Zones applied separately to no hunting and hunting periods	S(NHZone)
	% Mesic Flatwoods applied separately to no hunting and hunting periods	S(NHMF)
	% Dry Prairie applied separately to no hunting and hunting periods	S(NHDP)
IV Hunting Models	% Food Strips applied separately to no hunting and hunting periods	S(NHFP)
	% Burned applied separately to no hunting and hunting periods	S(NHBURN)
	Encounter period Hunting Pressure (Hunter Days/1000 ha)	S(PHP)
	Total Season Hunting Pressure (Hunter Days/1000 ha)	S(THP)
	Pre-hunt bobwhite density	S(DENS)
	Pre-hunt bobwhite density applied separately to no hunting and hunting periods	S(NHDENS)

I evaluated habitat covariates as well as hunting zone as factors influencing over-winter survival in the third model suite (Table 3.1). Hunting zone was a grouping variable. Bobwhites did occasionally move from zone to zone. For analysis purposes, each bobwhite was assigned to only one zone per over-winter period. If a bobwhite died, it was assigned to the zone in which it died. If a bobwhite survived the over-winter period, it was assigned to the zone in which it was located most frequently. Habitat covariates were specific to each hunt zone and varied from bird to bird according to the hunt zone in which they were assigned. The covariates were the percentage of mesic

flatwoods habitat within the hunt zone, the percentage of dry prairie habitat within the hunt zone, the percentage of the hunt zone that was burned the previous year, and the percentage of each zone in sesbania food strips. With the exception of the burn covariate, the habitat covariates were constant from year to year within zones. As with the climatic covariates, I evaluated the hunting zone and habitat covariates as a constant influence on survival throughout the season as well as separate influences during the no-hunting and hunting periods.

Saw palmetto is the primary escape cover for bobwhites on BWWMA in southwest Florida (Frye 1954). Mesic flatwoods and dry prairie cover types have an abundance of saw palmetto. I determined the percentages of those two cover types within each zone using ArcGIS and a habitat cover type layer of BWWMA developed by the Florida Fish and Wildlife Conservation Commission in 2005 – 2006 (Figure 3.2). The percentages of each of these cover types did not change over the six years of my study. I hypothesized that survival would be greater for bobwhites located in zones with greater percentages of one or both of the mesic flatwoods and dry prairie cover types because they would have access to more escape cover. I also hypothesized that the influences of the cover types on survival would differ between the no-hunting and hunting periods. By winter, most of the vegetation burned the previous year had recovered almost completely. However, with at least two growing seasons of growth, vegetation not burned the previous year was thicker and denser, possibly providing better escape cover. Because of this, I hypothesized that over-winter survival would decrease as the percentage of habitat burned the previous year increased. I included the percentage of the hunt zone in food strip coverage as a covariate. The food strips were planted in the spring, mainly as a food source for bobwhites and other wildlife in late winter when other seed sources had been depleted. Food strips also grew tall and dense providing cover for bobwhites. With zone F as the exception, the food plots did not meander over the entire zone (Figure 3.3). Nevertheless, I included the food strips as a covariate in this analysis to determine their effect, if any, on over-winter survival.

The fourth suite included models factoring pre-hunt bobwhite density (bobwhites/ha) and hunting pressure (hunter days/1000 ha) into over-winter survival

(Table 3.1). These covariates were specific to hunt zones and varied by year. I determined the pre-hunt bobwhite population for each zone using the Lincoln-Peterson estimate and the harvest records each year (Dimmick et al. 1982). I hypothesized that hunting zones with greater pre-hunt bobwhite densities would experience greater survival rates during the no-hunting periods because of predator satiation. However, hunter behavior may be influenced by pre-hunt density in that hunters concentrated their efforts on hunting zones with greater bobwhite densities. If that were the case, I would expect survival during the hunting periods to decrease with increasing pre-hunt density. I evaluated two measurements of hunting pressure, the hunting pressure per encounter period per zone and the total season hunting pressure per zone. I hypothesized that survival would decrease as hunting pressure increased.

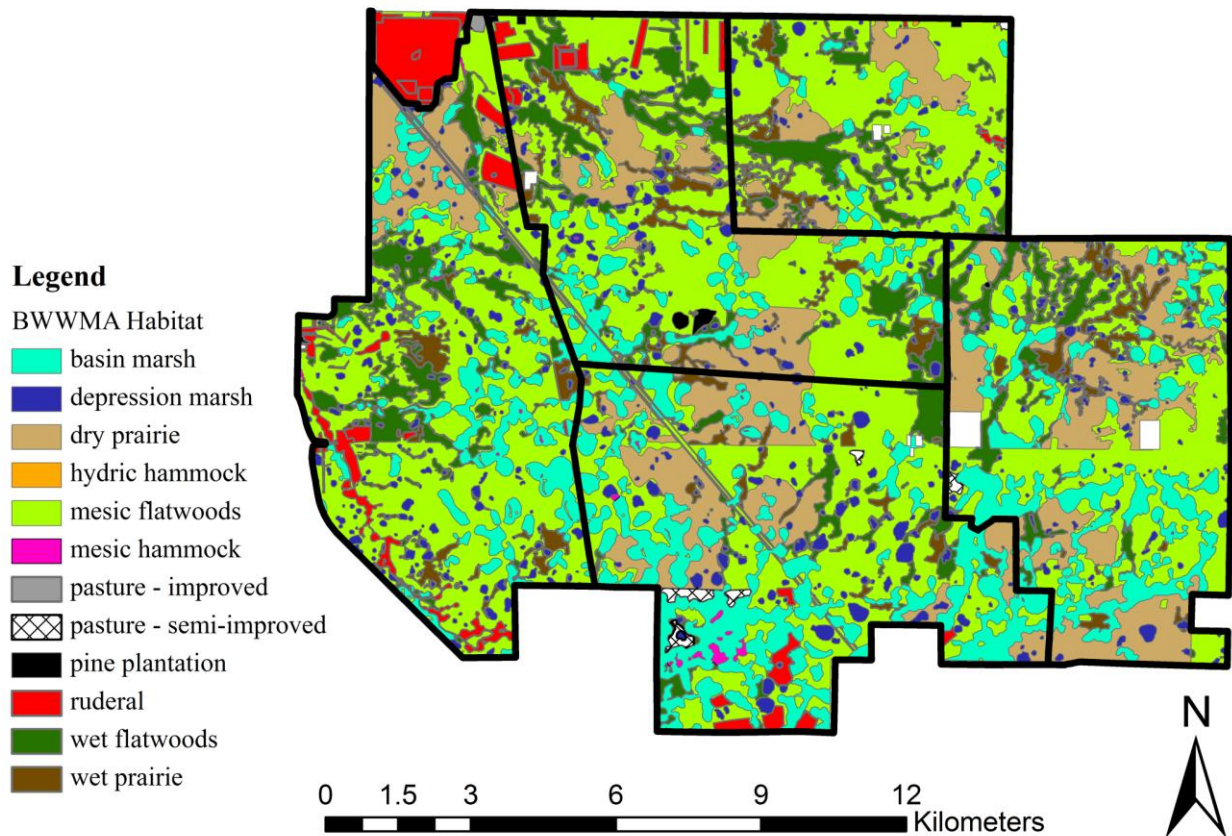


Figure 3.2: Habitat cover layer for Babcock-Webb WMA in southwest Florida depicting habitat categories available on the management area during the northern bobwhite study, 2002 - 2009. Hunting zones are labeled in figure 3.1.

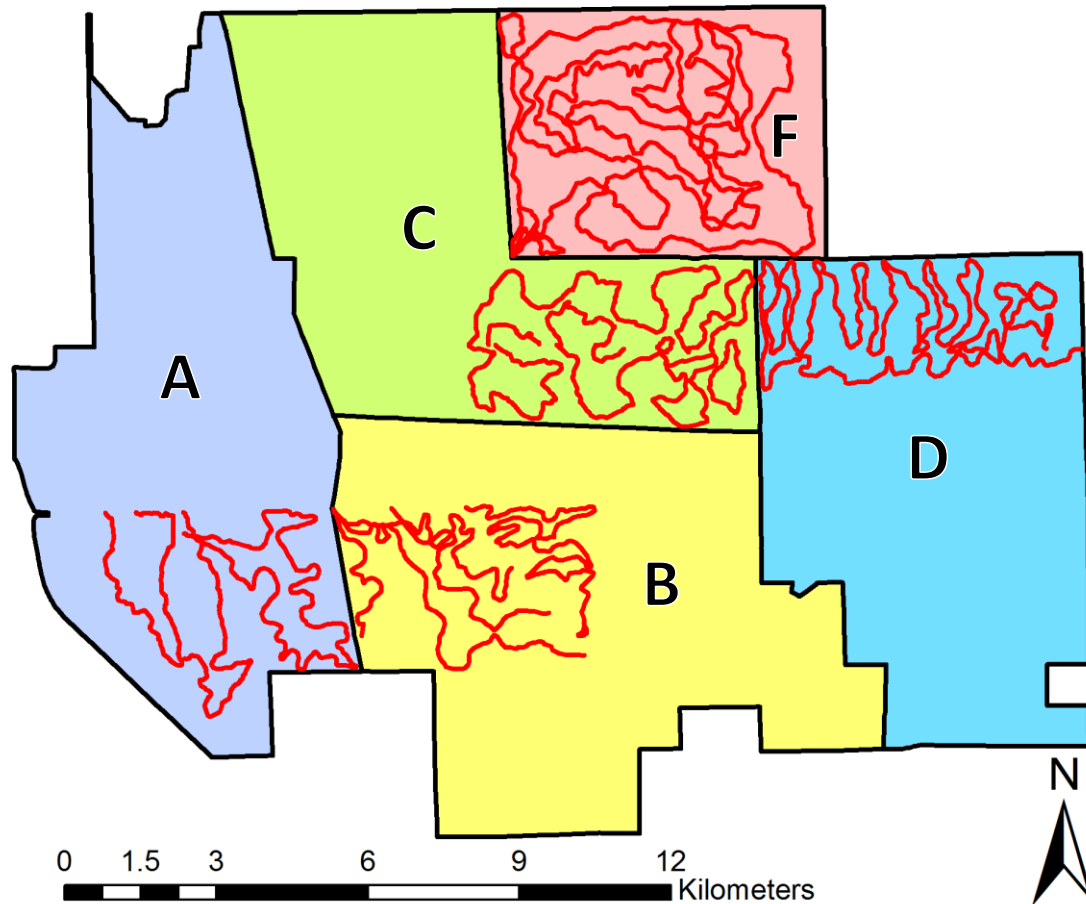


Figure 3.3: Babcock-Webb Wildlife Management Area in southwest Florida with food strips in red and five hunt management zones, 2002 - 2009.

In the fifth model suite, I compared the top models from the preliminary model suites. In the sixth suite, I evaluated plausible additive combinations of the models from the fifth suite to determine the most parsimonious model(s) that described bobwhite over-winter survival on my study area. I used model averaging to estimate the final survival parameter for each encounter period. In all model suites, I defined a covariate as important if the beta 95% confidence interval did not overlap zero (i.e., there was a significant relationship between the covariate and survival).

Management Questions: I answered six specific management oriented questions. Question 1: Do sesbania food strips affect over-winter survival and if so, how? Food

plots have been associated with increased late-winter survival (Robel and Kemp 1997). Sesbania food strips were planted on my study area to provide food for bobwhites and other wildlife during times of food shortage. They were planted each spring after the paths were disked and fertilized. There was much time and money allotted to establishing the food strips each year. Therefore, I evaluated the relationship between the percentage of food strip area within each hunt zone and over-winter survival. I did so by comparing a constant survival model with a model estimating survival as a function of the percentage of food strips. I hypothesized that there would be a positive relationship between the food strips and over-winter survival because of the additional food and cover supplied by the food strips.

Question 2: Does the percentage of a zone burned the previous year influence over-winter survival? Vegetation burned the previous winter had typically recovered by the following winter in southwest Florida. However, I addressed this question because burning is management that can be altered, and it is possible that even though the vegetation had recovered, it may not have provided adequate escape cover during winter. I evaluated a model estimating survival as a function of the percent of a hunting zone burned the previous year against a constant survival model first to determine if there was a relationship. I checked the beta estimates for burning to identify the direction of the relationship, if any, that burning had with survival.

Question 3: At what point does the amount of hunting pressure result in harvest rates of 15%, 20%, and 30%? Landers and Mueller (1986) reported that harvest rates >30% can cause a population to decline. Because the BWWMA bobwhite population was already thought to be low relative to area and declining, reducing the hunting season harvest rate to a more conservative 15% or 20% may be warranted. I answered this question by modeling total hunting pressure as a factor related to survival during the regular hunt encounter periods. I then took the intercept estimate and beta estimate for total hunting pressure and calculated the corresponding period survival rate estimates for hunting pressure amounts ranging from 0 to 100 hunter days/1000 ha. Not all mortality during the hunting period was related to hunting, so I assumed that non-hunting related mortality was the difference between one and the estimated survival rate when hunting

pressure equaled zero (i.e., $1 - \text{survival rate at hunting pressure of 0 hunter days/1000 ha}$). Therefore, to account for non-hunting related mortality, I added one minus the survival rate estimate when hunting pressure equaled zero to each survival rate calculated from the model. I graphed total hunting pressure against the adjusted hunting period mortality rate ($1 - \text{survival rate}$) with 95% confidence intervals to visualize the point which hunting mortality rate reached a desired threshold of 15 to 30%.

Question 4: What were the average harvest rates each year during the regular hunt and the zone F hunt? I answered this question so that I could compare harvest rates observed on BWWMA to other harvested bobwhite populations. If harvest rates on BWWMA were similar to harvest rates of stable or increasing bobwhite populations, then harvest rates on BWWMA may have little bearing on the population decline. I estimated harvest rates for each hunt each year as the proportion of radio-tagged bobwhites alive at the beginning of the hunt that were harvested and crippled (i.e., shot by a hunter but not retrieved).

Question 5: How did harvest rate relate to over-winter survival of bobwhites? I answered this question to assess whether harvest mortality was additive or compensatory to natural mortality during the over-winter period. If over-winter survival rates decreased as harvest rates increased, then harvest mortality was, to some degree, additive to natural mortality (Sparkman et al. 2011). If over-winter survival rates did not change as harvest rates increased, then harvest mortality was compensated by natural mortality. To answer this question, I evaluated a model relating the annual harvest rates for hunt zones to the over-winter survival rates. I then compared the model to the constant survival model. I considered harvest rate to be an important effect if the model was more parsimonious than the constant survival model and if the 95% confidence interval for the harvest rate parameter did not overlap zero.

Question 6: Is the pre-hunt density the following year related to over-winter survival? The answer to this question and the magnitude of the relationship may give insight into how the over-winter period survival one year affected density the following fall. If pre-hunt density the following year increased as over-winter survival increased, then over-winter survival could be an important predictor of the fall population the next

year. To answer this question, I evaluated a model with pre-hunt density the following year per hunting zone as a factor of over-winter survival. Because I had no pre-hunt population estimate for 2009, I used the average pre-hunt population estimation for years 2003 – 2008 for the 2009 estimation applied to over-winter survival in 2008. I compared this model to a constant survival model first to determine which had the most support. Then, I checked the beta estimate for following year's pre-hunt density for an important relationship.

RESULTS

I caught 711 bobwhites (393 males and 318 females) using the baited funnel trap method, and 755 bobwhites (658 males and 97 females) using the decoy funnel trap method over the duration of the study. Forty-four bobwhites (24 males and 20 females) were caught using the night cast net method. I caught 459 (225 males and 234 females) bobwhites using the dog cast net method, and 54 (27 males and 27 females) and 202 (93 males and 109 females) bobwhites by using the night telemetry cast net and diurnal telemetry cast net methods, respectively.

Over-winter Survival

I analyzed the over-winter survival histories for 1549 bobwhites from 1 October 2003 – 31 March 2009. Each encounter history spanned 175 days between 1 October and 31 March for each of the six yearly over-winter periods analyzed (Table 3.2).

In the first model suite, the additive model of year and time had the most support with $ER = 1$ (Table 3.3). Survival for each encounter period differed within years, but the pattern of survival estimates across each over-winter year was generally the same. With $ER < 3$, the additive models with year, time, sex, and age were also supported. Models evaluating differences in survival between sexes and ages alone had little support. There appeared to be no difference in survival between males and females or adults and juveniles because the beta estimates for sex and age included zero in their 95% confidence intervals (Table 3.4). However, when combined with the year plus time model, sex added some value by reducing the deviance from the year plus time model. The addition of age also appeared to be supported, but the model deviance was not

decreased by the addition and therefore, age did not explain variation in survival. None of the models with time divided into no-hunting and hunting periods had support relative to the most parsimonious models in this suite. Survival decreased during the hunting periods, but there was too much variation in survival within no-hunting and hunting periods to be constrained to singular estimates for each.

Table 3.2: Encounter period dates, lengths, and hunting for each over-winter period of the southwest Florida bobwhite study, 2003 - 2009. Hunting occurred during the highlighted periods.

Encounter Period		Year						Length (days)	Hunting?
		2003-2004	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009		
1	Start Date	10/1/2003	10/6/2004	10/5/2005	10/4/2006	10/3/2007	10/8/2008	14	No
	End Date	10/14/2003	10/19/2004	10/18/2005	10/17/2006	10/16/2007	10/21/2008		
2	Start Date	10/15/2003	10/20/2004	10/19/2005	10/18/2006	10/17/2007	10/22/2008	14	No
	End Date	10/28/2003	11/2/2004	11/1/2005	10/31/2006	10/30/2007	11/4/2008		
3	Start Date	10/29/2003	11/3/2004	11/2/2005	11/1/2006	10/31/2007	11/5/2008	14	No
	End Date	11/11/2003	11/16/2004	11/15/2005	11/14/2006	11/13/2007	11/18/2008		
4	Start Date	11/12/2003	11/17/2004	11/16/2005	11/15/2006	11/14/2007	11/19/2008	14	Hunt
	End Date	11/25/2003	11/30/2004	11/29/2005	11/28/2006	11/27/2007	12/2/2008		
5	Start Date	11/26/2003	12/1/2004	11/30/2005	11/29/2006	11/28/2007	12/3/2008	14	Hunt
	End Date	12/9/2003	12/14/2004	12/13/2005	12/12/2006	12/11/2007	12/16/2008		
6	Start Date	12/10/2003	12/15/2004	12/14/2005	12/13/2006	12/12/2007	12/17/2008	14	Hunt
	End Date	12/23/2003	12/28/2004	12/27/2005	12/26/2006	12/25/2007	12/30/2008		
7	Start Date	12/24/2003	12/29/2004	12/28/2005	12/27/2006	12/26/2007	12/31/2008	14	No
	End Date	1/6/2004	1/11/2005	1/10/2006	1/9/2007	1/8/2008	1/13/2009		
8	Start Date	1/7/2004	1/12/2005	1/11/2006	1/10/2007	1/9/2008	1/14/2009	14	Field Trial '09
	End Date	1/20/2004	1/25/2005	1/24/2006	1/23/2007	1/22/2008	1/27/2009		
9	Start Date	1/21/2004	1/26/2005	1/25/2006	1/24/2007	1/23/2008	1/28/2009	14	Field Trial '04 - '08
	End Date	2/3/2004	2/8/2005	2/7/2006	2/6/2007	2/5/2008	2/10/2009		
10	Start Date	2/4/2004	2/9/2005	2/8/2006	2/7/2007	2/6/2008	2/11/2009	14	No
	End Date	2/17/2004	2/22/2005	2/21/2006	2/20/2007	2/19/2008	2/24/2009		
11	Start Date	2/18/2004	2/23/2005	2/22/2006	2/21/2007	2/20/2008	2/25/2009	14	No
	End Date	3/2/2004	3/8/2005	3/7/2006	3/6/2007	3/4/2008	3/10/2009		
12	Start Date	3/3/2004	3/9/2005	3/8/2006	3/7/2007	3/5/2008	3/11/2009	14	No
	End Date	3/16/2004	3/22/2005	3/21/2006	3/20/2007	3/18/2008	3/24/2009		
13	Start Date	3/17/2004	3/23/2005	3/22/2006	3/21/2007	3/19/2008	3/25/2009	7	No
	End Date	3/23/2004	3/29/2005	3/28/2006	3/27/2007	3/25/2008	3/31/2009		

Table 3.3: Summary of model-selection results from the first model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(year+t)	18	4314.711	0	0.31045	1	4278.632
S(year+t+Sex)	19	4314.815	0.1042	0.29469	1.0535	4276.728
S(year+t+Sex+Age)	20	4316.366	1.6548	0.13572	2.2874	4276.269
S(year+t+Age)	19	4316.514	1.8028	0.12604	2.4631	4278.426
S(t)	13	4318.573	3.8626	0.045	6.8989	4292.532
S(t+Sex)	14	4318.665	3.9543	0.04299	7.2214	4290.617
S(t+Sex+Age)	15	4319.889	5.1782	0.02331	13.3183	4289.834
S(t+Age)	14	4320.151	5.4405	0.02045	15.1809	4292.103
S(year*t)	78	4325.569	10.8587	0.00136	228.2721	4168.146
S(year*PreHuntPostFTHPostFTH)	30	4345.226	30.5148	0	n/a	4285.012
S(year+PreHuntPostFTHPostFTH)	10	4353.645	38.9345	0	n/a	4333.62
S(PreHuntPostFTHPostFTH)	5	4357.687	42.976	0	n/a	4347.68
S(year*PreHuntPost)	18	4385.608	70.8977	0	n/a	4349.53
S(year+PreHuntPost)	8	4386.631	71.9203	0	n/a	4370.615
S(year*NoHunt)	12	4388.689	73.9787	0	n/a	4364.654
S(year+NoHunt)	7	4388.69	73.9791	0	n/a	4374.677
S(PreHuntPost)	3	4391.548	76.8376	0	n/a	4385.546
S(NoHunt)	2	4392.978	78.2676	0	n/a	4388.977
S(TTT)	4	4497.585	182.8738	0	n/a	4489.58
S(TT)	3	4560.415	245.7042	0	n/a	4554.412
S(T)	2	4617.42	302.7095	0	n/a	4613.419
S(year)	6	4634.174	319.4636	0	n/a	4622.165
S(Sex)	2	4637.581	322.8702	0	n/a	4633.58
S(.)	1	4638.271	323.5604	0	n/a	4636.271
S(Sex+Age)	3	4639.069	324.3579	0	n/a	4633.066
S(Age)	2	4640.075	325.3644	0	n/a	4636.074

Table 3.4: Parameter estimates and 95% confidence intervals (CI) for covariates in the S(year+t+Sex+Age) model in the first model suite for bobwhite over-winter survival in southwest Florida, 2003 - 2009.

Parameter	Estimate	SE	95% CI	
			Lower	Upper
Intercept	3.0900	0.2613	2.5779	3.6021
2003 - 2004	-0.3098	0.1837	-0.6699	0.0502
2004 - 2005	-0.3952	0.1507	-0.6907	-0.0997
2005 - 2006	-0.4676	0.1551	-0.7715	-0.1636
2006 - 2007	-0.3576	0.1623	-0.6758	-0.0395
2007 - 2008	-0.5096	0.1542	-0.8118	-0.2074
2008 - 2009	0.0000	0.0000	0.0000	0.0000
Encounter Period 1	-0.0125	0.2768	-0.5550	0.5300
Encounter Period 2	0.9708	0.3401	0.3043	1.6374
Encounter Period 3	0.9630	0.3247	0.3265	1.5994
Encounter Period 4	-1.4152	0.2427	-1.8909	-0.9394
Encounter Period 5	-1.1524	0.2488	-1.6400	-0.6648
Encounter Period 6	-0.4987	0.2674	-1.0228	0.0254
Encounter Period 7	-0.0054	0.2895	-0.5728	0.5619
Encounter Period 8	0.5229	0.3076	-0.0800	1.1259
Encounter Period 9	-0.2391	0.2663	-0.7611	0.2829
Encounter Period 10	0.2807	0.2850	-0.2779	0.8393
Encounter Period 11	0.3431	0.2848	-0.2151	0.9014
Encounter Period 12	0.3129	0.2820	-0.2399	0.8656
Encounter Period 13	0.0000	0.0000	0.0000	0.0000
Sex ^a	-0.1267	0.0865	-0.2962	0.0429
Age ^b	0.0594	0.0877	-0.1124	0.2312

^a Male = 1 and female = 0

^b Adult = 1 and juvenile = 0

In the second model suite, all models with the climatic variables had more support than the constant survival model indicating climatic influences on survival (Table 3.5). The model with average temperature explaining survival differently in the no-hunting and hunting periods had the most support with ER = 1 (Table 3.5). Survival decreased with

increasing temperature during both periods (hunting period $\beta = -0.04$; no-hunting period $\beta = -0.02$; Table 3.6). Models with average rainfall and days of rain alone did not have enough support to be included in the fifth model suite; however, they did provide some value to model fit by reducing the deviance when added to the average temperature model (Table 3.5). Average rainfall and days of rain were not important effects because their β 95% confidence intervals included zero (Table 3.6).

Table 3.5: Summary of model-selection results from the second model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	Δ AIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(NHAvgTemp)	3	4376.823	0	0.53613	1	4370.82
S(NHAvgTemp+NHDayRain)	5	4378.341	1.5179	0.251	2.1360	4368.334
S(NHAvgTemp+NHAvgRain)	5	4378.67	1.8474	0.21287	2.5186	4368.663
S(NHDayRain)	3	4523.315	146.4924	0	n/a	4517.312
S(NHAvgRain)	3	4590.236	213.4136	0	n/a	4584.234
S(AvgTemp)	2	4634.639	257.8167	0	n/a	4630.638
S(DayRain)	2	4634.73	257.907	0	n/a	4630.728
S(AvgRain)	2	4637.209	260.386	0	n/a	4633.207
S(.)	1	4638.271	261.4484	0	n/a	4636.271

Table 3.6: Parameter estimates and 95% confidence intervals (CI) for the three most supported models in the second suite for over-winter survival of bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(NHAvgTemp)	Intercept	4.3969	0.5641	3.2913	5.5026
	No Hunting Avg. Temp	-0.0196	0.0082	-0.0356	-0.0036
	Hunting Avg. Temp	-0.0411	0.0087	-0.0581	-0.0240
S(NHAvgTemp+NHDayRain)	Intercept	4.3743	0.5706	3.2559	5.4927
	No Hunting Avg. Temp	-0.0178	0.0083	-0.0340	-0.0016
	Hunting Avg. Temp	-0.0416	0.0087	-0.0586	-0.0245
	No Hunting Days of Rain	-0.0349	0.0292	-0.0922	0.0224
	Hunting Days of Rain	0.0260	0.0255	-0.0239	0.0760
S(NHAvgTemp+NHAvgRain)	Intercept	4.3930	0.5657	3.2843	5.5017
	No Hunting Avg. Temp	-0.0187	0.0082	-0.0347	-0.0026
	Hunting Avg. Temp	-0.0412	0.0087	-0.0582	-0.0242
	No Hunting Avg. Rain	-0.2663	0.1835	-0.6260	0.0934
	Hunting Avg. Rain	0.1269	0.3175	-0.4953	0.7492

In the third model suite, the model with the most support was the hunting-zone model set to explain survival differently in the no-hunting and hunting periods (Table 3.7). In this model, all zones had positive relationships with survival during the no-hunting period (Table 3.8). Zones A and F were the only hunting zones that did not have important negative survival during the hunting period (Table 3.8). During the no-hunting period there was no difference in encounter period survival estimates among zones (Table 3.9). Zone F had greater encounter period survival estimates during the hunting period than zones B, C, and D (Table 3.9). With the exception of zones A and F, zones had greater encounter period survival estimates during the no-hunting period than during the hunting period (Table 3.9). The models with habitat covariates describing zones did not explain the variation in survival as well as the model with the categorical zone descriptions.

Table 3.7: Summary of model-selection results from the third model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	Δ AIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(NHZone)	10	4323.343	0	0.99965	1	4303.318
S(NHMF+NHDP+NHFP+NHBURN)	9	4339.844	16.5009	0.00026	3844.8077	4321.824
S(NHDP+NHFP+NHBURN)	7	4341.978	18.6347	0.00009	11107.2222	4327.965
S(NHMF+NHDP+NHFP)	7	4352.348	29.0047	0	n/a	4338.335
S(NHMF+NHFP+NHBURN)	7	4356.865	33.5217	0	n/a	4342.852
S(NHMF+NHDP+NHBURN)	7	4368.924	45.5806	0	n/a	4354.911
S(NHDP+NHFP)	5	4372.393	49.0502	0	n/a	4362.387
S(NHDP+NHBURN)	5	4375.432	52.0888	0	n/a	4365.425
S(NHFP+NHBURN)	5	4375.78	52.437	0	n/a	4365.773
S(NHMF+NHFP)	5	4384.045	60.702	0	n/a	4374.038
S(NHMF+NHDP)	5	4384.19	60.8472	0	n/a	4374.184
S(NHDP)	3	4386.829	63.4858	0	n/a	4380.826
S(NHMF+NHBURN)	5	4387.351	64.0074	0	n/a	4377.344
S(NHBURN)	3	4396.025	72.6818	0	n/a	4390.022
S(NHMF)	3	4419.934	96.5909	0	n/a	4413.931
S(NHFP)	3	4546.24	222.8963	0	n/a	4540.237
S(MF)	2	4628.076	304.7326	0	n/a	4624.074
S(Zone)	5	4629.154	305.8112	0	n/a	4619.148
S(MF+DP+FP+BURN)	5	4630.279	306.9358	0	n/a	4620.272
S(DP)	2	4633.682	310.3387	0	n/a	4629.681
S(FP)	2	4638.086	314.7428	0	n/a	4634.085
S(.)	1	4638.271	314.9279	0	n/a	4636.271
S(BURN)	2	4638.465	315.1221	0	n/a	4634.464

Table 3.8: Parameter estimates and 95% confidence intervals (CI) for the top model in the third model suite for over-winter survival of bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(NHZone)	Intercept	2.3437	0.1330	2.0831	2.6043
	No Hunt Zone A	0.6187	0.1869	0.2525	0.9850
	Hunt Zone A	-0.1367	0.1928	-0.5145	0.2411
	No Hunt Zone B	0.8962	0.2196	0.4657	1.3267
	Hunt Zone B	-1.1658	0.1750	-1.5088	-0.8228
	No Hunt Zone C	1.1461	0.2171	0.7207	1.5716
	Hunt Zone C	-0.9493	0.1763	-1.2950	-0.6037
	No Hunt Zone D	0.7182	0.2023	0.3216	1.1147
	Hunt Zone D	-0.7745	0.1805	-1.1284	-0.4207
	No Hunt Zone F	0.3953	0.1730	0.0563	0.7343
	Hunt Zone F	0.0000	0.0000	0.0000	0.0000

Table 3.9: Encounter period survival estimates and 95% confidence intervals (CI) for northern bobwhites in each hunt zone on BWWMA in southwest Florida, 2003 - 2009. Estimates calculated from the top model in suite 3.

Zone	Survival Estimates					
	No Hunting	95% CI		Hunting	95% CI	
		Lower	Upper		Lower	Upper
A	0.9508	0.9118	0.9731	0.9009	0.8276	0.9451
B	0.9623	0.9275	0.9808	0.7646	0.6398	0.8559
C	0.9704	0.9429	0.9849	0.8013	0.6874	0.8809
D	0.9553	0.9172	0.9763	0.8277	0.7221	0.8988
F	0.9393	0.8947	0.9657	0.9124	0.8892	0.9311

In the fourth model suite, the additive model with period hunting pressure and pre-hunt density had the most support with ER = 1 (Table 3.10). Two other models, period hunting pressure alone and additive period hunting pressure with no hunting and hunting effects of pre-hunt density, had enough support to pass to the fifth model suite with ER <3. In all three top models, period hunting pressure had an important negative relationship (beta = -0.07) with survival (Table 3.11). Pre-hunt density effects were not

important in the two models in which it was included, but in both cases pre-hunt density did explain some of the variation in the data as evidenced by lower deviances.

Table 3.10: Summary of model-selection results from the fourth model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	Δ AIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(PHP+DENS)	3	4256.15	0	0.46097	1	4250.147
S(PHP)	2	4256.928	0.778	0.31241	1.4755	4252.927
S(PHP+NHDENS)	4	4257.57	1.4201	0.22662	2.0341	4249.566
S(NHDENS)	3	4563.853	307.7027	0	n/a	4557.85
S(DENS)	2	4630.312	374.162	0	n/a	4626.311
S(THP+DENS)	3	4631.867	375.7173	0	n/a	4625.865
S(THP)	2	4636.557	380.4073	0	n/a	4632.556
S(.)	1	4638.271	382.121	0	n/a	4636.271

Table 3.11: Parameter estimates and 95% confidence intervals (CI) for the three most supported models in the fourth model suite for over-winter survival of bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(PHP+DENS)	Intercept	2.7970	0.0777	2.6446	2.9494
	Period hunting pressure	-0.0723	0.0037	-0.0796	-0.0651
	Pre-hunt density	0.3261	0.1982	-0.0624	0.7145
S(PHP)	Intercept	2.8959	0.0511	2.7958	2.9960
	Period hunting pressure	-0.0728	0.0037	-0.0801	-0.0656
S(PHP+NHDENS)	Intercept	2.8104	0.0797	2.6541	2.9667
	Period hunting pressure	-0.0740	0.0043	-0.0825	-0.0655
	No Hunting Density	0.2246	0.2365	-0.2389	0.6881
	Hunting Density	0.4367	0.2483	-0.0500	0.9234

Twelve models were compared in the fifth model suite, four from suite 1, three from suite 2, one from suite 3, three from suite 4, and the constant survival model (Table 3.12). The models from suite 4, hunting pressure and density, had all the support when compared to models from the other preliminary suites. The models with year, time, sex, and age from suite 1 were second to the suite 4 models. The zone model from suite 3 fit the data better than the climatic models from suite 2. However, all the models explained survival better than the constant survival model.

Table 3.12: Summary of model-selection results from the fifth model suite for over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(PHP+DENS)	3	4256.15	0	0.46097	1	4250.147
S(PHP)	2	4256.928	0.778	0.31241	1.4755	4252.927
S(PHP+NHDENS)	4	4257.57	1.4201	0.22662	2.0341	4249.566
S(year+t)	18	4314.711	58.5606	0	n/a	4278.632
S(year+t+Sex)	19	4314.815	58.6648	0	n/a	4276.728
S(year+t+Sex+Age)	20	4316.366	60.2154	0	n/a	4276.269
S(year+t+Age)	19	4316.514	60.3634	0	n/a	4278.426
S(NHZone)	10	4323.343	67.1931	0	n/a	4303.318
S(NHAvgTemp)	3	4376.823	120.6726	0	n/a	4370.82
S(NHDayRain+NHAvgTemp)	5	4378.341	122.1905	0	n/a	4368.334
S(NHAvgRain+NHAvgTemp)	5	4378.67	122.52	0	n/a	4368.663
S(.)	1	4638.271	382.121	0	n/a	4636.271

In the sixth model suite, I combined models from the fifth suite to compile a model set to average and calculate my final over-winter survival estimates (Table 3.13). Ten models had reasonable support with ER <10, and 17 total models were averaged to get the final survival estimates. All of the top models (i.e., ER <10) included year, time, period hunting pressure, and no-hunting and hunting applications of density, average temperature, and zone. Sex was included in six of the top ten models (Table 3.13). However, there was no difference in survival between males and females. Hunting pressure had an important negative relationship with survival (Table 3.14). Density was

an important factor explaining variation in survival, the greater the pre-hunt density, the greater the survival during the hunting period (Table 3.14). The relationship of average temperature to survival was also positive during the hunting period with an increase in survival as temperature increased (Table 3.14). Hunting zone remained an important factor related to survival. However, the differences among zones and between no-hunting and hunting periods were not evident when the zone effect was included in models with other covariates, indicating that other covariates explained survival more effectively than zone. Model averaged period survival estimates declined within years during the regular hunt periods (periods 4 – 6; Figure 3.4). Among years, the model-averaged over-winter survival rate estimates ranged from 0.310 (2007 – 2008) to 0.480 (2008 – 2009), but did not differ except between 2007 – 2008 and 2008 – 2009 (Figure 3.5). Average over-winter survival rate was 0.402 (SE = 0.023).

Table 3.13: Summary of model-selection results from the sixth model suite with additive combinations of the best models from each preliminary suite for over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Only models with support are shown. Model notation is described in Table 3.1.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(year+t+Sex+PHP+NHDENS+NHAvgTemp+NHZone)	32	4154.791	0	0.23401	1	4090.549
S(year+t+PHP+NHDENS+NHAvgTemp+NHZone)	31	4155.661	0.87	0.15147	1.5449	4093.433
S(year+t+Sex+PHP+NHDENS+NHAvgTemp+NHDDayRain+NHZone)	34	4155.918	1.127	0.1332	1.7568	4087.645
S(year+t+Sex+Age+PHP+NHDENS+NHAvgTemp+NHZone)	33	4156.32	1.5288	0.10896	2.1477	4090.062
S(year+t+PHP+NHDENS+NHAvgTemp+NHDDayRain+NHZone)	33	4156.763	1.9723	0.08729	2.6808	4090.506
S(year+t+Sex+Age+PHP+NHDENS+NHAvgTemp+NHDDayRain+NHZone)	35	4157.384	2.5929	0.064	3.6564	4087.094
S(year+t+Age+PHP+NHDENS+NHAvgTemp+NHZone)	32	4157.505	2.7135	0.06026	3.8833	4093.262
S(year+t+Sex+PHP+NHDENS+NHAvgTemp+NHAvgRain+NHZone)	34	4157.921	3.1301	0.04893	4.7825	4089.648
S(year+t+Age+PHP+NHDENS+NHAvgTemp+NHDDayRain+NHZone)	34	4158.57	3.7788	0.03537	6.6161	4090.296
S(year+t+PHP+NHDENS+NHAvgTemp+NHAvgRain+NHZone)	33	4158.784	3.9926	0.03179	7.3611	4092.526
S(year+t+Sex+Age+PHP+NHDENS+NHAvgTemp+NHAvgRain+NHZone)	35	4159.418	4.6271	0.02315	10.1084	4089.129
S(year+t+Age+PHP+NHDENS+NHAvgTemp+NHAvgRain+NHZone)	34	4160.608	5.8173	0.01277	18.3250	4092.335
S(year+t+Sex+PHP+DENS+NHAvgTemp+NHZone)	31	4163.11	8.3188	0.00365	64.1123	4100.882
S(year+t+PHP+DENS+NHAvgTemp+NHZone)	30	4163.945	9.1534	0.00241	97.0996	4103.731
S(year+t+Sex+Age+PHP+DENS+NHAvgTemp+NHZone)	32	4164.592	9.8005	0.00174	134.4885	4100.349
S(year+t+Age+PHP+DENS+NHAvgTemp+NHZone)	31	4165.76	10.9686	0.00097	241.2474	4103.532
S(PHP+NHDENS+NHZone)	13	4171.86	17.0692	0.00005	4680.2000	4145.819

Table 3.14: Parameter estimates and 95% confidence intervals (CI) for covariates in the best model of the sixth model suite for bobwhite over-winter survival in southwest Florida, 2003 - 2009.

Parameter	Estimate	SE	95% CI	
			Lower	Upper
2003 - 2004	-0.1969	0.2132	-0.6147	0.2209
2004 - 2005	-0.2398	0.1585	-0.5505	0.0709
2005 - 2006	-0.2889	0.1693	-0.6208	0.0430
2006 - 2007	-0.3519	0.1697	-0.6845	-0.0194
2007 - 2008	-0.5999	0.1686	-0.9304	-0.2693
2008 - 2009	0.0000	0.0000	0.0000	0.0000
Encounter Period 1	-0.2715	0.3445	-0.9466	0.4037
Encounter Period 2	0.7813	0.3581	0.0795	1.4831
Encounter Period 3	0.8472	0.3247	0.2109	1.4836
Encounter Period 4	0.4651	0.5298	-0.5734	1.5036
Encounter Period 5	-0.0125	0.5167	-1.0253	1.0003
Encounter Period 6	0.4653	0.5009	-0.5164	1.4470
Encounter Period 7	0.1030	0.3109	-0.5063	0.7122
Encounter Period 8	0.8257	0.3515	0.1368	1.5147
Encounter Period 9	0.6765	0.4759	-0.2562	1.6092
Encounter Period 10	0.4470	0.3335	-0.2066	1.1005
Encounter Period 11	0.4265	0.2987	-0.1590	1.0120
Encounter Period 12	0.3422	0.2853	-0.2169	0.9013
Encounter Period 13	0.0000	0.0000	0.0000	0.0000
Sex	-0.1484	0.0877	-0.3203	0.0235
Period hunting pressure	-0.0743	0.0077	-0.0894	-0.0593
No Hunting Density	-0.3932	0.4673	-1.3092	0.5227
Hunting Density	1.5644	0.4999	0.5847	2.5442
No Hunting Avg. Temp	0.0184	0.0242	-0.0291	0.0659
Hunting Avg. Temp	0.0311	0.0094	0.0128	0.0495
No Hunting Zone A	1.7931	1.7028	-1.5444	5.1305
Hunting Zone A	0.6699	0.2802	0.1207	1.2191
No Hunting Zone B	2.0193	1.7047	-1.3220	5.3606
Hunting Zone B	-0.2520	0.3008	-0.8416	0.3377
No Hunting Zone C	2.3512	1.7078	-0.9962	5.6986
Hunting Zone C	0.9065	0.3133	0.2924	1.5207
No Hunting Zone D	1.9317	1.7111	-1.4221	5.2856
Hunting Zone D	0.3685	0.2729	-0.1663	0.9034
No Hunting Zone F	1.7558	1.7105	-1.5967	5.1083
Hunting Zone F	0.0000	0.0000	0.0000	0.0000

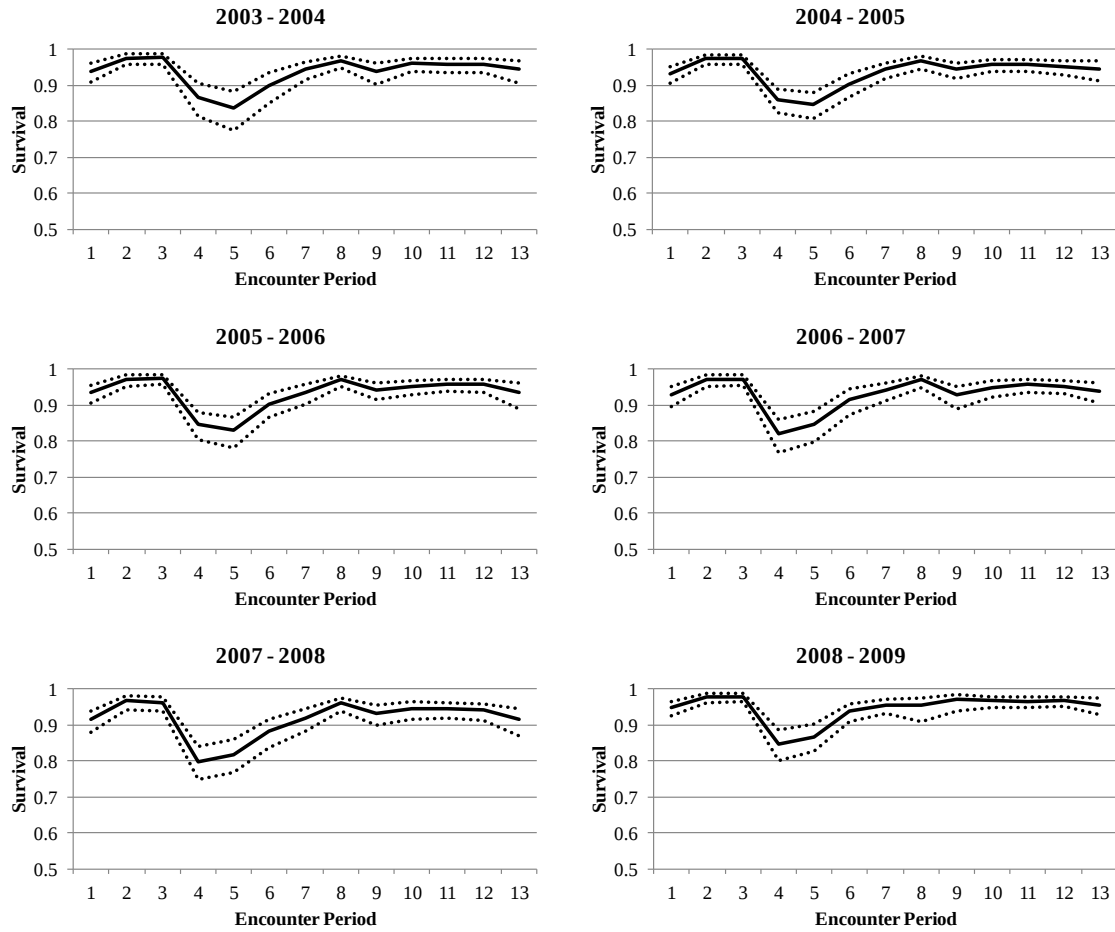


Figure 3.4: Encounter period survival rate estimates (solid line) and 95% confidence intervals (dotted lines) for each year of the northern bobwhite study in southwest Florida, 2003 – 2009. Estimates were calculated from model averaging.

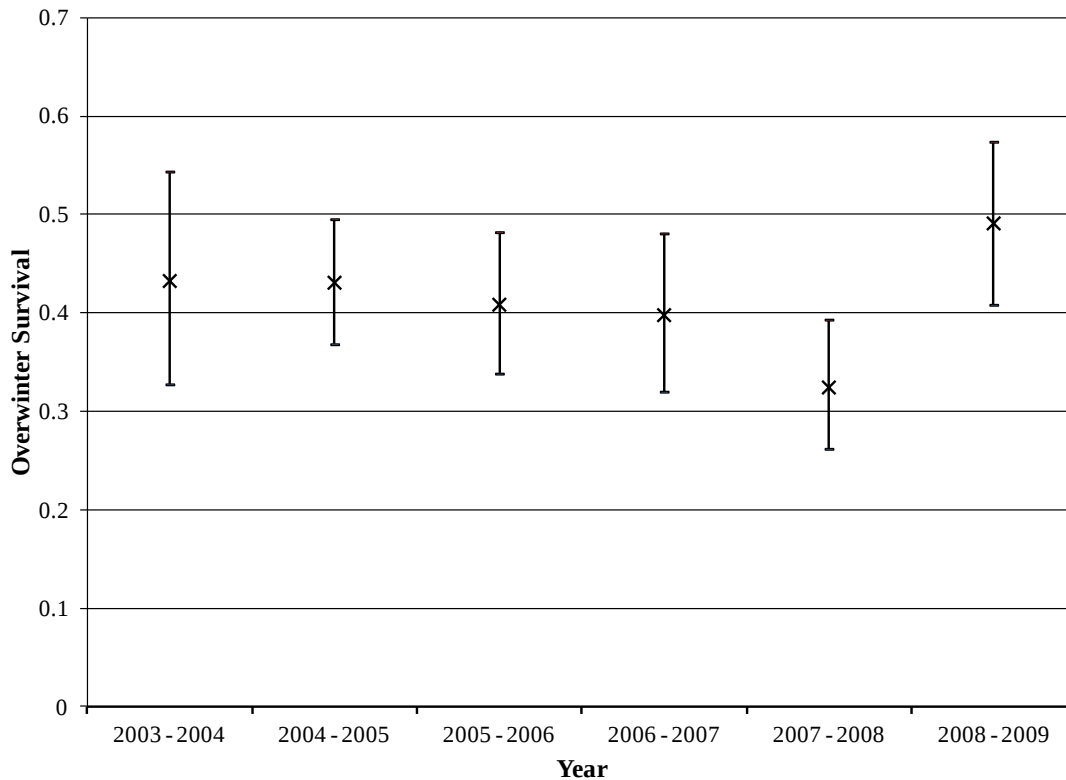


Figure 3.5: Over-winter survival rate estimates and 95% confidence intervals for each year of the northern bobwhite study in southwest Florida, 2003 – 2009. Yearly estimates were calculated from the final model averaged estimates.

Management Questions

The six management related questions and answers are summarized in Table 3.15. When modeled alone, the proportion of a hunt zone covered in sesbania food strips did not have an important effect on over-winter survival. The model evaluating a relationship between food strips and over-winter survival had only slightly more support than the constant survival model (Table 3.16). Therefore, food strips did not appear to influence over-winter survival. The model with the interaction between food strips and hunting pressure had the most support in the model set with $ER = 1$ (Table 3.16). The only important beta estimate in this model was the period hunting pressure (-0.08 ; Table 3.17). The constant food strip effect and the interaction term both had beta estimate 95% confidence intervals that included zero (Table 3.17). Because the interaction term was

not important, there was no indication that hunting was concentrated around the food strips causing survival to decrease in zones with more food strips. The interaction model was likely the best because hunting pressure was a much more important factor affecting over-winter survival than the amount of food strips.

Table 3.15: Questions and answers for the six management related analyses for northern bobwhites in southwest Florida, 2003 - 2009.

Question 1: Does the percentage of a hunt zone covered in sesbania food strips affect over-winter survival and if so, how?
Answer: No
Question 2: Does the percentage of a zone burned the previous year affect over-winter survival and if so, how?
Answer: No
Question 3: On average, at what point does the amount of hunting pressure (hunter days/1000 ha) during the regular hunt result in harvest rates of 15%, 20%, and 30%?
Answer: Hunting pressure = 27.3 (633 total hunter days for season) → 15% harvest rate
Hunting pressure = 35.3 (818 total hunter days for season) → 20% harvest rate
Hunting pressure = 50.5 (1170 total hunter days for season) → 30% harvest rate
Question 4: What were the harvest rates observed during the regular hunting period and the zone F hunting period each year?
Answer: Regular Hunt = 38%; Zone F Hunt = 11%
Question 5: How did the harvest rates for each hunt zone relate to the zonal over-winter survival rates of bobwhites each year?
Answer: Overwinter survival decreased with increasing harvest rates
Question 6: Is pre-hunt density the following year related to over-winter survival?
Answer: No.

Table 3.16: Summary of model-selection results from management Question 1 relating food strips to over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(FP*PHP)	4	4260.5614	0	1	1	4252.5568
S(FP)	2	4638.0860	377.5246	0	n/a	4634.0846
S(.)	1	4638.2711	377.7097	0	n/a	4636.2706

Table 3.17: Parameter estimates and 95% confidence intervals (CI) for the models evaluated for Question 1 relating food strips to over-winter survival of bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(FP+PHP+FP*PHP)	Intercept	2.9406	0.0904	2.7633	3.1178
	Food strips	-6.1443	10.1000	-25.9403	13.6516
	Period hunting pressure	-0.0755	0.0077	-0.0906	-0.0605
	Food strips * Period hunting pressure	0.4178	1.1344	-1.8056	2.6411
S(FP)	Intercept	2.3844	0.0706	2.2460	2.5227
	Food strips	11.8920	8.1177	-4.0187	27.8026

The proportion of the hunting zone burned each year also was not related to over-winter survival. The model with burning as a covariate had slightly less support than the constant survival model (Table 3.18), and the 95% confidence interval for the burning parameter estimate included zero (Table 3.19).

Table 3.18: Summary of model-selection results from management Question 2 relating burning to over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(.)	1	4638.2711	0	0.52426	1	4636.2706
S(BURN)	2	4638.4653	0.1942	0.47574	1.1020	4634.4639

Table 3.19: Parameter estimates and 95% confidence intervals (CI) for the model evaluated for Question 2 relating burning to over-winter survival of bobwhites in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(BURN)	Intercept	2.3247	0.1145	2.1003	2.5490
	Burn	0.2357	0.1745	-0.1063	0.5778

The model with total hunting pressure as a factor describing the regular hunt period survival had more support than the constant survival model (Table 3.20). The relationship was negative and important (Table 3.21). Survival decreased as hunting pressure increased. The estimate for the total number of hunter days/1000 ha that resulted in 30% hunting related mortality was 50.5 (95% CI = 31.3 to 94.7; Figure 3.6). That hunting intensity would equate to 1,170 total hunter days for hunt zones A – D, which total 23,170 ha. The estimates for 20% and 15% harvest rates were 35.3 (95% CI = 21.5 to 67.8) and 27.3 (95% CI = 16.4 to 53.1) hunter days/1000 ha (818 and 633 total hunter days for the regular hunting season), respectively (Figure 3.6).

Table 3.20: Summary of model-selection results from management Question 3 relating hunting pressure to survival of bobwhites during the regular hunting season on BWWMA in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(THP)	2	1575.5081	0	1	1	1571.5004
S(.)	1	1600.0318	24.5237	0	n/a	1598.0292

Table 3.21: Parameter estimates and 95% confidence intervals (CI) for the model evaluated for Question 3 relating hunting pressure to survival of bobwhites during the regular hunting season on BWWMA in southwest Florida, 2003 - 2009. Model notation is described in Table 3.1.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(THP)	Intercept	2.10934	0.1628	1.79017	2.428504
	Total hunting pressure	-0.0167	0.0032	-0.0229	-0.01054

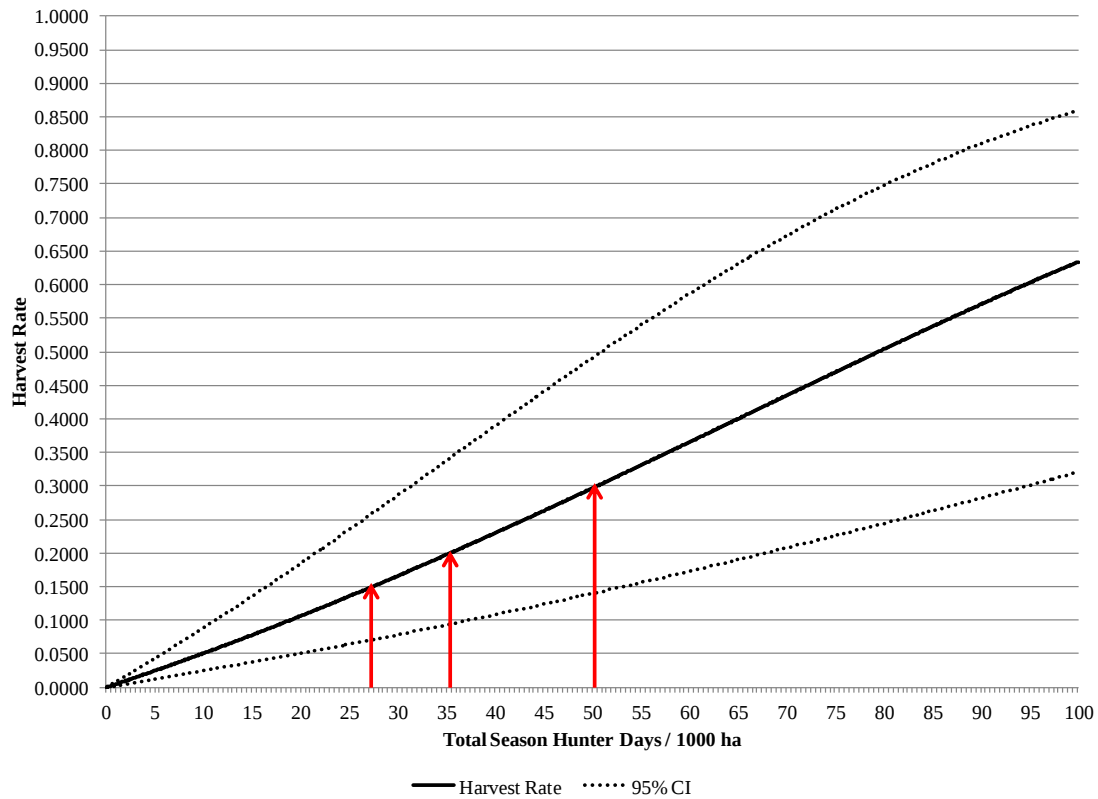


Figure 3.6: Relationship between total hunting pressure and harvest rate of northern bobwhites in southwest Florida, 2003–2009. Red lines indicate total hunting pressure amounts yielding 15, 20, and 30% hunting mortality.

On average, the harvest rate during the regular hunting period was 38% (Table 3.22). Yearly harvest rates ranged from 28% in 2008 – 2009 to 48% in 2004 – 2005. The average harvest rate during the zone F hunt was 11% (Table 3.23). Yearly harvest rates ranged from 2% in 2008 – 2009 to 22% in 2003 – 2004.

Table 3.22: Estimated harvest rates of northern bobwhites during the regular hunting season on BWWMA in southwest Florida, 2003 - 2009.

Year	Radio-tagged	Radio-tagged Mortality			% Radio-tagged Mortality		
	Alive Pre-Hunt	Harvest	Cripple	Total	Harvest	Cripple	Total
2003 - 2004	39	15	1	16	38%	3%	41%
2004 - 2005	184	68	20	88	37%	11%	48%
2005 - 2006	145	52	6	58	36%	4%	40%
2006 - 2007	99	25	8	33	25%	8%	33%
2007 - 2008	117	41	5	46	35%	4%	39%
2008 - 2009	103	25	4	29	24%	4%	28%
Average					33%	6%	38%

Table 3.23: Estimated harvest rates of northern bobwhites during the zone F hunting season on BWWMA in southwest Florida, 2003 - 2009.

Year	Radio-tagged	Radio-tagged Mortality			% Radio-tagged Mortality		
	Alive Pre-Hunt	Harvest	Cripple	Total	Harvest	Cripple	Total
2003 - 2004	54	11	1	12	20%	2%	22%
2004 - 2005	58	5	0	5	9%	0%	9%
2005 - 2006	53	7	0	7	13%	0%	13%
2006 - 2007	59	3	1	4	6%	2%	7%
2007 - 2008	50	2	4	6	4%	7%	11%
2008 - 2009	40	0	1	1	0%	2%	2%
Average					9%	2%	11%

Estimated harvest rates for each hunt zone ranged from 2% in zone F (2008 – 2009) to 67% in zones B and C (2003 – 2004). The model relating harvest rate to over-winter survival was more parsimonious than the constant survival model (Table 3.24). The harvest-rate effect was supported ($\beta = -1.23$) and the relationship was important (Table 3.25). Over-winter survival declined as harvest rate increased (Figure 3.7).

Table 3.24: Summary of model-selection results from management Question 5 about the effects of harvest rates (HR) on over-winter survival of northern bobwhites in southwest Florida, 2003 - 2009.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(HR)	2	4612.3242	0	1	1	4636.2706
S(.)	1	4638.2711	25.9469	0	n/a	4634.4639

Table 3.25: Parameter estimates and 95% confidence intervals (CI) for the model evaluated for Question 5 on the effects of harvest rates on over-winter survival of bobwhites in southwest Florida, 2003 - 2009.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(HR)	Intercept	2.8817	0.0914	2.7025	3.0608
	Harvest Rate	-1.2346	0.2346	-1.6943	-0.7748

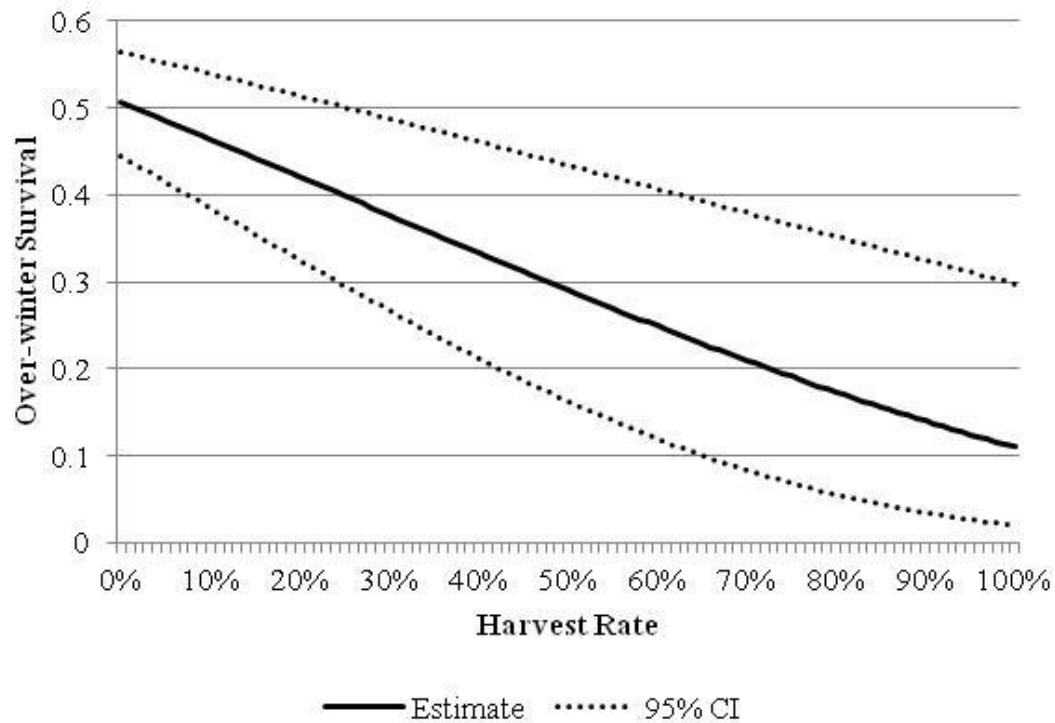


Figure 3.7: Over-winter survival rate estimates and 95% confidence intervals related to harvest rates of the northern bobwhites in southwest Florida, 2003 – 2009.

Pre-hunt density the following year was not related to over-winter survival. The constant survival model had more support than the model relating pre-hunt density the following year (NYDENS) to over-winter survival (Table 3.26). Compared to the constant survival model, the deviance did not decrease, meaning that over-winter survival did not explain any variation in the pre-hunt density the following year. Furthermore, the beta estimate for pre-hunt density the following year was not important (Table 3.27).

Table 3.26: Summary of model-selection results from management Question 6 about the relationship between over-winter survival and pre-hunt density the following year (NYDENS) of northern bobwhites in southwest Florida, 2003 - 2009.

Model	K	AIC _c	ΔAIC _c	AIC _c Weights	Evidence Ratio	Deviance
S(.)	1	4638.2711	0	0.73107	1	4636.2706
S(NYDENS)	2	4640.2712	2.0001	0.26893	2.7184	4636.2698

Table 3.27: Parameter estimates and 95% confidence intervals (CI) for the model evaluated for Question 6 on the relationship between over-winter survival and pre-hunt density the following year (NYDENS) of bobwhites in southwest Florida, 2003 - 2009.

Model	Parameter	Estimate	SE	95% CI	
				Lower	Upper
S(NYDENS)	Intercept	2.4689	0.0687	2.3341	2.6036
	Next year's pre-hunt density	0.0048	0.1672	-0.3230	0.3325

DISCUSSION

The objectives of this analysis were to estimate the bobwhite over-winter survival rate, to model factors related to over-winter survival, and to address specific management related questions. Model selection indicated that year, time, and hunting zone were factors that influenced over-winter survival of bobwhites on BWWMA. These results are similar to those reported by Terhune et al. (2007). They evaluated temporal and spatial factors affecting survival of bobwhites in Georgia and found them to be important.

Terhune et al. (2007) attributed the variation to differences in habitat suitability, predator abundance, and habitat manipulations among study sites and years. The same underlying factors may have been responsible for the variation in survival rates during the over-winter period and among hunt zones on my study area. However, the habitat among zones on BWWMA was generally managed similarly (i.e., prescribed fire and roller chopping). Furthermore, the models I evaluated that specifically related habitat characteristics to survival were not as well supported as the model that explained survival influenced by hunting zone. Predator abundance could have varied from one zone to another and certainly among encounter periods and years. However, an important factor that varied over time and space and explained variation in my data was the amount of hunting pressure.

Over-winter survival in BWWMA decreased as hunting pressure increased. In Iowa, Suchy and Munkel (2000) reported that the over-winter survival rate was lower on the more heavily hunted site of two sites with different levels of hunting pressure. Likewise, Williams et al. (2009) reported lower over-winter survival on their study site with greater harvest mortality. In North Carolina, the difference in over-winter survival rates between hunted (0.45) and non-hunted (0.65) study sites was significant (Robinette and Doerr 1993). Curtis et al. (1988) also reported lower winter and annual survival rates for a hunted population in North Carolina compared to a non-hunted population in north Florida. Concurring with my results, these other studies indicated that any hunting or increased hunting generally reduces over-winter survival. It appears that, at least in some cases, some level of hunting mortality is additive to natural mortality.

During the no-hunting period, pre-hunt bobwhite density was not related to survival. Therefore, there was no evidence that predator satiation (i.e., maximum predation threshold) was reached during the no-hunting period. Conversely, during the hunting period, survival increased as pre-hunt density increased. My hypothesis that hunters chose to hunt more frequently, and harvest birds at greater rates, in zones with greater bobwhite densities was not supported by the results. However, access limitations to some hunting zones over the duration of the study likely influenced hunter behavior

more than free will. Consequently, I cannot conclude that hunters chose to hunt locations with greater densities of bobwhites.

Survival during the hunting period increased as average temperature increased. My hypothesis about the relationship between temperature and survival during the hunting period was supported. Bird dogs may not be able to track bobwhites effectively in warmer temperatures. Also, hunters may not exert as much hunting effort during periods of warmer weather. Rainfall, during the no-hunting period and the hunting period, was not an important factor related to survival. The days of rain covariate did explain a small amount of variation in the data as seen by the slight reduction in deviance when added to models (Table 3.12). My hypothesis, that increased rainfall during the hunting periods would decrease survival because bird dogs would detect bobwhites more effectively in the moist conditions, was not supported.

My model-averaged estimates for over-winter survival ranged from 0.310 in 2007 – 2008 to 0.480 in 2008 – 2009. These estimates are in the top half of the range of estimates from studies examined by Sandercock et al. (2009). One study in Georgia reported more variable over-winter survival estimates ranging from 0.238 – 0.647 over an 8-year study (Terhune et al. 2007). Hughes et al. (2005) reported a range of over-winter survival estimates of 0.25 – 0.36 on an agricultural area in Georgia and 0.51 – 0.58 on an intensively managed bobwhite plantation in Georgia. My results compare well to these studies, however, my results are less variable and the upper end of my range is lower. Average harvest rates (38%) during the regular hunting period on BWWMA were much greater than the <12% harvest rates on study sites in Georgia (Hughes et al. 2005, Terhune et al. 2007) and the 23.3% reported from north Florida (Pollock et al. 1989). The low variability of my estimates suggests that over-winter survival is relatively stable on BWWMA. However, the great level of hunting mortality during my study may have resulted in the upper range of my survival estimates being lesser than those reported from Georgia.

The percentage of a hunting zone covered in food strips was not related to over-winter survival. Increased hunting-related mortality because of more food strips was not supported because the interaction between food strips and hunting pressure was

not an important factor. Madison et al. (2002) reported similar findings in Kansas that bobwhite survival was no different near food plots. In my analysis, I simply used the amount of food strips at the zone level as a covariate to evaluate this relationship. A more fine-scaled assessment of food strips within individual bobwhite home ranges may have yielded more precise results. Future analyses may consider this when relating food plots to over-winter survival.

The percentage of the hunting zone burned the previous year also was not related to over-winter survival. This is not surprising because the vegetation appeared to have recovered to the pre-burned state by the following winter. As with food strips, it may be of interest to analyze the amount of an individual bird's home range that was burned the previous year to obtain more precise results.

The results of my analysis relating survival to harvest rate indicated that harvest was at least partially additive to mortality during the over-winter period. I could not compare hunting pressure with other studies because it was either not reported, or not translatable to my measure of hunting pressure. Dixon et al. (1996) reported that a harvest mortality rate of 33% for a population on a managed hunting plantation in South Carolina may have been additive to bobwhite mortality in late winter, and concluded that hunting pressure should be restricted to ensure bobwhite population persistence. In North Carolina, Curtis et al. (1988) reported 19% and Robinette and Doerr (1993) reported 14% harvest mortality. Both of these studies were conducted on Fort Bragg Military Reservation where the bobwhite population had declined from the early 1970s to the mid-1980's (Curtis et al. 1988) and was described as "low" by Robinette and Doerr (1993). Madison et al. (2002) estimated harvest mortality rates in Kansas of 19% and 17% in areas near to and far from food plots, respectively. Other studies have reported greater harvest mortality rates. Burger et al. (1995) estimated a harvest mortality rate of 28% for a declining population in Missouri. Utilizing census data in Illinois, Roseberry and Klimstra (1984) and Vance and Ellis (1972) reported harvest rates of 44% and 70%, respectively. However, these harvest rates were estimated during times when natural predator population levels may have been lower and also may have been biased by the methods used. Bobwhite harvest rate during the regular hunting season on BWWMA

appears to be high compared to other studies. Hunting pressure may have been greater on BWWMA resulting in greater harvest mortality rates. I concur with Dixon et al. (1996) that in the future it would be useful for studies estimating over-winter survival and harvest mortality to report a standardized measurement of hunting pressure so that results are more comparable.

The confidence intervals for the effect of total season hunting pressure on survival during the regular hunting period were wide; however, the model does give some idea of the amount of hunting pressure that should be allowed for desired harvest rates. I plotted the observed hunting pressures and corresponding harvest rates for the 2003 to 2008 regular hunting seasons (Figure 3.8). The model seemed to underestimate harvest rates because the range between the estimated harvest rate and the more conservative confidence interval appeared to provide the most realistic harvest rate predictions. Terhune et al. (2007) concluded that the harvest rates <12% on their study sites were adequate to maintain consistent bobwhite population levels. Although the disparity is large, this is in agreement with the conclusion that harvest rates >30% can cause population decline (Landers and Mueller 1986). The average harvest rate during the zone F hunt over the six years of my study was 11%. Pre-hunt density estimates for zone F were consistently greater than any other hunt zone (Table 3.28). This result strengthens the indication that the harvest rate during the BWWMA regular hunting season. If the goal of management is to increase the bobwhite population on BWWMA, the target harvest rate during the regular hunting season should be much lower than observed.

Pre-hunt density the following year was not related to the over-winter survival rates observed during my study. This result suggests that other factors during the summer (i.e., number of nesting attempts and brood survival) were affecting the pre-hunt density in the fall. In their sensitivity analysis, Sandercock et al. (2009) identified bobwhite winter survival, summer survival, and chick survival as the key factors related to variance in population change. Sub-adult fertility and over-winter survival were the two demographic parameters most influential to bobwhite population change in Alabama (Folk et al. 2007). One possible explanation for my result is that the range of over-winter survival evaluated in my study was below the threshold for a positive population

response the following year. Over-winter survival rates above the threshold may increase the breeding season population to a level that increases overall reproduction and, therefore, the fall population. Nevertheless, further investigation into bobwhite demographic parameters during the summer on BWWMA may identify other factors that are limiting population growth.

Table 3.28: Pre-hunt density estimates for bobwhites in each hunting zone on BWWMA in southwest Florida, 2003 - 2009.

Year	Pre-hunt Bobwhite Density Estimates (birds/ha) by Zone				
	A	B	C	D	F
2003-2004	0.213	0.068	0.116	0.106	0.276
2004-2005	0.257	0.120	0.178	0.302	0.625
2005-2006	0.227	0.185	0.216	0.116	0.392
2006-2007	0.268	0.139	0.203	0.600	0.747
2007-2008	0.104	0.081	0.151	0.154	0.782
2008-2009	0.154	0.101	0.524	0.081	0.920

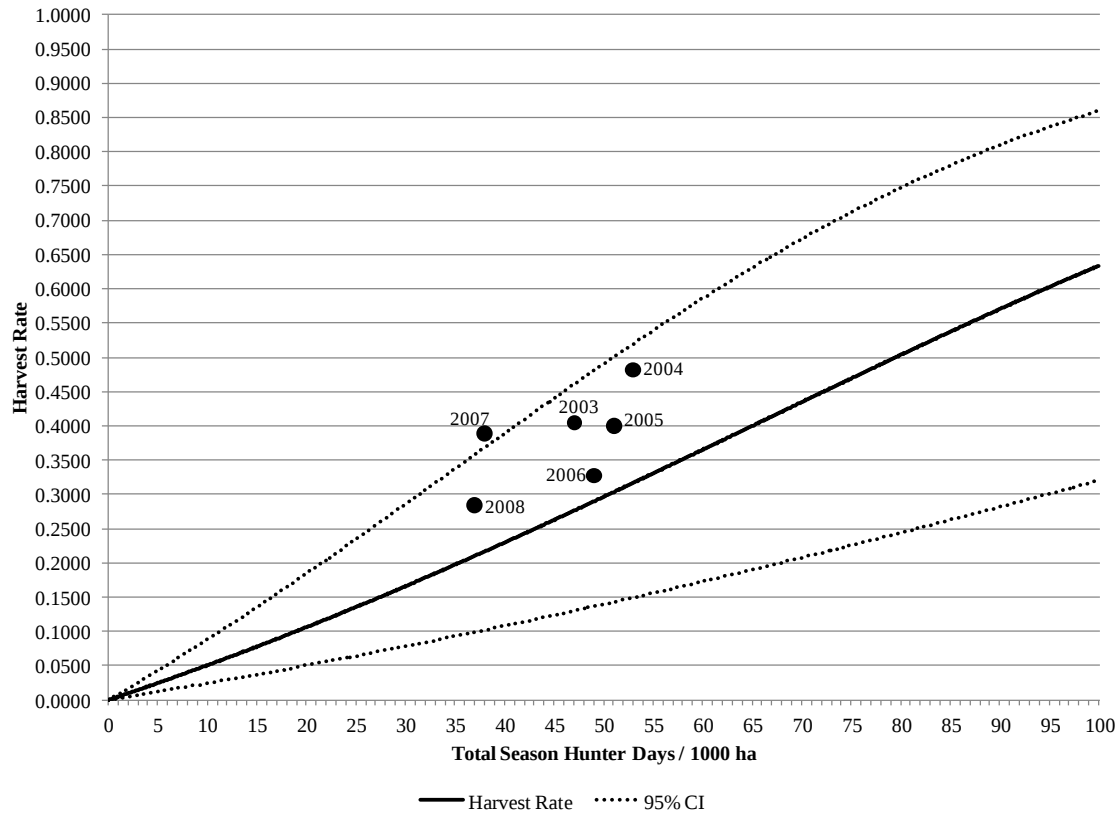


Figure 3.8: Predicted harvest rates in relation to observed hunting pressures and associated harvest rates during the northern bobwhite study in southwest Florida, 2003 – 2009. The predicted relationship (solid line) and 95% confidence intervals (dashed lines) were derived and extrapolated in Program MARK from the relationship between over-winter survival and hunting pressure. The observed hunting pressure and associated harvest rates (dots) are the actual data for each year.

MANAGEMENT IMPLICATIONS

My results indicated that food strips and prescribed burning appeared to have a minimal effect on over-winter survival. As food-strip planting and prescribed burning are two of the main management practices on BWWMA, I believe more information and more specific analyses (i.e., food strip and burning proportions of individual home ranges) are needed to truly understand the relationships food strips and burning have with survival.

Hunting pressure was the most important factor influencing over-winter survival on BWWMA. For example, in the 2008 – 2009 over-winter period, survival was the greatest of the six years studied and hunting pressure was the least. Hunting pressure and the related harvest rates observed on BWWMA may be additive to natural mortality and too great to sustain the bobwhite population according to other research (Landers and Mueller 1986, Terhune et al. 2007). The habitat appeared to be adequate for bobwhites and management practices that I evaluated did not seem to be negatively impacting the bobwhites. Predator management is an option to reduce natural predation, but to be done effectively, it is expensive and time consuming. Also, federal laws prevent the control of avian predators. Therefore, for BWWMA, under the current management regime, the only pragmatic option to increase the bobwhite population appears to be harvest management. Reducing the target harvest rate may be the most reasonable way to increase the population. Reductions in bag limits affect only a small number of hunters and do not contribute much to harvest rate reduction (Guthery et al. 2004). Individual bird quotas (i.e., seasonal limits to the number of bobwhites harvested) are difficult to regulate. According to my model, harvest rate reduction can be achieved by reducing the number of hunter days (Table 3.29). A desired harvest rate could be achieved by a zonal hunter-day quota. For example, if a 15% harvest rate is desired, zone A could be closed after reaching 131 hunter days. Or, the current season length could be maintained and the number of hunters allowed to hunt in each zone each day reduced to the zone season total hunter days divided by the number of hunt days in the season (i.e., for 15% harvest rate in zone C, $118/24$ hunt days ≈ 5 hunter days per bobwhite hunt day). Finally, the number of bobwhite hunt days per week could be reduced from four to allow more hunting opportunity each hunt day, but for fewer days during the 6-week bobwhite hunting season.

Table 3.29: Harvest rates and associated hunting pressures for bobwhite hunting on BWWMA in southwest Florida.

Harvest Rate	Hunter days/1000 ha*	Hunting Pressure				Total Hunter Days
		Zone A (5,977 ha)	Zone B (6,258 ha)	Zone C (5,396 ha)	Zone D (5,539 ha)	
12%	18.3	109	115	99	101	424
15%	21.9	131	137	118	121	506
20%	28.4	170	178	153	157	658
30%	40.9	244	256	221	227	948

* Average of the low- and mid- range estimates from the model relating hunting pressure to harvest rate in Question 4.

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PART IV

CONCLUSIONS

The two primary objectives of my research were to (1) determine factors related to nest survival of northern bobwhites on Babcock-Webb Wildlife Management Area (BWWMA) in southwest Florida (Part II); and (2) determine the factors related to over-winter survival of northern bobwhites on BWWMA in southwest Florida (Part III). My key conclusions from the analyses are briefly discussed below.

Nest survival has not been found to be an important factor related to bobwhite population change (Sandercock et al. 2009). Incubation period nest survival rates on BWWMA were similar to other estimates reported from studies throughout the bobwhite range (Burger et al. 1995, Terhune et al. 2006, Collins et al. 2009, Potter et al. 2011). Reproductive parameter estimates from BWWMA were very comparable to those from a Georgia study (Terhune et al. 2006) which supported far greater bobwhite densities. These results suggest that recruitment in the population is probably not a key limiting factor for bobwhites on BWWMA. Nest survival was best described as a function of quadratic time and broad-scale habitat characteristics. Daily nest survival decreased throughout the nesting period, slightly leveled off at the end, and was positively related to the proportion of the 1000-m radius area around a nest comprised of basin marsh habitat. The peak nesting occurred between late April and late June. Managers should keep this in mind when conducting habitat management (i.e., chopping and burning) during the breeding season. An effort should be made to reduce the impact of management on bobwhite nest survival during this period as survival of these nests may be extremely important to fall populations.

Based on my results, harvest appeared to be additive to natural mortality and hunting pressure was the main factor related to bobwhite over-winter survival (Part III). Over-winter survival has been identified as a parameter highly associated with bobwhite population change (Folk et al. 2007, Sandercock et al. 2009). Other factors found to be associated with over-winter survival in my analysis (i.e., temperature and pre-hunt density) are not directly manageable. Therefore, until factors affecting other important bobwhite demographic parameters are identified, reducing over-winter mortality by regulating hunting pressure may be the best opportunity to increase the BWWMA bobwhite population. The significant reduction in over-winter mortality in 2008 in

response to reduction in hunting pressure is an indication that this management strategy will be effective.

Finally, future research could investigate summer adult survival, chick survival (Sandercock et al. 2009), and sub-adult fertility (Folk et al. 2007) which are other parameters that have been identified as highly associated with bobwhite population change. All factors (i.e., spatial, temporal, biological, climatic) should be evaluated as to their relation to bobwhite demographic parameters, because it is important to understand how these factors affect bobwhites. However, an emphasis should be placed on factors controlled via management. If other manageable variables strongly related to these population parameters can be identified and understood, bobwhite population recovery could be expedited by addressing limiting factors on all fronts. In all likelihood, the BWWMA bobwhite population is not being limited by simply one factor but instead by the complex interaction of several key factors linked to survival and recruitment. Managing for improvement in both recruitment and survival is likely to have the best chance for successful restoration of the bobwhite population.

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VITA

Steven was born and raised in Columbia, TN. Though his parents lived in a neighborhood, there was a creek nearby and wooded areas around that were his playgrounds. He also spent time during summers at family farms in Rives, TN and Fayetteville, TN, where he gained a love and appreciation for nature and the outdoors. At the age of ten, Steven met a couple of excellent birders who taught him bird identification and banding. Steven also grew up in the Boy Scouts of America and was lucky to have two excellent scoutmasters who took him on local and national high adventure camping, canoeing, and backpacking trips. He earned his Eagle Scout honor and graduated from Columbia Central High School in the spring of 1998, and enrolled in the University of Tennessee, Knoxville as a Wildlife and Fisheries Science major the following fall. Steven interned with the U.S. Fish and Wildlife Service at Seedskadee National Wildlife Refuge in southwestern Wyoming during the summer of 2001. His main duties there were surveying and reporting results of raptor, waterfowl, and sage grouse populations on the refuge. After receiving his Bachelor of Science degree in the spring of 2002, Steven returned to Seedskadee NWR as a seasonal biotech performing many of the same duties he had as an intern. He also met his future wife, Amy, in Wyoming. In September of 2002, he accepted a job with the Florida Fish and Wildlife Conservation Commission studying northern bobwhites in southwest Florida. After two years as a field technician, Steven was promoted to field supervisor and retained that position until the end of the study in June of 2009. The research involved trapping and radio tracking wild bobwhites to determine survival rates of adults and nest survival. In the spring of 2010, with permission from the State of Florida, Steven took the data he collected on the bobwhite study to the University of Tennessee to pursue a Master of Science degree. He graduated with that degree in December 2011. Steven is married to his beautiful wife, Amy. They have two English pointers, Scout and Nash. Someday, they hope to be able to put them on bobwhites again.