IMPROVING MANAGEMENT FOR NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*): RE-EVALUATION OF MOVEMENTS, NESTING HABITAT AND FEEDING ECOLOGY

By

DARRELL EUGENE TOWNSEND II

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Thesis Approved:

Robert L Lochmiller by James H Shaw

Thesis Advisor

D. M. Leslie Jr.

E J Bidwell

Ronald E. Masters

Wayne B. Powell

Dean of the Graduate College

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CHAPTER I

USE OF SUPPLEMENTAL FOOD AND ITS INFLUENCE ON SURVIVAL OF NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*)

Abstract: Biologists have debated the effectiveness of supplemental feeders as a management tool for northern bobwhites (*Colinus virginianus*), but few extensive evaluations have been conducted. We examined 783 crops from harvested bobwhite during 1992–1996 to determine effects of climatic stress in winter on use of supplemental feeders and their impact on survival rate in winter. Crops of bobwhites harvested from areas with supplemental feeders contained 28.2% supplemental food compared with 5.5% ($P < 0.001$) for those from areas without supplemental feeders. Winter climate was not a significant predictor of the proportional use of supplemental feeders. Rates of winter survival were greater on areas with supplemental feeders compared with non-supplemented areas in winters 1992–1993 ($P = 0.001$) and 1993–1994 ($P = 0.002$), but in 1994–1995 rates were greater on non-supplemented areas ($P = 0.032$). Cause-specific mortality rates indicated that supplemental feeders did not pre-dispose bobwhites to hunter harvest or predators. Results suggested that bobwhite can gain nutritional benefits from supplemental feeders during times of severe winter stress.

Key words: *Colinus virginianus*, hunting, northern bobwhite, Oklahoma, survival, supplemental feed, winter

Introduction

Declining numbers of northern bobwhite in the United States have been well documented (Klimstra 1982, Church et al. 1993); Oklahoma experienced a 16% decrease from 1961 to 1988 (Brennan 1991). Winter survival can be extremely low in many populations (Robel and Fretwell 1970; Curtis et al. 1988; Robinette and Doerr 1993;

Burger et al. 1994, 1995). To improve winter survival of bobwhite, managers of intensively hunted areas have used supplemental feeders believing that nutritional deficiencies and severe climatic stress can contribute to population declines. However, supplemental feeders have not been universally regarded as an effective management tool (Lehmann 1984, Guthery 1986, Landers and Mueller 1986). In addition to a lack of solid evidence that populations of bobwhite are nutritionally stressed during winter, several biologists have suggested that supplemental feeders could concentrate predators and facilitate spread of disease, thereby having an overall detrimental effect on populations (Lehmann 1984, Guthery 1986, Landers and Mueller 1986).

The suggestion that supplemental feeders may enhance survival during stressful winters when foods become limited has never been fully evaluated (Lehmann 1984, Guthery 1986, Landers and Mueller 1986). Our study was designed to evaluate use of supplemental feeders by northern bobwhite in response to changing climatic conditions in winter and assess their effect on winter survival. We hypothesized that prevalence of supplemental food in crops of harvested bobwhites would be greater on areas with supplemental feeders in winter and that use of supplemental feed would be correlated with climatic winter stresses. We further hypothesized that survival rates would be greater for populations with access to supplemental feeders.

Study area and methods

We collected crops from harvested quail during the regular hunting season on the Packsaddle Wildlife Management Area (PWMA) in western Oklahoma. This 6,475-ha area of mixed-prairie habitat was located 40 km north of Cheyenne, Oklahoma, where elevation ranged from 579 to 762 m above mean sea level and annual precipitation averaged 53 cm. Ambient temperatures averaged 2.1°C during winter and 27.0°C in summer (Cole et al. 1966). Soils consisted of sandy Nobscot-Brownfield and Pratt Tivoli, moderately sandy Broken land-Berthoud-Enterprise and Pratt-Carwile, and loamy Quinlan-Woodward (Cole et al. 1966). Dominant species of grasses included sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), sand paspalum (*Paspalum stramineum*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and sand dropseed (*Sporobolus cryptandrus*). Common forbs on the area included western ragweed (*Ambrosia psilostachaya*), Texas croton (*Croton texensis*), erect dayflower (*Commelina erecta*), and prairie sunflower (*Helianthus petiolaris*). Woody vegetation included shinnery oak (*Quercus harvardii*), sand sage (*Artemisia filifolia*), and sand plum (*Prunus angustifolia,* Cole et al. 1966).

The experimental design incorporated 2 284-ha areas (control, feeder) separated by a 243-ha buffer zone. The feeder area contained 55-gallon barrels modified to serve as supplemental feeders. We filled each barrel with sorghum and located it in the center of each 8 ha of the 284-ha area. We checked barrels for moldy feed and refilled them as needed. We located randomly placed food plots (0.5−1.5 ha) of wheat, milo, and millet on both experimental areas as part of the normal management practices on PWMA. We collected crops from all birds harvested from each area during 1992−1996. Due to the pseudo-replicated nature of our study, we acknowledge that area effects were confounded with treatment effects (Guthery 1987).

We controlled quail hunts at Packsaddle WMA, where 440 hunters were selected by a lottery system in each season. Five parties of 4 hunters each were permitted to hunt on Tuesday and Saturday of their selected week from 1 November to 13 February and were required to check in and out daily. Crops from each area were identified and returned to the laboratory where food items were divided into 5 categories: miscellaneous debris, insects, vegetation, native seeds, and supplemental seeds (seeds obtained from supplemental feeders or planted food plots). We weighed items in each category to the nearest 0.001 g, and we calculated a ratio of supplemental feed as a percentage of total crop contents (Jensen and Korschgen 1947, Korschgen 1948).

To evaluate effect of supplemental feeders on winter survival, we trapped bobwhites on control and treatment areas using modified Stoddard funnel traps baited with sorghum (Wilbur 1967) and by nightlighting throughout the year (Huempfner et al. 1975). We marked captured birds with radio-transmitters weighing <7 g (Holohill Systems Ltd., Ontario, Canada and Wildlife Materials, Inc., Carbondale, Illinois), sexed, aged, and banded with aluminum leg-bands (Webb and Guthery 1982). We monitored birds ≥5 times/week using a radio-receiver and yagi antenna. Mortalities were classified as: avian or mammalian predator, hunting, capture related, missing, or unknown. We determined mammalian and avian mortalities by evidence found at the kill site (Dumke and Pils 1973). We determined hunting mortalities from hunter returns at the check station. We classified bobwhite that survived ≤7 days after the initial capture as capture-related mortalities and excluded them from analyses (Kurzejeski et al. 1987, Pollock et al.1989). Birds classified into the missing category were censored, but included in the analysis until the day they were censored (Pollock et al. 1989).

We compared percentage of supplemental food in quail crops between control and feeder areas with analysis of variance (ANOVA; SAS Institute, Inc. 1996). Data were arcsine-transformed prior to analysis (Steel and Torrie 1980). To assess influence of climatic variables on the intake of supplemental food in quail, we used stepwise regression analysis (PROC REG; SAS Institute, Inc. 1996), with amount of supplemental food as the dependent variable and climatic conditions as independent variables. Variables selected for inclusion into the model were deemed to be significant when $P \leq 0.15$ (Hosmer and Lemeshow 1989, Sams et al. 1996, Cody and Smith 1997, Boyer et al. 1999). Prevalent weather conditions at time of harvest (maximum and minimum temperature, precipitation, and snowfall; National Oceanic and Atmospheric Administration 1992, 1993, 1994, 1995, 1996) and ≤7-day averages just prior to harvest were included as independent variables. We also examined associations with climatic variables using Pearson correlation analysis (PROC CORR, SAS Institute, Inc. 1996). We computed survival rates using a modification of the SAS program by White and Garrott (1990), which uses the staggered-entry design of the Kaplan−Meier procedure or product-limit estimator (Kaplan and Meier 1958). We estimated winter survival over a 5-month period (1 November−31 March). We calculated cause-specific mortality rates using the computer program MICROMORT (Heisey 1985) that incorporates the Heisey−Fuller method to estimate the probability of dying from a given mortality agent in the presence of other competing agents (Heisey and Fuller 1985). We used log-rank chi-square analysis to determine differences in survival curves and a Z-statistic to examine differences in 5-month survival rates and cause-specific mortality (Pollock et al 1989) between feeder and control study areas. Differences we deemed significant at $P \leq 0.05$.

Results

Percentage of supplemental food in the winter diet of quail was consistently greater in birds harvested from the feeder area compared with the control area in all years ($F = 116.74_{1,781}$, $P < 0.001$). Supplemental food in the diet reached a peak in winter, 1992–1993, comprising 45.2% of the diet on the feeder area.

Multiple regression models that predicted supplemental food use by quail in winter on the feeder ($R^2 = 15.0$, 7 variable model) and control ($R^2 = 20.0$, 10 variable model) areas were very significant, but explained only a small percentage of variation in supplemental food use at time of harvest (Table 2). The 7-day mean maximum temperature prior to harvest accounted for most of the variation (1.0–2.9%) in supplemental food use on these 2 areas, where supplemental feed became more important as mean maximum temperature declined (Table 3). Both mean minimum and maximum temperatures during the previous 1–7 days prior to harvest were correlated negatively with percentage of supplemental food in crops of birds harvested from the feeder area (Table 3). Variables associated with temperature generally were not correlated with use of supplemental food on the control area, except for 6- or 7-day mean maximums (Table 3). Amount of precipitation or snowfall 1–3 days prior to harvest was correlated positively with supplemental food use on the feeder study area. Amount of snowfall 1–7 days prior to harvest was correlated negatively with supplemental food in crops of birds from the control area, indicating that birds did not have access or they elected not to use food plots during snow events. Although many significant correlations existed between climatic variables and percentage of supplemental food in crops of harvested birds, all correlation coefficients were small ($r < 0.22$, Table 3), indicating that combinations of other extrinsic factors influenced supplemental food use by quail in western Oklahoma.

Considering all forms of mortality, the 5-month over winter survival rate was greater in the population from the feeder area compared with the control in 2 of 4 winters ($P < 0.05$, Table 4). Survival rate was 6-fold greater in 1992-1993 and 2-fold greater in 1993-1994 on the feeder area compared with the control. In winter 1994-1995, the population on the control area had a survival rate 2-fold greater than the population on the feeder area.

Because mortality risks may be elevated from hunters and predators concentrating their activities in the vicinity of supplemental feeders, we estimated cause-specific mortality rates (Table 5). Although we did not detect a significant difference, in winter 1993-1994, avian mortality tended to be greater on the feeder ($M = 0.45$) than on the control ($M = 0.33$, $P = 0.064$; Table 5). In winter 1995-1996, hunter mortality was greater on the feeder ($M = 0.33$) than on the control ($M = 0.21$), but was not statistically significant ($P = 0.074$; Table 5). However, in 3 of 4 years, raptor and mammalian cause-specific mortality rates were greater on the control than on the feeder area, but did not differ statistically (Table 5). Cause-specific mortality rates indicated that neither hunters nor predators were able to benefit by concentrating their activities near supplemental feeders (Table 5).

Discussion

Our data demonstrated that bobwhites with access to supplemental feeders used this nutritional resource even when food plots are available. Results suggest, however, that bobwhites on the control area were denied access or did not utilize food plots during periods of snow cover. Further, bobwhites with access to feeders took greater advantage of supplemental feed during precipitation and snowfall events that occurred 1 – 3 days prior to harvest. Bobwhites progressively increased the proportion of supplemental feeder use with decreasing ambient temperatures, but low correlation coefficients suggest that winter climatic conditions, alone, were not strong predictors of the proportional use of supplemental feeders. We attribute low correlation coefficients to the year-round availability and daily use of feeders by bobwhites, regardless of prevalent weather conditions.

Our results support the hypothesis that supplemental feeders can increase survival during winter when climatic conditions are especially stressful (Lehmann 1984, Guthery 1986, Landers and Mueller 1986). Kendeigh (1969, 1970) proposed that daily fluctuations in body weights were greatest at low temperatures because of increased energy demands to maintain core body temperatures, causing greater depletion of fat reserves. Leif and Smith (1993) reported that bobwhites that consumed low-energy foods were unable to accumulate as much body fat as bobwhites that consumed high-energy foods. Supplemental feeding not only provides bobwhites with a high-energy food source that is required to maintain existence energy during low ambient temperatures (Robel et al. 1979), but also may help to preserve energy reserves and increase predator avoidance by decreasing foraging activities (movements) (Johnson and Gaines 1990).

Raynor (1980) reported an inverse correlation between mean population density of bobwhites and days of snow cover (r = -0.51) and total snowfall (r = -0.32) during preceding winters. Roseberry and Klimstra (1984) also documented population declines in winter that varied from 36% to 81% in 1953–1980 ($\bar{x}$ = 63%) with the greatest natural mortality in January-March. Peoples et al. (1994) documented benefits of essential and nonessential amino acids to supplementally fed bobwhites in winter and Robel (1969) observed that bobwhites with access to a supplemental food source had greater body weights, body fat, and food in their crops than those without access to supplemental food. However, Guthery (1999) believed that those differences were negligible and that supplemental food merely added excess energy when energy was readily available. Thus, winter periods of food (energy deficiencies) and climate stress may cause bobwhites to reach a critical nutritional threshold; birds with access to supplemental feeders can receive nutritional benefits that ultimately affect their winter rates of survival. Although climatic conditions were not strong predictors of the proportion of supplemental food in quail crops in our study area, the combination of decreased native foods and severe winter stresses could have acted in concert to regulate the proportion of supplemental food use.

If hunters or predators concentrated their activity in the vicinity of supplemental feeders, they apparently did not receive any benefit by doing so. Cause-specific mortality rates did not differ between areas, indicating that supplemental feeders did not predispose bobwhites to hunter harvest or predators. Hence, our data does not support the hypotheses of Lehmann (1984), Guthery (1986), and Landers and Mueller (1986) that supplemental feeders can adversely concentrate predators. Greater winter survival on the feeder area in 2 of 4 years suggested that supplemental feeders can positively impact winter survival of bobwhite in western Oklahoma during some years.

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Table 1. Relative percentage of food items in the crops of hunter-harvested northern bobwhites from study areas with (feeder) and without (control) supplemental feeders during winters of 1992–1996. An ANOVA was used to test for differences in food items between study areas.

	Control			Feeder			
Winter season	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
1992–1993							
% Supplemental	100	16.69	3.60	83	45.22	4.85	<0.001
% Native	100	74.82	2.88	83	46.49	4.48	<0.001
% Vegetation	100	1.38	0.53	83	1.22	0.49	0.489
% Insects	100	2.46	0.94	83	2.91	1.07	0.821
% Miscellaneous	100	4.64	0.53	83	4.15	0.58	0.120
1993–1994							
% Supplemental	100	3.48	1.61	100	24.51	3.77	<0.001
% Native	100	82.26	2.37	100	64.97	3.73	<0.001
% Vegetation	100	6.91	1.51	100	4.17	1.06	0.043
% Insects	100	0.46	0.21	100	0.28	0.11	0.353
% Miscellaneous	100	6.89	1.09	100	6.07	0.87	0.376
1994–1995							
% Supplemental	100	0.27	0.15	100	25.20	3.96	<0.001
% Native	100	77.01	2.81	100	61.15	3.96	0.001
% Vegetation	100	14.62	2.58	100	7.49	1.96	0.003
% Insects	100	1.50	0.41	100	2.07	0.86	0.594
% Miscellaneous	100	6.59	1.19	100	4.09	0.62	0.003
1995–1996							
% Supplemental	100	1.51	1.04	100	20.65	3.31	<0.001
% Native	100	89.63	1.89	100	75.23	3.35	0.001
% Vegetation	100	6.90	1.59	100	1.77	0.43	<0.001
% Insects	100	1.26	0.33	100	2.04	0.49	0.382
% Miscellaneous	100	0.70	0.12	100	0.31	0.01	0.006

Table 1. Continued

	Control			Feeder			
Winter season	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Winters pooled							
% Supplemental	400	5.49	0.89	383	28.17	2.02	<0.001
% Native	400	80.93	1.29	383	62.65	1.99	<0.001
% Vegetation	400	7.45	0.89	383	3.77	0.61	<0.001
% Insects	400	1.42	0.28	383	1.78	0.35	0.806
% Miscellaneous	400	4.70	0.44	383	3.63	0.32	<0.001

Table 2. Climatic variables selected by a stepwise multiple regression analysis to predict prevalence of supplemental foods in crops of hunter-harvested northern bobwhite from study areas with (feeder) and without (control) supplemental feeders in winter (data from 1992–1996 pooled).

Area	Variable[a]	Parameter estimate	SE	Partial R^2	F	P
Control	Intercept	0.230	0.094	--	5.97	0.015
	7-day max	-0.010	0.003	3.3	8.71	0.003
	4-day prec	1.602	0.653	1.9	6.02	0.015
	4-day snow	-0.293	0.060	2.9	23.92	<0.001
	2-day prec	-3.54	0.562	1.5	39.79	<0.001
	1-day max	-0.007	0.002	0.7	10.63	0.001
	1-day min	0.007	0.002	1.7	10.41	0.001
	3-day prec	2.693	1.040	0.9	6.70	0.010
	6-day max	0.010	0.004	0.5	6.52	0.011
	2-day snow	0.150	0.045	0.5	10.96	0.001
	7-day prec	1.544	0.369	0.9	17.54	<0.001
Feeder	Intercept	1.358	0.197	--	47.66	<0.001
	7-day max	-0.029	0.007	4.5	15.63	<0.001
	2-day prec	1.233	0.335	2.9	13.56	<0.001
	6-day snow	-0.374	0.106	2.7	12.42	<0.001
	3-day snow	0.241	0.093	2.4	6.68	0.010
	7-day prec	-1.949	0.668	0.9	8.50	0.004
	7-day min	0.025	0.012	0.7	4.47	0.035
	1-day min	-0.006	0.003	0.9	3.87	0.050

[a] 1- to 7-day (n-day) averages for maximum (max) or minimum (min) daily temperature, precipitation (prec), and snowfall (snow).

Table 3. Correlation coefficients for the relationships between prevalence of supplemental food in northern bobwhite crops and mean prevalent climatic conditions that existed 1 to 7 days prior to their harvest in Oklahoma, winters 1992–1996 (all data pooled).

Area	Precipitation		Maximum Temperature		Minimum Temperature		Snowfall	
Mean period prior to harvest	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Control								
1 day	-0.09	0.067	0.04	0.389	0.11	0.026	-0.12	0.011
2 days	-0.13	0.009	0.02	0.559	0.07	0.122	-0.16	0.001
3 days	-0.06	0.182	0.02	0.574	0.07	0.144	-0.16	0.001
4 days	0.03	0.485	0.01	0.738	0.07	0.155	-0.14	0.004
5 days	0.02	0.645	-0.03	0.516	0.03	0.430	-0.14	0.004
6 days	0.04	0.324	-0.11	0.021	-0.05	0.315	-0.15	0.002
7 days	0.08	0.086	-0.18	<0.001	-0.10	0.029	-0.11	0.020
Feeder								
1 day	0.11	0.026	-0.18	<0.001	-0.09	0.068	0.09	0.059
2 days	0.20	<0.001	-0.19	<0.001	-0.15	0.002	0.17	0.001
3 days	0.19	<0.001	-0.14	0.004	-0.11	0.028	0.15	0.002
4 days	0.09	0.075	-0.12	0.014	-0.10	0.038	0.00	0.978
5 days	0.04	0.429	-0.15	0.002	-0.14	0.004	-0.06	0.220
6 days	0.05	0.291	-0.18	<0.001	-0.15	0.002	-0.06	0.188
7 days	0.05	0.299	-0.21	<0.001	-0.16	0.001	-0.02	0.649

Table 4. Estimated 5-month survival rate in winter with 95% confidence interval for northern bobwhite residing in study areas with (feeder) and without (control) supplemental feeders in Oklahoma from 1992–1996. Differences in survival curves and survival rates between study areas were tested using chi-square analysis and *Z*-statistics.

	Control			Feeder			Survival curves		Survival rates	
Winter	*n*	$\hat{s}$	95% CI	*n*	$\hat{s}$	95% CI	χ^2	*P*	*Z*	*P*
1992–1993	294	0.0304	0.0046–0.0561	255	0.1886	0.1154–0.2619	0.295	0.587	3.997	0.001
1993–1994	202	0.1259	0.0609–0.1908	168	0.3050	0.2036–0.4064	0.014	0.903	2.914	0.002
1994–1995	188	0.2200	0.1237–0.3163	200	0.1069	0.0363–0.1774	0.861	0.353	1.857	0.032
1995–1996	193	0.2251	0.1394–0.3107	200	0.1562	0.0841–0.2283	0.456	0.499	1.205	0.114

Table 5. Estimated 5-month cause-specific mortality rates (*M*) and associated standard errors (SE) in winter for northern bobwhite residing in study areas with (feeder) and without (control) supplemental feeders in Oklahoma from 1992–1996. Differences in mortality rates between study areas were tested using *Z*-statistics.

Winter	Control			Feeder				
Agent	*n*	*M*	SE	*n*	*M*	SE	*Z*	*P*
1992–1993								
Raptor	24	0.44	0.066	20	0.36	0.064	0.87	0.808
Mammal	11	0.20	0.054	9	0.16	0.049	0.55	0.709
Hunting	12	0.22	0.055	14	0.25	0.058	-0.38	0.352
1993–1994								
Raptor	20	0.33	0.034	21	0.45	0.071	-1.52	0.064
Mammal	16	0.26	0.056	1	0.02	0.021	4.01	0.999
Hunting	18	0.30	0.058	10	0.21	0.059	1.09	0.862
1994–1995								
Raptor	22	0.43	0.068	19	0.38	0.067	0.52	0.699
Mammal	8	0.16	0.050	8	0.16	0.051	0.00	
Hunting	12	0.23	0.058	14	0.28	0.063	-0.58	0.281
1995–1996								
Raptor	19	0.34	0.062	16	0.29	0.052	0.62	0.732
Mammal	12	0.21	0.054	8	0.15	0.048	0.83	0.797
Hunting	12	0.21	0.054	18	0.33	0.063	-1.45	0.074
Pooled								
Raptor	85	0.38	0.032	76	0.37	0.033	0.22	0.587
Mammal	47	0.21	0.027	26	0.13	0.023	2.26	0.988
Hunting	54	0.24	0.028	56	0.27	0.031	-0.72	0.236

CHAPTER II

CHARACTERISTICS OF NEST SITES OF NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*) IN WESTERN OKLAHOMA

Abstract: Previous studies have described the nesting habitat of the northern bobwhite (*Colinus virginianus*) throughout its range, but few have compared structural or compositional differences of vegetation between random non-use sites and successful and non-successful nest sites. From 1996-1998, we compared cover and structure of 85 plant species from 80 nest sites of northern bobwhite in western Oklahoma. Bobwhite nest sites were consistently associated with greater structural complexity than what was available at random non-use sites. Bobwhites selected nest sites that had greater coverage of grass and woody vegetation with a relatively low percentage of bare ground, presumably because these attributes maximizes their chance for successful reproduction by providing protection against weather and predators. Successful bobwhite nest sites had greater concealment in 1996 and 1997 (12.37 and 10.74% visibility, respectively) than non-successful nest sites (21.6 and 27.65% visibility), but they did not differ in 1998. We found no differences in composition or structure at successful and non-successful nest sites.

Key words: bobwhite, *Colinus virginianus*, cover, detrended correspondence analysis, DCA, gallinaceous, habitat, nest, northern, Oklahoma, quail, upland game, vegetation.

INTRODUCTION

Ground-nesting birds in shrub and grassland habitats suffer greater nesting mortality than other species, and many are documented to be in long-term population declines (Martin 1993a). Declining populations of the northern bobwhite (*Colinus virginianus*) are no exception and have been well documented (Klimstra 1982, Church et al. 1993). Oklahoma experienced a 16% decrease from 1961 to 1988 (Brennan 1991). Although the reason for these declines remain unknown, successful reproduction is an important factor of bobwhite ecology that depends on adequate nesting and brood rearing habitat (Berner and Gysel 1969). Previous studies have described the macrohabitat of bobwhite nest sites throughout their range (Klimstra and Roseberry 1975, Lehmann 1984:78-83, Roseberry and Klimstra1984:18-23, Taylor 1991), but few have compared structure and composition of vegetation between successful and non-successful nest sites and nest sites vs. random non-use sites. Our study was designed to determine if nest-site selection by bowhites was related to specific site characteristics and if such characteristics influenced the likelihood of nest success.

STUDY AREA

Research was conducted at the Packsaddle Wildlife Management Area (PWMA) in western Oklahoma. This 6,475-ha area of mixed-prairie habitat is located 40 km north of Cheyenne, Oklahoma, where elevation ranged from 579 to 762 m above mean sea level. Mean precipitation throughout the breeding season (April-September) was 11.32 cm in 1996, 9.42 cm in 1997 and 4.29 cm in 1998. Ambient temperatures averaged 2.1 °C during winter and 27.0 °C in summer (Cole et al. 1966). Soils consisted of sandy Nobscot-Brownfield and Pratt Tivoli, moderately sandy Broken land-Berthoud-Enterprise and Pratt-Carwile, and loamy Quinlan-Woodward (Cole et al. 1966). Dominant species of grasses included sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), sand paspalum (*Paspalum stramineum*), blue grama (*Bouteloua gracilis*), hairy grama (*B.*

hirsuta), and sand dropseed (*Sporobolus cryptandrus*). Common forbs on the area included western ragweed (*Ambrosia psilostachaya*), croton (*Croton sp.*), and prairie sunflower (*Helianthus petiolaris*). Woody vegetation included shinnery oak (*Quercus harvardii*), sand sage (*Artemisia filifolia*), and sand plum *(Prunus angustifolia*) (Cole et al. 1966).

METHODS

Radio-telemetry

Birds were trapped on the area using modified Stoddard funnel traps (Wilbur 1967) baited with sorghum throughout the year and by nightlighting (Huempfner 1975) sessions prior to the nesting season (March-April). Captured birds were marked with radio transmitters (Holohill Systems Limited, Ontario, Canada and Wildlife Materials, Incorporated, Carbondale, Illinois) weighing < 7 g, sexed, aged and banded with aluminum leg bands (Webb and Guthery 1982). Birds were monitored at least once daily throughout the nesting and brood rearing season (May - October).

Nesting Cover

Nest sites were marked and microhabitat characterized after parents permanently left the nest. Successful nests were defined by a hatch of ≥ 1 chick from each nest. Lost nests were characterized as: (1) predation (mammal or snake) and (2) abandoned. Ten 0.10 m quadrats were used to characterize plant cover (Daubenmire 1959) in a 1-m^2 plot positioned directly over the nest site. We took habitat measurements at each of 2 plots: a plot centered directly over the nest and a plot 20 m from the nest selected at a random direction (Badyaev 1995). Estimates of percent cover by species and bare ground were recorded using Daubenmire's coverage classes (Daubenmire 1959).

Nesting Characteristics

Physiographic variables such as aspect (degree), slope (%) (Sieg and Becker 1990), distance to nearest shinnery oak stand or any other noticeable abrupt change in habitat (edge), or major disturbance (roads, burns, food plots, etc.) were recorded. Diameter of the nest at the top, and depth and thickness of the nest lining were recorded (Lehmann 1984). Tradeoffs for nest-site selection between the bobwhite's visibility of its surroundings and its concealment from predators were evaluated (Gotmark et al. 1995). Visual obstruction was evaluated using a vertical profile board placed 3 m from each nest or non-use site (Nudds 1977). Obstruction was recorded in 4 profiles: <0.25 m, 0.25-0.50 m, >0.50-1.00 m, and >1.00-2.00 m. Percentage of vegetation cover was differentiated into 6 categories; <2.5%, 2.5-25%, >25-50%, >50-75%, >75-95%, and >95% (Schmutz et al. 1989). Measurements from within each nest site (a bobwhite's view from the nest) was taken at a height of 0.5 m in 4 different directions (Angelstam 1986): the first direction was random and subsequent directions were taken at 90° intervals.

We quantified nest concealment by placing a 10-cm diameter disc marked by 5 equivalent pie shaped triangles. Nest concealment from outside the nest (predator's view) was quantified by 9 points; 8 at 45° compass intervals 1 m from the nest and 1 overhead view taken at 0.5 m from the nest (Keppie and Herzog 1978, Martin and Roper 1988, Holway 1991, Gotmark et al. 1995). Concealment was quantified by placing a 10-cm disc divided into 5 equivalent sections and each section was assigned a visibility percentage as follows: 0 = 0 %; 1 = 20 %, 2 = 40 %, 3 = 60 %, 4 = 80 %, 5 = 100 % (Holway 1991). Density of little bluestem patches around the nest and non-use site within 1 m^2 and at 1 m, 2 m, and 5 m radii was recorded (Martin and Roper 1988). This density was compared with nest success in relation to predation.

We measured shrub densities at 1 m, 2 m, and 5 m radii around each nest and non-use site. Shrubs were defined as woody vegetation >0.50 m in height and with a stem diameter <2 cm (Holway 1991). Effective plant height directly over the nest was measured using a meter tape (Higgins et al. 1994).

Statistical Analyses

We compared percent plant cover and nest characteristics between successful and non-successful nests and nest sites vs. random non-use sites with analysis of variance (SAS Institute, Incorporated 1996). Sources of variation were distributed among main factor effects (site and year) and the interaction terms (site by year). If there were significant interaction terms, main effects were compared separately by each year. We examined relationships between coverage variables and nesting success using a stepwise forward logistic regression model (PROC LOGISTIC; SAS Institute, Inc. 1996). The suitability of this model was tested using the Hosmer-Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 1989), where $P > 0.05$ indicated that the model was a suitable fit.

A detrended correspondence analysis (DCA) was used to find patterns in the coverage of species composition of plants between successful and non-successful nests and nest sites vs. random non-use sites using the program CANOCO (ter Braak 1998);

data were square-root transformed to minimize the effect of potential outliers. The DCA was performed on 85 plant species and 80 nest sites that were analyzed with rare plant species down-weighted.

RESULTS

Vegetation Cover

We analyzed 80 nests of northern bobwhites that were located in 1996–1998 and their respective random sites. A species-by-species analysis of bobwhite nest and random sites yielded few differences (Appendix A and B), respectively. As a result, we summarized vegetation cover in the following categories: bare ground, leaf litter, grasses, forbs, woodies, sedges and legumes. Bobwhites selected nest sites associated with greater coverage of woody and grass vegetation and less coverage of bare ground. In 1996 and 1997, percent cover of grass ($P = 0.001$ and $P = 0.056$) and woody ($P = 0.015$ and $P = 0.023$) vegetation, respectively, was greater at nest sites than at random non-use sites (Table 1). In 1998, woody vegetation was also greater at nest sites than at random non-use sites ($P = 0.017$; Table 1). Coverage of bare ground was 1.6-fold greater in 1996 ($P = 0.003$) and 5-fold greater in 1997 ($P = 0.001$) at random non-use sites than at nest sites (Table 1).

Coverage of plant species generally did not differ between successful and non-successful nest sites. However, in 1996 successful nest sites had less bare ground than non-successful nest sites ($P = 0.001$), but they did not differ in 1997 and 1998 (Table 2). Univariate logistic regression indicated that there was a nearly significant negative relationship between probability of nesting success (P_{ns}) and percent coverage of bare ground ($\chi^2 = 3.01$, *d.f.* = 1, $P = 0.088$; Figure 1).

Results of the detrended correspondence analysis are shown in Figure 2. Due to the small amount of variance explained by axis 3 (eigenvalue = 0.128) and axis 4 (eigenvalue = 0.104), valid biological gradients were difficult to interpret, and as a result, we concentrated only on the first 2 axes. The ordination diagram suggested that low DCA axis 1 scores consisted of plant species closely associated with bare ground and high DCA axis 1 scores consisted of plant species associated with litter. DCA second axis scores were grouped along a disturbance gradient with low disturbance occupying low DCA axis 2 scores and high disturbance occupying high DCA axis 2 scores.

Species cover suggested that bobwhites selected for less disturbed sites associated with an intermediate litter coverage than what was expected from random non-use sites. The DCA revealed no discernable differences between successful and non-successful nest sites. DCA axis 1 mean sample scores were greater at both successful ($\bar{x}$ = 1.48) and non-successful ($\bar{x}$= 1.42) nest sites than at random non-use sites ($\bar{x}$= 1.18), and DCA axis 2 mean sample scores were lower at successful ($\bar{x}$= 0.83) and non-successful ($\bar{x}$ = 0.77) nest sites than at random non-use sites ($\bar{x}$= 0.99) (Table 3). DCA mean sample scores did not differ between successful and non-successful nest sites (Table 4).

Nest Site Characteristics

We found no differences in vegetation characteristics between successful and non-successful nest sites (Table 5). However, nest success was related to nest concealment.

Successful bobwhite nests were less visible than non-successful nests in 1996 ($P = 0.026$) and 1997 ($P = 0.012$) but did not differ in 1998 ($P = 0.536$) (Figure 3).

Bobwhites selected nest sites associated with dense vegetation cover and higher densities of little bluestem. Density of little bluestem at 1 m and visual obstruction estimates (0 – 1 m high) were consistenlty greater at nest sites than at random non-use sites (Table 6). In 1996, little bluestem density within 1 m^2 of nest sites ($\bar{x} = 7.07$) was greater than that of their respective random non-use sites ($\bar{x} = 4.07$; $P < 0.001$), but it did not differ in 1997 and 1998.

DISCUSSION

Nest-site selection can be a critical factor in determining the reproductive success of bobwhites. Individuals that select nest sites in more favorable environments are likely to increase their chances of successful reproduction (Wilson and Cooper 1998). Microhabitat selection is best described by a nonrandom distribution of nest sites within dense vegetation (Gloutney and Clark 1997). Bobwhite nests were consistently associated with greater structural complexity than what was available at random. Badyaev (1995) documented that the eastern Wild Turkey (*Meleagris gallopavo silvestris*) also selected nest sites with greater vegetation complexity. Meseke (1992) documented that nest site selection by bobwhites on Conservation Reserve Program (CRP) fields in Illinois did not differ from random sites. In contrast, our data was collected on native rangeland where landscape composition tends to be more heterogenous (Patten and Ellis 1995; Fuhlendorf and Smeins 1999) than grassland monocultures typically found in CRP fields. As a result, bobwhites in western Oklahoma apparently select nest sites that have a greater coverage of grass and woody vegetation with a relatively low percentage of bare ground. Kopp et al. (1998) documented that bobwhites in Texas avoided areas with < 20% coverage of woody vegetation and that they preferred patches with 20-60% coverage of woody vegetation. Our data, suggests that nest sites associated with 20-30 % woody and 50% grass vegetation may provide bobwhites greater protection from potential predators throughout the breeding season in western Oklahoma. Sites associated with dense vegetation are thought to be less vulnerable to predation (Rands 1988, Filliater et al. 1994) because these sites presumably offer superior cover that helps prevent predation by inhibiting chemical, auditory, or visual clues (Martin and Roper 1988) and protects incubating bobwhites from weather and other disturbances (Colwell 1992, Riley et al. 1992). McKee et al. (1998) found similar results in nest site selection of greater-prairie chicken (*Tympanuchus cupido pinnatus*). They documented litter and woody cover or forb and grass cover to be the best predictors of nest success of greater-prairie chickens.

Unlike McKee et al. (1998), plant cover around bobwhite nest sites was not a predictor of nest success. Wilson and Cooper (1998) found similar results and documented that nest placement was similar between successful and non-successful nests of the Acadian Flycatcher (*Empidonax virescens*). LaHaye et al. (1997) also reported that reproductive success was unrelated to nest-site characteristics in California Spotted Owls (*Strix occidentalis occidentalis*). Martin and Roper (1988) hypothesized that increased density of nest-site foliage (within a habitat patch surrounding the nest) decreases a predators chance of finding the nest. Bobwhite nest sites in western Oklahoma primarily were constructed within patches of little bluestem, but we found that the mean density of little bluestem patches at successful nest sites did not differ from non-successful nest sites.

Estimates of concealment have been documented to be an important component of nest success (Keppie and Herzog 1978, Riley et al. 1992). Bowman and Harris (1980) found spatial heterogeneity (disturbance) to be more important than concealment in reducing nest predation. However, in 1996 and 1997, our results were consistent with Martin and Roper (1988) and Martin (1993b) who found that greater concealment reduced the chance of nest predation in Audubon's Hermit Thrushes (*Catharus gattatus auduboni*). Angelstam (1986) also documented higher predation rates on less concealed artificial ground nests. Riley et al. (1992) documented that greater basal composition and taller plants were associated with successful nest sites of lesser paraire chickens (*Tympanuchus pallidicinctus*) presumably because they provided greater concealment. Increased coverage of bare ground at nests sites appears to predispose nesting bobwhite to greater predation risk, likely because nests associated with a high percentage of bare ground are highly visible to predators. We conclude that concealment may be an important component in bobwhite nest success primarily because bobwhites select nest sites associated with greater structural complexity that inherently maximizes their chance for successful reproduction.

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Table 1. Nest-site selection by northern bobwhites based on percent ground cover of nest and random sites on PWMA, Ellis County Oklahoma, 1996-1998.

Year	Nest			Random			
	Site			Site			
Coverage	n	$\bar{x}$	*SE*	n	$\bar{x}$	*SE*	P
1996							
Bare ground	41	22.79	2.88	41	37.40	4.50	0.003
Leaf Litter	41	11.06	2.22	41	12.66	3.43	0.679
Grasses	41	49.72	2.95	41	32.82	3.35	0.001
Forbs	41	6.36	1.45	41	8.88	2.06	0.365
Woodies	41	19.58	3.05	41	9.55	2.12	0.015
Sedges	41	0.13	0.05	41	0.26	0.10	0.585
Legumes	41	1.15	0.57	41	0.64	0.23	0.294
1997							
Bare ground	21	5.64	2.34	21	28.00	5.12	0.001
Leaf Litter	21	15.03	2.22	21	12.36	3.55	0.623
Grasses	21	49.47	5.15	21	36.33	5.32	0.056
Forbs	21	9.65	2.92	21	13.60	3.08	0.310
Woodies	21	28.63	5.14	21	15.62	3.90	0.023
Sedges	21	0.68	0.63	21	0.01	0.01	0.052
Legumes	21	0.54	0.37	21	0.71	0.34	0.792
1998							
Bare ground	18	14.35	3.22	18	18.44	5.79	0.575
Leaf Litter	18	19.26	4.77	18	15.88	4.24	0.563
Grasses	18	49.78	4.78	18	46.42	6.34	0.648
Forbs	18	6.83	1.41	18	12.10	4.32	0.211
Woodies	18	29.78	4.78	18	15.04	4.00	0.017
Sedges	18	0	0	18	0	0	
Legumes	18	0.04	0.03	18	0.10	0.08	0.939

Table 2. Percent ground cover of successful and non-successful nests sites on PWMA, Ellis County Oklahoma, 1996-1998.

Year	Successful			Non-Successful			
Coverage	*n*	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*	*P*
1996							
Bare ground	23	15.53	2.83	18	32.06	4.72	0.001
Leaf Litter	23	13.23	3.14	18	8.29	3.06	0.288
Grasses	23	53.36	4.62	18	45.07	3.01	0.206
Forbs	23	8.03	2.22	18	4.22	1.62	0.227
Woodies	23	22.76	4.41	18	15.51	3.97	0.274
Sedges	23	0.12	0.05	18	0.14	0.09	0.968
Legumes	23	1.71	0.99	18	0.43	0.23	0.149
1997							
Bare ground	12	8.29	3.94	9	2.11	0.87	0.346
Leaf Litter	12	11.54	2.83	9	19.67	3.07	0.212
Grasses	12	49.33	7.44	9	49.67	7.23	0.971
Forbs	12	12.05	4.94	9	6.44	1.63	0.204
Woodies	12	24.56	6.93	9	34.06	7.72	0.306
Sedges	12	1.11	1.11	9	0.11	0.08	0.136
Legumes	12	0.90	0.64	9	0.06	0.06	0.494
1998							
Bare ground	7	14.18	5.77	11	14.45	4.01	0.969
Leaf Litter	7	27.00	8.99	11	14.34	5.11	0.078
Grasses	7	46.04	8.57	11	52.16	5.84	0.542
Forbs	7	5.54	1.95	11	7.66	1.97	0.660
Woodies	7	30.11	9.12	11	29.57	5.64	0.958
Sedges	7	0	0	11	0	0	
Legumes	7	0.04	0.04	11	0.05	0.05	0.994

Table 3. DCA mean sample scores of successful and non-successful nest sites vs. their random non-use sites at PWMA, Ellis county Oklahoma, 1996-1998 (all data pooled).

Nest Success		Nest Site			Random Site			
DCA Axis	Eigenvalue	*n*	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*	*P*
Successful								
Axis 1	0.276	42	1.48	0.08	80	1.18	0.07	0.010
Axis 2	0.230	42	0.83	0.07	80	0.99	0.05	0.060
Axis 3	0.128	42	1.27	0.05	80	1.22	0.04	0.485
Axis 4	0.104	42	1.05	0.03	80	1.07	0.04	0.729
Non-Successful								
Axis 1	0.276	38	1.42	0.10	80	1.18	0.07	0.051
Axis 2	0.230	38	0.77	0.08	80	0.99	0.05	0.016
Axis 3	0.128	38	1.32	0.05	80	1.22	0.04	0.158
Axis 4	0.104	38	1.09	0.03	80	1.07	0.04	0.744

Table 4. DCA mean sample scores of bobwhite successful and non-successful nest sites at PWMA, Ellis county Oklahoma, 1996-1998 (all data pooled).

DCA		Successful			Non-Successful			
Axis	Eigenvalue	*n*	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*	*P*
Axis 1	0.276	42	1.48	0.08	38	1.42	0.10	0.629
Axis 2	0.230	42	0.83	0.07	38	0.77	0.08	0.595
Axis 3	0.128	42	1.27	0.05	38	1.32	0.05	0.514
Axis 4	0.104	42	1.05	0.03	38	1.09	0.03	0.561

Table 5. Comparison of vegetation characteristics between successful and non-successful bobwhite nest sites at PWMA, Ellis County Oklahoma, 1996-1998.

	Successful			Non-Successful			
Characteristic	n	$\bar{x}$	SE	n	$\bar{x}$	SE	P
Shrub Stem Count, 1 m	42	36.52	5.39	38	42.84	6.00	0.575
Shrub Stem Count, 2 m	42	102.81	15.72	38	83.39	12.41	0.467
Shrub Stem Count, 5 m	42	244.74	34.51	38	211.55	29.34	0.662
Little Bluestem Patch, 1 m	42	12.98	0.91	38	11.05	0.82	0.298
Little Bluestem Patch, 2 m	42	23.98	1.70	38	20.71	1.61	0.286
Little Bluestem Patch, 5 m	42	48.62	3.65	38	43.63	3.28	0.494
Cover Board, 0-0.25 m	42	66.96	1.43	38	64.74	1.73	0.657
Cover Board, 0.25-0.50 m	42	49.77	2.79	38	42.91	3.57	0.227
Cover Board, 0.50-1.00 m	42	32.39	3.27	38	27.34	4.04	0.453
Cover Board, 1.00-2.00 m	42	7.43	2.55	38	8.75	2.38	0.816
Total Height	41	850.12	40.64	37	831.89	25.11	0.737
Clump Width	41	802.98	52.92	37	790.00	47.27	0.815
Clump Length	41	677.54	49.45	37	667.03	34.28	0.847
Bowl Width	42	145.17	14.90	38	121.71	1.88	0.337
Bowl Length	42	143.29	12.52	38	123.62	2.50	0.372
Depth Dome	40	89.22	5.43	35	85.66	7.32	0.542
Depth Bowl	33	54.59	3.61	32	49.76	3.81	0.368
Lining Thickness	42	48.91	2.23	37	48.16	1.84	0.550

Table 6. Nest site selection based on a comparison of vegetation characteristics of bobwhite nest sites and their respective random sites on PWMA, Ellis County Oklahoma, 1996-1998.

Nest Success	Nest Site			Random Site			
Characteristic	*n*	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*	*P*
Successful Nests							
Shrub Stem Count, 1 m	80	39.53	4.01	80	34.43	3.85	0.336
Shrub Stem Count, 2 m	80	93.59	10.14	80	71.45	7.13	0.142
Shrub Stem Count, 5 m	80	228.98	22.80	80	172.16	17.20	0.064
Little Bluestem Patch, 1 m	80	12.06	0.62	80	9.83	0.64	0.036
Little Bluestem Patch, 2 m	80	22.43	1.18	80	19.24	1.12	0.140
Little Bluestem Patch, 5 m	80	46.25	2.47	80	43.61	2.78	0.828
Cover Board, 0-0.25 m	80	65.90	1.11	80	58.15	2.01	0.005
Cover Board, 0.25-0.50 m	80	46.51	2.26	80	34.23	2.21	0.001
Cover Board, 0.50-1.00 m	80	29.99	2.57	80	17.59	1.77	0.001
Cover Board, 1.00-2.00 m	80	8.06	1.74	80	4.84	1.13	0.285

Figure 1. Relationships between percent coverage of bare ground and probability of nest success (Pns) at PWMA, Ellis County, Oklahoma. Values calculated from probability equations derived from univariate logistic regression models ($P = 0.088$).

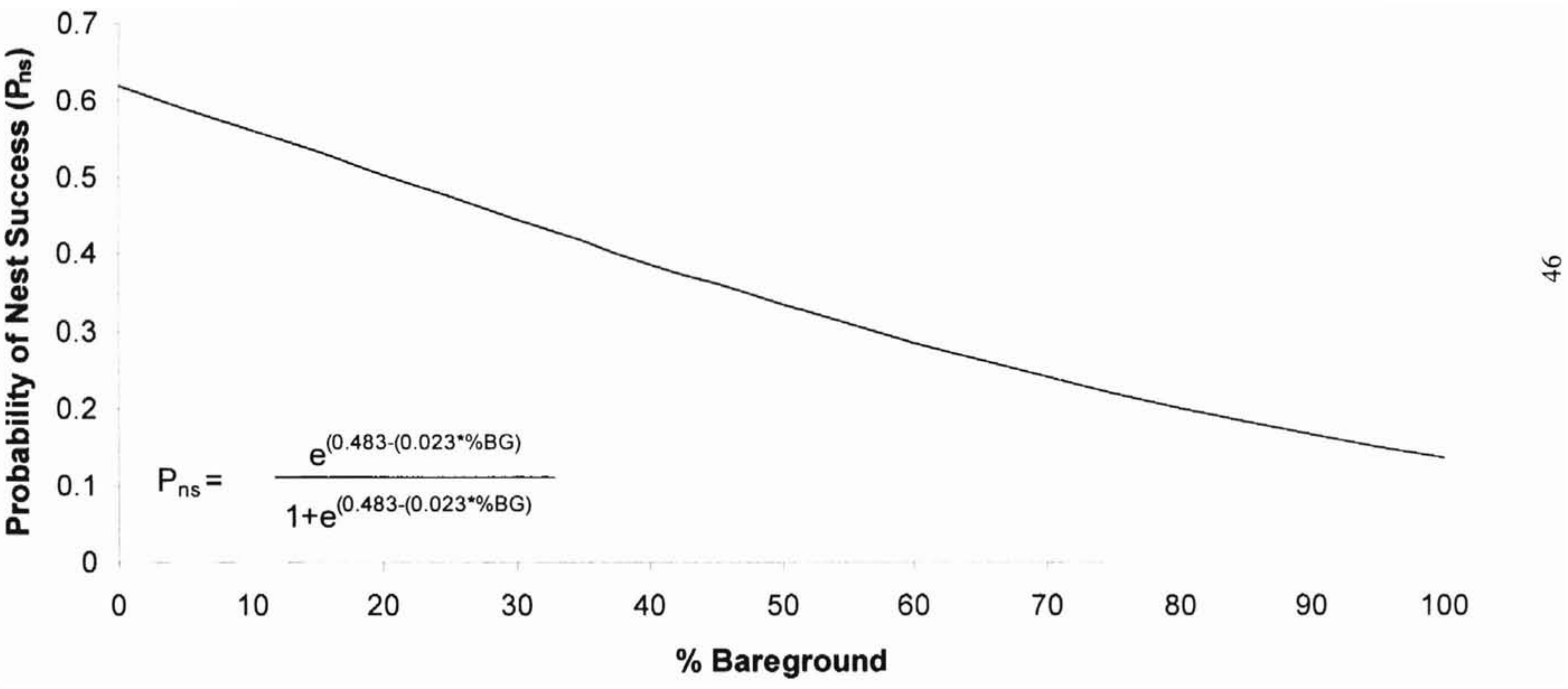

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Probability of Nest Success (P_{ns})
$P_{ns} = \frac{e^{(0.483-(0.023*\%BG)}}{1+e^{(0.483-(0.023*\%BG)}}$
0
10
20
30
40
50
60
70
80
90
100
% Bareground

Figure 2. Results of a detrended correspondence analysis of 85 plant species from 81 individual bobwhite nest sites and their corresponding random sites at PWMA, Ellis County Oklahoma, 1996-1998 (all data pooled). Species scores have a minimum weight of 1.

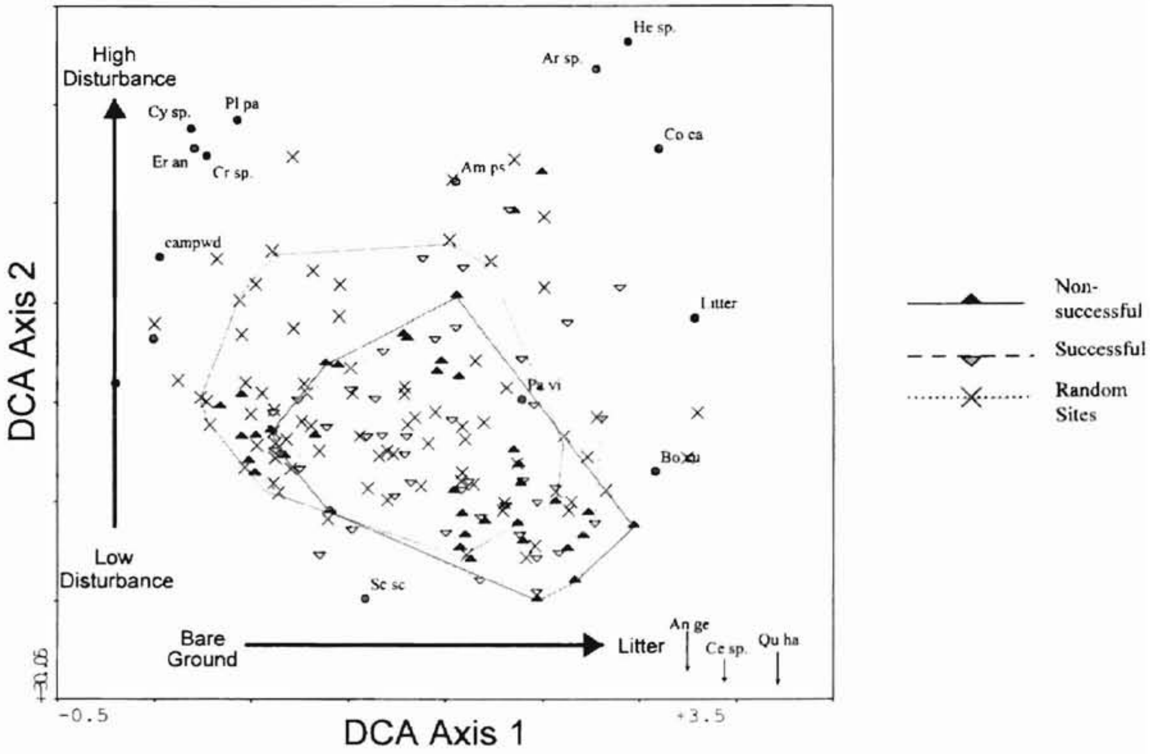
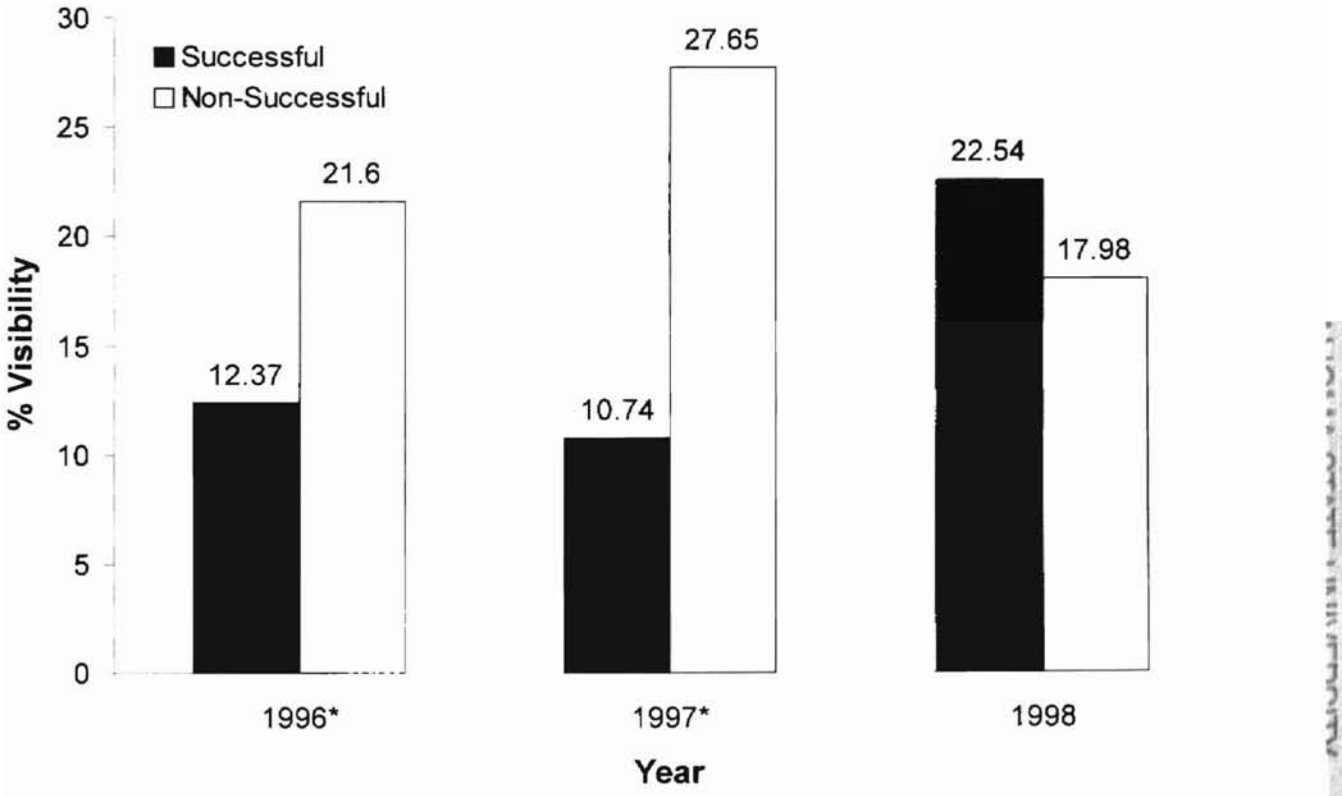

He sp.
Ar sp.
High Disturbance
Cy sp.
Pl pa
Er an
Cr sp.
Co ca
Am ps
campwd
Litter
Pa vi
Bo cu
Low Disturbance
Sc sc
Bare Ground
Litter
An ge
Ce sp.
Qu ha
DCA Axis 2
-0.05
-0.5
+3.5
DCA Axis 1
Non-successful
Successful
Random Sites

Figure 3. Mean estimates of nest concealment for successful and non-successful bobwhite nest sites at PWMA, Ellis County, Oklahoma, 1996-1998 ($* = P < 0.05$).



30
25
20
15
10
5
0
% Visibility
■ Successful
☐ Non-Successful
12.37
21.6
10.74
27.65
22.54
17.98
1996*
1997*
1998
Year

Appendix A. Comparison of percent cover by species of successful and non-successful bobwhite nest sites vs their respective random sites on PWMA, Ellis County, Oklahoma 1996-1998.

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Successful Nests 1996							
Bare Ground	23	15.53	2.83	23	30.23	6.17	0.035
Leaf Litter	23	13.22	3.14	23	16.33	4.38	0.566
Schizachyrium scoparium	23	47.02	4.85	23	24.01	3.76	<0.001
Andropogon gerrardii	23	0.61	0.42	23	0.66	0.60	0.922
Paspalum sp.	23	2.20	0.55	23	2.59	1.41	0.762
Panicum virgatum	23	1.20	0.56	23	2.11	0.77	0.206
Ambrosia psilostachya	23	3.25	1.33	23	3.33	1.54	0.968
Eriogonum annuum	23	0.14	0.08	23	0.23	0.18	0.821
Bouteloua curtipendula	23	0.42	0.21	23	0.26	0.20	0.477
Croton sp.	23	0.05	0.05	23	0.07	0.07	0.969
Cyperus sp.	23	0.12	0.05	23	0.36	0.15	0.111
Plantago patagonica	23	0.01	0.01	23	0.41	0.27	0.651
Quercus havardii	23	10.45	2.37	23	10.51	3.08	0.986
Artemisia sp.	23	11.54	4.33	23	1.18	0.97	0.004

Appendix A. Continued.

Nest Success	Nest Site			Random Site			
Year	n	$\bar{x}$	SE	n	$\bar{x}$	SE	P
Celtis sp.	23	0.48	0.46	23	0.38	0.25	0.847
Heterotheca sp.	23	0.27	0.15	23	0.08	0.07	0.149
Conyza Canadensis	23	0	0	23	0	0	0
1997							
Bare Ground	12	8.29	3.94	12	24.60	6.69	0.036
Leaf Litter	12	11.54	2.83	12	9.63	4.08	0.728
Schizachyrium scoparium	12	45.00	8.29	12	35.65	8.05	0.354
Andropogon gerrardii	12	0.17	0.15	12	0.27	0.25	0.964
Paspalum sp.	12	0.15	0.13	12	0.90	0.52	0.308
Panicum virgatum	12	0.37	0.20	12	0	0	0.865
Ambrosia psilostachya	12	6.29	2.75	12	4.79	1.77	0.589
Eriogonum annuum	12	0.13	0.13	12	0.08	0.05	0.785
Bouteloua curtipendula	12	2.77	2.77	12	0	0	0.197
Croton sp.	12	0	0	12	0	0	0
Cyperus sp.	12	1.11	1.11	12	0	0	0.197
Plantago patagonica	12	0.06	0.03	12	0.71	0.35	0.493
Quercus havardii	12	13.81	5.63	12	11.17	4.80	0.724
Artemisia sp.	12	7.98	4.34	12	4.21	3.92	0.532
Celtis sp.	12	2.77	2.64	12	0.46	0.46	0.487

Appendix A. Continued.

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*P*
Heterotheca sp.	12	0.44	0.44	12	0	0	0.224
Conyza Canadensis	12	0.04	0.03	12	0.83	0.41	0.500
1998							
Bare Ground	7	14.18	5.77	7	14.50	11.58	0.977
Leaf Litter	7	27.00	8.99	7	21.50	9.02	0.590
Schizachyrium scoparium	7	33.61	7.65	7	27.54	9.07	0.603
Andropogon gerrardii	7	0.04	00.04	7	0.07	0.07	0.955
Paspalum sp.	7	0	0	7	0.04	0.04	0.881
Panicum virgatum	7	0	0	7	0	0	0
Ambrosia psilostachya	7	3.36	1.79	7	6.04	3.01	0.406
Eriogonum annuum	7	0.21	0.21	7	0	0	0.348
Bouteloua curtipendula	7	0	0	7	0	0	0
Croton sp.	7	0	0	7	0	0	0
Cyperus sp.	7	0	0	7	0	0	0
Plantago patagonica	7	0.64	0.53	7	0	0	0.906
Quercus havardii	7	23.18	6.12	7	17.07	6.86	0.510
Artemisia sp.	7	2.11	1.87	7	0.43	0.43	0.738
Celtis sp.	7	0	0	7	0.46	0.46	0.780
Heterotheca sp.	7	0.25	0.21	7	0.04	0.04	0.156

Appendix A. Continued.

Nest Success	Nest Site			Random Site			
Year	n	$\bar{x}$	SE	n	$\bar{x}$	SE	P
Conyza Canadensis	7	0.50	0.33	7	0.04	0.04	0.428
Non-Successful Nests 1996							
Bare Ground	18	33.87	4.82	18	47.93	5.91	0.066
Leaf Litter	18	7.86	2.93	18	7.57	5.12	0.961
Schizachyrium scoparium	18	38.72	3.29	18	22.33	4.61	0.011
Andropogon gerrardii	18	0.05	0.05	18	0.22	0.16	0.779
Paspalum sp.	18	1.36	0.37	18	3.55	0.98	0.126
Panicum virgatum	18	0.34	0.19	18	0.09	0.09	0.752
Ambrosia psilostachya	18	0.91	0.63	18	3.95	1.70	0.144
Eriogonum annuum	18	0.72	0.52	18	0.37	0.28	0.404
Bouteloua curtipendula	18	0	0	18	0.12	0.12	0.639
Croton sp.	18	0.08	0.08	18	0.47	0.43	0.198
Cyperus sp.	18	0.13	0.08	18	0.13	0.12	1.000
Plantago patagonica	18	0.13	0.13	18	0.03	0.02	0.658
Quercus havardii	18	9.71	3.43	18	4.67	1.78	0.222
Artemisia sp.	18	4.28	1.99	18	0.20	0.16	0.294
Celtis sp.	18	0.79	0.49	18	0.20	0.20	0.289
Heterotheca sp.	18	0.13	0.08	18	0.03	0.03	0.478

Appendix A. Continued.

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Conyza Canadensis	18	0	0	18	0	0	0
1997							
Bare Ground	9	2.11	0.87	9	32.53	8.16	0.001
Leaf Litter	9	19.67	3.07	9	16.000	6.34	0.565
Schizachyrium scoparium	9	38.72	7.38	9	19.03	3.96	0.095
Andropogon gerrardii	9	6.00	3.64	9	2.72	1.71	0.220
Paspalum sp.	9	0.61	0.52	9	2.33	0.93	0.046
Panicum virgatum	9	2.11	1.39	9	3.94	3.54	0.464
Ambrosia psilostachya	9	2.00	1.11	9	2.94	1.75	0.768
Eriogonum annuum	9	0.03	0.03	9	0.31	0.20	0.121
Bouteloua curtipendula	9	00.33	0.22	9	0	0	0.892
Croton sp.	9	0	0	9	0.03	0.03	0.132
Cyperus sp.	9	0.11	0.08	9	0.03	0.03	0.933
Plantago patagonica	9	0.28	0.20	9	2.61	1.58	0.037
Quercus havardii	9	21.36	6.92	9	8.11	5.20	0.131
Artemisia sp.	9	7.69	5.71	9	6.58	4.21	0.873
Celtis sp.	9	4.97	4.61	9	0.06	0.06	0.204
Heterotheca sp.	9	0.06	0.06	9	1.39	1.36	0.597
Conyza canadensis	9	2.03	1.30	9	2.39	1.51	0.789

Appendix A. Continued.

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
1998							
Bare Ground	11	14.45	4.01	11	20.95	6.36	0.459
Leaf Litter	11	14.34	5.11	11	12.30	3.97	0.801
Schizachyrium scoparium	11	50.84	5.81	11	44.05	6.93	0.466
Andropogon gerrardii	11	0.66	0.32	11	0.89	0.54	0.652
Paspalum sp.	11	0.05	0.03	11	0.45	0.24	0.038
Panicum virgatum	11	0	0	11	0.18	0.14	0.109
Ambrosia psilostachya	11	4.59	1.33	11	7.27	1.96	0.298
Eriogonum annuum	11	0.18	0.18	11	0.05	0.03	0.453
Bouteloua curtipendula	11	1.57	1.57	11	0.16	0.16	0.267
Croton sp.	11	0.14	0.14	11	0	0	0.215
Cyperus sp.	11	0	0	11	0	0	0
Plantago patagonica	11	0.02	0.02	11	5.66	5.41	0.198
Quercus havardii	11	21.39	6.43	11	7.41	3.43	0.065
Artemisia sp.	11	8.18	4.30	11	3.98	2.28	0.297
Celtis sp.	11	0	0	11	1.64	1.64	0.222
Heterotheca sp.	11	0.05	0.05	11	0.09	0.05	0.702
Conyza Canadensis	11	0.05	0.05	11	0.55	0.55	0.287

Appendix B. Comparison of percent cover by species for successful and non-successful bobwhite nest sites on PWMA, Ellis County, Oklahoma 1996-1997.

Year	Successful			Non-successful			
Species	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
1996							
Bare Ground	23	15.53	2.83	18	33.87	4.82	0.013
Leaf Litter	23	13.22	3.14	18	7.86	2.93	0.345
Schizachyrium scoparium	23	47.02	4.85	18	38.72	3.29	0.171
Andropogon gerrardii	23	0.61	0.42	18	0.05	0.05	0.342
Paspalum sp.	23	2.20	0.55	18	1.36	0.37	0.537
Panicum virgatum	23	1.20	0.56	18	0.34	0.19	0.261
Ambrosia psilostachya	23	3.25	1.33	18	0.91	0.63	0.238
Eriogonum annuum	23	0.14	0.08	18	0.72	0.52	0.154
Bouteloua curtipendula	23	0.42	0.21	18	0	0	0.081
Croton sp.	23	0.05	0.05	18	0.08	0.08	0.933
Cyperus sp.	23	0.12	0.05	18	0.13	0.08	0.939
Plantago patagonica	23	0.01	0.01	18	0.13	0.13	0.595
Quercus havardii	23	10.45	2.37	18	9.71	3.43	0.851
Artemisia sp.	23	11.54	4.33	18	4.28	1.99	0.053
Celtis sp.	23	0.48	0.46	18	0.79	0.49	0.558
Heterotheca sp.	23	0.27	0.15	18	0.13	0.08	0.324

Appendix B. Continued

Year	Successful			Non-successful			
Species	n	$\bar{X}$	SE	n	$\bar{X}$	SE	P
Conyza Canadensis	23	0	0	18	0	0	0
1997							
Bare Ground	12	8.29	3.94	9	2.11	0.87	0.450
Leaf Litter	12	11.54	2.83	9	19.67	3.07	0.177
Schizachyrium scoparium	12	45.00	8.29	9	38.72	7.38	0.563
Andropogon gerrardii	12	0.17	0.15	9	6.00	3.64	0.023
Paspalum sp.	12	0.15	0.13	9	0.61	0.52	0.557
Panicum virgatum	12	0.37	0.20	9	2.11	1.39	0.457
Ambrosia psilostachya	12	6.29	2.75	9	2.00	1.11	0.157
Eriogonum annuum	12	0.13	0.13	9	0.03	0.03	0.557
Bouteloua curtipendula	12	2.77	2.77	9	0.33	0.22	0.292
Croton sp.	12	0	0	9	0	0	0
Cyperus sp.	12	1.11	1.11	9	0.11	0.08	0.281
Plantago patagonica	12	0.06	0.03	9	0.28	0.20	0.832
Quercus havardii	12	13.81	5.63	9	21.36	6.92	0.354
Artemisia sp.	12	7.98	4.34	9	7.69	5.71	0.965
Celtis sp.	12	2.77	2.64	9	4.97	4.61	0.540
Heterotheca sp.	12	0.44	0.44	9	0.06	0.06	0.203

Appendix B. Continued

Year	Successful			Non-successful			
Species	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Conyza Canadensis	12	0.04	0.03	9	2.03	1.30	0.122
1998							
Bare Ground	7	14.18	5.77	11	14.45	4.01	0.978
Leaf Litter	7	27.00	8.99	11	14.34	5.11	0.175
Schizachyrium scoparium	7	33.61	7.65	11	50.84	5.81	0.109
Andropogon gerrardii	7	0.04	0.04	11	0.66	0.32	0.278
Paspalum sp.	7	0	0	11	0.05	0.03	0.833
Panicum virgatum	7	0	0	11	0	0	0
Ambrosia psilostachya	7	3.36	1.79	11	4.59	1.33	0.671
Eriogonum annuum	7	0.21	0.21	11	0.18	0.18	0.874
Bouteloua curtipendula	7	0	0	11	1.57	1.57	0.275
Croton sp.	7	0	0	11	0.14	0.14	0.273
Cyperus sp.	7	0	0	11	0	0	0
Plantago patagonica	7	0.64	0.53	11	0.02	0.02	0.899
Quercus havardii	7	23.18	6.12	11	21.39	6.43	0.830
Artemisia sp.	7	2.11	1.87	11	8.18	4.30	0.186
Celtis sp.	7	0	0	11	0	0	0
Heterotheca sp.	7	0.25	0.21	11	0.05	0.05	0.135
Conyza Canadensis	7	0.50	0.33	11	0.05	0.05	0.392

Appendix C. Comparison of nest vegetation characteristics of successful and non-successful bobwhite nest sites vs. their respective random sites on PWMA, Ellis County Oklahoma, 1996-1998.

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Successful Nests							
1996							
Shr1	23	32.96	6.13	23	40	8.25	0.456
Shr2	23	112.22	23.91	23	86.91	15.32	0.307
Shr5	23	256.48	51.18	23	207.57	35.03	0.342
Topwdth (cm)	23	15.99	2.69	0	.	.	.
Toplngth (cm)	23	15.53	2.26	0	.	.	.
Dpthdme (cm)	22	10.36	0.78	0	.	.	.
Dpthbwl (cm)	15	6.76	0.49	0	.	.	.
Linthick (cm)	23	4.68	0.33	0	.	.	.
Asdwn	23	186.83	18.33	23	170.39	22.33	0.605
Asnest	23	153.22	18.94	0	.	.	.
Slope	23	4.78	1.03	23	4.48	0.93	0.884
Totalht (cm)	23	85.71	6.05	0	.	.	.
Clumpwth (cm)	23	73.53	7.39	0	.	.	.
Clumplth (cm)	23	65.91	7.23	0	.	.	.
Lbp1	23	14.65	1.37	23	11.17	1.36	0.072
Lbp2	23	26.74	2.26	23	21	2.34	0.087
Lbp5	23	54.83	5.25	23	48.17	4.87	0.326
Lbpm2	23	7.09	0.73	23	3.78	0.64	<0.001
Nconceal	23	12.37	1.43	23	80.77	3.53	<0.001

Appendix C. Continued

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Cba25	23	66.57	1.79	23	59.63	3.83	0.143
Cba50	23	51.19	3.55	23	36.91	4.22	0.018
Cba10	23	37.50	4.81	23	21.78	3.44	0.016
Cba20	23	8.47	2.81	23	4.86	1.52	0.366
Noeggs	23	12.30	0.63	0	.	.	.
Nohtched	23	11.30	0.59	0	.	.	.
Orgcnt	17	13.18	0.66	0	.	.	.
1997							
Shr1	12	31.75	10.03	12	32.42	10.40	0.966
Shr2	12	81.17	25.14	12	70.33	21.21	0.728
Shr5	12	199.33	51.28	12	170.42	49.43	0.703
Topwdth (cm)	12	12.65	0.47	0	.	.	.
Toplngth (cm)	12	13.05	0.42	0	.	.	.
Dpthdme (cm)	12	6.91	0.64	0	.	.	.
Dpthbwl (cm)	11	4.70	0.50	0	.	.	.
Linthick (cm)	12	5.01	0.33	0	.	.	.
Asdwn	12	158.92	30.79	11	163.36	34.11	0.918
Asnest	12	173.75	30.68	0	.	.	.
Slope	12	6.25	1.16	11	5.73	0.96	0.814
Totalht (cm)	11	80.54	7.11	0	.	.	.
Clumpwth (cm)	11	94.55	9.93	0	.	.	.
Clumplth (cm)	11	73.09	8.81	0	.	.	.
Lbp1	12	11	1.34	12	7.42	1.44	0.056
Lbp2	12	20.58	3.57	12	16.17	3.47	0.305
Lbp5	12	39.67	6.61	12	38.33	7.09	0.868

Appendix C. Continued

Nest Success		Nest Site			Random Site		
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Lbpm2	12	4.83	0.84	12	4.08	1.03	0.487
Nconceal	12	10.74	3.43	12	82.59	4.46	<0.001
Cba25	12	70.22	1.33	12	60.35	4.8	0.057
Cba50	12	51.55	4.09	12	34.51	5.86	0.039
Cba10	12	28.77	4.83	12	12.52	3.81	0.017
Cba20	12	1.77	0.35	12	2.03	0.78	0.884
Noeggs	12	11.08	1.15	0	.	.	.
Nohtched	12	10.67	1.04	0	.	.	.
Orgcnt	9	12.89	0.93	0	.	.	.
1998							
Shr1	7	56.43	18.51	7	50.86	19.39	0.786
Shr2	7	109	32.74	7	96.86	36.37	0.752
Shr5	7	284	89.94	7	238.86	95.4	0.661
Topwdth (cm)	7	12.84	0.40	0	.	.	.
Toplngth (cm)	7	12.59	0.59	0	.	.	.
Dpthdme (cm)	6	7.66	0.88	0	.	.	.
Dpthbwl (cm)	7	3.85	0.43	0	.	.	.
Linthick (cm)	7	5.37	0.53	0	.	.	.
Asdwn	4	105	23.1	3	126.67	11.32	0.778
Asnest	7	136.29	37.54	0	.	.	.
Slope	7	1.29	0.61	7	1.14	0.63	0.995
Totalht (cm)	7	89.71	7.90	0	.	.	.
Clumpwth (cm)	7	80.14	9.95	0	.	.	.
Clumplth (cm)	7	65.43	10.55	0	.	.	.
Lbp1	7	10.86	1.53	7	9.29	1.78	0.460

Appendix C. Continued

Nest Success	Nest	Site		Random	Site		
Year	n	$\bar{x}$	SE	n	$\bar{x}$	SE	P
Lbp2	7	20.71	2.69	7	18.29	3.43	0.514
Lbp5	7	43.57	5.24	7	40.00	5.7	0.806
Lbpm2	7	4.00	0.53	7	3.71	0.84	0.793
Nconceal	7	22.54	2.24	7	87.62	8.28	<0.001
Cba25	7	62.64	5.8	7	60.79	6.69	0.809
Cba50	7	42.04	10.16	7	40.88	9.19	0.921
Cba10	7	21.81	7.12	7	15.73	5.82	0.540
Cba20	7	13.71	12.46	7	9.89	8.64	0.691
Noeggs	7	12	0.79	0	.	.	.
Nohtched	7	9.86	1.75	0	.	.	.
Orgcnt	7	12	0.79	0	.	.	.
Non-Successful Nests							
1996							
Shr1	18	36.28	7.87	18	19.78	4.75	0.125
Shr2	18	73.83	19.09	18	43.50	8.78	0.279
Shr5	18	155.89	31.2	18	93.50	18.44	0.284
Topwdth (cm)	18	12.31	0.23	0	.	.	.
Toplngth (cm)	18	12.35	0.28	0	.	.	.
Dpthdme (cm)	17	11.05	1.17	0	.	.	.
Dpthbwl (cm)	13	6.93	0.49	0	.	.	.
Linthick (cm)	17	4.85	0.33	0	.	.	.
Asdwn	18	153.39	26.87	18	146.67	28.78	0.851
Asnest	18	232.72	24.44	0	.	.	.
Slope	18	4.11	0.92	18	7.56	2.93	0.146
Totalht (cm)	17	84.29	2.61	0	.	.	.

Appendix C. Continued

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Clumpwth (cm)	17	73.71	5.47	0	.	.	.
Clumplth (cm)	17	55.05	4.31	0	.	.	.
Lbp1	18	11.56	1.48	18	9.39	1.51	0.317
Lbp2	18	22.5	2.87	18	18.78	2.54	0.324
Lbp5	18	46.67	5.01	18	38.56	4.77	0.290
Lbpm2	18	7.06	0.55	18	4.44	0.700	0.012
Nconceal	18	21.6	3.47	18	94.94	2.56	<0.001
Cba25	18	64.23	3.13	18	51.46	4.98	0.018
Cba50	18	45.52	5.7	18	29.7	4.41	0.020
Cba10	18	34.11	6.41	18	19.15	4.51	0.041
Cba20	18	14.67	4.52	18	6.5	2.97	0.072
Noeggs	18	1.22	0.77	0	.	.	.
Nohtched	18	0	0	0	.	.	.
Orgcnt	14	12.07	0.65	0	.	.	.
1997							
Shr1	9	57.78	17.64	9	39	8.96	0.305
Shr2	9	106.67	31.01	9	62.78	9.15	0.227
Shr5	9	280.33	90.75	9	158.11	19.16	0.167
Topwdth (cm)	9	12.52	0.47	0	.	.	.
Toplngth (cm)	9	13.09	0.46	0	.	.	.
Dpthdme (cm)	7	5.81	0.51	0	.	.	.
Dpthbwl (cm)	8	3.65	0.25	0	.	.	.
Linthick (cm)	9	5.19	0.28	0	.	.	.
Asdwn	9	131	33.51	9	147.89	27.44	0.729
Asnest	9	228.56	33.05	0	.	.	.

Appendix C. Continued

Nest Success	Nest	Site		Random	Site		
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Slope	9	7.11	2.35	9	6.56	2.24	0.825
Totalht (cm)	9	92.44	4.61	0	.	.	.
Clumpwth (cm)	9	95.44	13.57	0	.	.	.
Clumplth (cm)	9	76.33	7.19	0	.	.	.
Lbp1	9	8.22	1.1	9	8.44	1.46	0.916
Lbp2	9	15.67	2.3	9	16.78	2.51	0.822
Lbp5	9	30.67	3	9	34.33	4.34	0.692
Lbpm2	9	3.89	0.48	9	3.11	0.39	0.532
Nconceal	9	27.65	5.46	9	88.64	4.88	<0.001
Cba25	9	65.56	3.04	9	63.99	4.99	0.787
Cba50	9	42.35	7.28	9	33.32	7.38	0.332
Cba10	9	25.36	7.14	9	16.28	3.78	0.235
Cba20	9	4.7	2.39	9	3.31	1.71	0.502
Noeggs	9	3.33	1.82	0	.	.	.
Nohtched	9	0	0	0	.	.	.
Orgcnt	7	12.43	0.95	0	.	.	.
1998							
Shr1	11	41.36	7.66	11	34.73	9.48	0.686
Shr2	11	80	16.27	11	77	17.34	0.922
Shr5	11	246.36	43.52	11	197.82	45.93	0.555
Topwdth (cm)	11	11.66	0.33	0	.	.	.
Toplngth (cm)	11	11.78	0.60	0	.	.	.
Dpthdme (cm)	11	6.48	0.67	0	.	.	.
Dpthbwl (cm)	11	3.62	0.40	0	.	.	.
Linthick (cm)	11	4.44	0.25	0	.	.	.

Appendix C. Continued

Nest Success	Nest Site			Random Site			
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Asdwn	9	171	40.63	10	203.5	31.82	0.484
Asnest	11	200.91	28.67	0	.	.	.
Slope	11	29.64	23.58	11	4.82	0.96	0.193
Totalht (cm)	11	73.91	5.45	0	.	.	.
Clumpwth (cm)	11	73.72	6.84	0	.	.	.
Clumplth (cm)	11	76.82	4.86	0	.	.	.
Lbp1	11	12.55	0.87	11	11.82	1.28	0.667
Lbp2	11	21.91	2.02	11	22.27	1.57	0.902
Lbp5	11	49.27	6.57	11	58	12.1	0.455
Lbpm2	11	4.91	0.41	11	5.45	0.8	0.532
Nconceal	11	17.98	4.23	11	87.47	4.49	<0.001
Cba25	11	64.9	2.21	11	57.13	4.88	0.209
Cba50	11	39.08	5.95	11	32.28	5.34	0.465
Cba10	11	17.89	6.62	11	14.05	4.68	0.628
Cba20	11	2.39	0.87	11	3.16	1.91	0.919
Noeggs	7	5.71	2.1	0	.	.	.
Nohtched	11	0	0	0	.	.	.
Orgcnt	6	10	1.57	0	.	.	.

Appendix D. Comparison of nest vegetation characteristics of successful and non-successful bobwhite nest sites on PWMA, Ellis County Oklahoma, 1996-1998.

Year	Successful			Non-successful			
Species	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
1996							
Shr1	23	32.96	6.13	18	36.28	7.87	0.742
Shr2	23	112.22	23.91	18	73.83	19.09	0.148
Shr5	23	256.48	51.18	18	155.89	31.2	0.069
Topwdth (cm)	23	15.99	2.69	18	12.31	0.23	0.235
Toplngth (cm)	23	15.53	2.26	18	12.35	0.28	0.225
Dpthdme (cm)	22	10.36	0.78	17	11.05	1.17	0.615
Dpthbwl (cm)	15	6.76	0.49	13	6.93	0.49	0.815
Linthick (cm)	23	4.68	0.33	17	4.85	0.33	0.721
Asdwn	23	186.83	18.33	18	153.39	26.87	0.325
Asnest	23	153.22	18.94	18	232.72	24.44	0.013
Slope	23	4.78	1.03	18	4.11	0.92	0.763
Totalht (cm)	23	85.71	6.05	17	84.29	2.61	0.849
Clumpwth (cm)	23	73.53	7.39	17	73.70	5.47	0.986
Clumplth (cm)	23	65.91	7.23	17	55.05	4.32	0.246
Lbp1	23	14.65	1.37	18	11.56	1.48	0.132
Lbp2	23	26.74	2.26	18	22.5	2.87	0.235
Lbp5	23	54.83	5.25	18	46.67	5.01	0.259
Lbpm2	23	7.09	0.73	18	7.06	0.55	0.974
Nconceal	23	12.37	1.43	18	21.6	3.47	0.026
Cba25	23	66.57	1.79	18	64.23	3.13	0.641
Cba50	23	51.19	3.55	18	45.52	5.7	0.371

Appendix D. Continued

Year Species	Successful *n*	 $\bar{x}$	 SE	Non-successful *n*	 $\bar{x}$	 SE	 *P*
Cba10	23	37.50	4.81	18	34.11	6.41	0.620
Cba20	23	8.47	2.81	18	14.67	4.52	0.147
Noeggs	23	12.30	0.63	18	1.22	0.77	<0.001
Nohtched	23	11.30	0.59	18	0	0	<0.001
Orgcnt	17	13.18	0.66	14	12.07	0.65	0.248
1997							
Shr1	12	31.75	10.03	9	57.78	17.64	0.132
Shr2	12	81.17	25.14	9	106.67	31.01	0.450
Shr5	12	199.33	51.28	9	280.33	90.75	0.325
Topwdth (cm)	12	12.65	0.47	9	12.52	0.47	0.842
Toplngth (cm)	12	13.05	0.42	9	13.09	0.46	0.947
Dpthdme (cm)	12	6.91	0.64	7	5.81	0.51	0.254
Dpthbwl (cm)	11	4.70	0.50	8	3.65	0.25	0.117
Linthick (cm)	12	5.01	0.33	9	5.19	0.28	0.699
Asdwn	12	158.92	30.79	9	131	33.51	0.540
Asnest	12	173.75	30.68	9	228.56	33.05	0.244
Slope	12	6.25	1.16	9	7.11	2.35	0.714
Totalht (cm)	11	80.54	7.11	9	92.44	4.61	0.199
Clumpwth (cm)	11	94.55	9.93	9	95.44	13.57	0.957
Clumplth (cm)	11	73.09	8.81	9	76.33	7.19	0.785
Lbp1	12	11	1.34	9	8.22	1.1	0.165
Lbp2	12	20.58	3.57	9	15.67	2.3	0.291
Lbp5	12	39.67	6.61	9	30.67	3	0.301
Lbpm2	12	4.83	0.84	9	3.89	0.48	0.418
Nconceal	12	10.74	3.43	9	27.65	5.46	0.012

Appendix D. Continued

Year	Successful			Non-successful			
Species	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Cba25	12	70.22	1.33	9	65.56	3.04	0.396
Cba50	12	51.55	4.09	9	42.35	7.28	0.292
Cba10	12	28.77	4.83	9	25.36	7.14	0.631
Cba20	12	1.77	0.35	9	4.7	2.39	0.135
Noeggs	12	11.08	1.15	9	3.33	1.82	0.001
Nohtched	12	10.67	1.04	9	0	0	<0.001
Orgcnt	9	12.89	0.93	7	12.43	0.95	0.738
1998							
Shr1	7	56.43	18.51	11	41.36	7.66	0.420
Shr2	7	109	32.74	11	80	16.27	0.407
Shr5	7	284	89.94	11	246.36	43.52	0.686
Topwdth (cm)	7	12.84	0.40	11	11.66	0.33	0.040
Toplngth (cm)	7	12.59	0.59	11	11.78	0.60	0.380
Dpthdme (cm)	6	7.66	0.88	11	6.48	0.67	0.308
Dpthbwl (cm)	7	3.85	0.43	11	3.62	0.40	0.715
Linthick (cm)	7	5.37	0.53	11	4.44	0.25	0.096
Asdwn	4	105	23.1	9	171	40.63	0.281
Asnest	7	136.29	37.54	11	200.91	28.67	0.186
Slope	7	1.29	0.61	11	29.64	23.58	0.190
Totalht (cm)	7	89.71	7.90	11	73.90	5.45	0.108
Clumpwth (cm)	7	80.14	9.95	11	73.72	6.84	0.590
Clumplth (cm)	7	65.43	10.55	11	76.81	4.86	0.286
Lbp1	7	10.86	1.53	11	12.55	0.87	0.381
Lbp2	7	20.71	2.69	11	21.91	2.02	0.722
Lbp5	7	43.57	5.24	11	49.27	6.57	0.665

Appendix D. Continued

Year	Successful			Non-successful			
Species	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*P*
Lbpm2	7	4.00	0.53	11	4.91	0.41	0.360
Nconceal	7	22.54	2.24	11	17.98	4.23	0.536
Cba25	7	62.64	5.8	11	64.9	2.21	0.745
Cba50	7	42.04	10.16	11	39.08	5.95	0.779
Cba10	7	21.81	7.12	11	17.89	6.62	0.661
Cba20	7	13.71	12.46	11	2.39	0.87	0.198
Noeggs	7	12	0.79	7	5.71	2.1	0.016
Nohtched	7	9.86	1.75	11	0	0	<0.001
Orgcnt	7	12	0.79	6	10	1.57	0.258

CHAPTER III

FITNESS COSTS AND BENEFITS ASSOCIATED WITH LONG-DISTANCE DISPERSAL IN NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*)

Abstract: Northern bobwhites (*Colinus virginianus*) generally are considered the least mobile of all gallinaceous species, but dispersal events of bobwhite (commonly referred to as "shuffling") are well known. Few studies have attempted to explain relationships between dispersal, mortality, and nest success of northern bobwhite. To examine these relationships, we monitored 957 radio-marked bobwhite from 1991 to 1996. Mean dispersal and non-dispersal distance did not differ between sex ($P = 0.699$) and age ($P = 0.572$), respectively. Adult (2,821 m) dispersal distances were shorter than those of juveniles (3,411 m; $P = 0.042$). We found no sex or age related differences in survival rates among dispersers and non-dispersers. Despite associated risks with increased movement activity, survival rate was 1.5-times greater for dispersers ($\hat{S} = 0.72$) than non-dispersers ($\hat{S} = 0.50$). We found no relationships between nest success and dispersal distance, suggesting that dispersal distance had little effect on reproductive output of northern bobwhite.

Key words: *Colinus virginianus*, dispersal, distance, movements, northern bobwhite, Oklahoma.

INTRODUCTION

Dispersal is a highly observed behavioral trait that is intrinsic to nearly all vertebrate populations (Lidicker and Caldwell 1982). Among avian species, juveniles are the primary dispersers as they depart natal ranges, and dispersal is often female-biased (Greenwood 1980). Greenwood (1980) hypothesized that sex-biased dispersal was related to the species' mating system and female-biased dispersal was the product of monogamy, the principal mating system of birds. Liberg and von Schantz (1985) proposed the "oedipus hypothesis" to explain why among polygynous species, both sexes should disperse to avoid potential conflicts over future reproductive resources between parents and offspring. Howard (1960) hypothesized that innate dispersal events allowed populations to extend their range into favorable habitats and repopulate depleted areas caused by catastrophy. Range extension (Howard 1960, Johnston 1961, Johnson and Gaines 1990), regulation of population densities (Lidicker 1962), and inbreeding avoidance (Redmond and Jenni 1982) are hypothesized advantages of dispersal. In contrast, philopatry may be advantageous because individuals benefit from prior experience with vital resources and local predators (Oring and Lank 1984).

Although animals may experience future benefits from dispersing, they inherently face increased mortality risks for several reasons. Increased movement activity has been shown to decrease fitness (Baker 1978, Swingland and Greenwood 1983, Rappole et al. 1989, Woollard and Harris 1990, Bensch et al. 1998) and make dispersers more conspicuous to predators (Ambrose 1972, Smith 1974, Johnson and Gaines 1990). It is also thought that dispersers are less effective at escaping predators in unfamiliar territories (Metzgar 1967, Dias and Blondel 1996). Regardless of mating system or sex bias, animals are forced to entertain trade-off decisions between philatropy and dispersal.

The northern bobwhite (*Colinus virginianus*) is an interesting model for examining dispersal because this ground-nesting galliform is relatively immobile and typically lives ≤ 1 km of their birth site (Lehmann 1984); relatively few bobwhites have been documented moving > 1 km. However, dispersal movements > 104 km were documented by Lehmann (1984). In contrast, > 40% of the birds in our study dispersed > 2, 000 m. Because of inherent risks associated with dispersal, our objective was to determine associations between long-distance dispersal, mortality, and reproductive success for bobwhites. Understanding these relationships may be an important factor in isolating causes of bobwhite population declines, which have become common throughout the United States. Consequently, our study was designed to understand evolution of dispersal in this species by examining associations between movement distance and fitness components such as survival and nesting success. We hypothesized that 1) non-dispersing bobwhite would have greater survival than dispersers, 2) survival would decrease with dispersal distance, 3) reproductive success of non-dispersers would be greater than dispersers and 4) nest success would increase with days post-dispersal prior to nest initiation.

MATERIALS AND METHODS

Study Area

Our study was conducted in short-grass-shrub habitat on Packsaddle Wildlife Management Area (PWMA) in Ellis County, Oklahoma. This 6,475-ha area of mixed-prairie habitat was located 40 km north of Cheyenne, where elevation ranged from 579 to 762 m above mean sea level and mean annual precipitation was 53 cm. Ambient temperatures averaged 2.1°C during winter and 27.0°C in summer (Cole et al. 1966). Soils consisted of sandy Nobscot-Brownfield and Pratt Tivoli, moderately sandy Broken land-Berthoud-Enterprise and Pratt-Carwile, and loamy Quinlan-Woodward (Cole et al. 1966).

Dominant species of grasses included sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), sand paspalum (*Paspalum stramineum*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and sand dropseed (*Sporobolus cryptandrus*). Common forbs on the area included western ragweed (*Ambrosia psilostachaya*), Texas croton (*Croton texensis*), erect dayflower (*Commelina erecta*), and prairie sunflower (*Helianthus petiolaris*). Woody vegetation included shinnery oak (*Quercus harvardii*), sand sage (*Artemisia filifolia*), and sand plum *(Prunus angustifolia*) (Cole et al. 1966).

Collection and Radiotelemetry

We captured 957 birds from 1991 to 1996 using modified Stoddard funnel traps (Wilbur 1967) baited with sorghum and by night-lighting (Huempfner et al. 1975) prior to the nesting season (March−April). Captured birds were marked with aluminum leg bands (Webb and Guthery 1982) and radiotransmitters that weighed <7 g (Holohill Systems Ltd., Ontario, Canada and Wildlife Materials, Inc., Carbondale, Illinois); birds also were sexed and aged as adults or juveniles prior to their release. We monitored birds ≥5 times a week using a radio receiver (Wildlife Materials, Carbondale, Illinois) and a 3-element yagi antenna. Mortalities were classified as avian or mammalian predator, hunting, capture related, missing, or unknown. We attributed the cause of death from mammalian and avian predators from evidence found at the kill site (Dumke and Pils 1973). Harvest mortalities were determined from hunter returns at a check station where hunters were required to check in and out of the management area. We initially classified all mortalities of bobwhite that died ≤ 7 days of their capture as capture-related mortalities and excluded them from all statistical analyses (Kurzejeski et al. 1987, Pollock et al. 1989). However, preliminary analysis of telemetry data indicated that birds dying within 30 days of initial capture were most likely capture related; as a result, those observations were excluded from further analysis. When radio contact was lost for several days, birds were classified into a missing category and subsequently were censored, but they were included in the analysis until the day they were censored (Pollock et al. 1989). To locate all missing birds, we used vehicles to circle their last known coordinates up to a 16-km radius. When vehicle searches failed to locate missing birds, a final attempt was initiated with fixed-wing aircraft to cover all surrounding areas up to 48-km from the last known location.

During the breeding season (May–September) when radio-signals indicated that a bird was not moving, we cautiously circled its location to determine if it was incubating. Each nest site was marked, and nests were monitored daily throughout the 23-day incubation period. When radio telemetry determined parents were no longer incubating, we attempted to observe the nest to get an accurate determination of its status. As a measure of reproductive success, all nests were classified as successful (≥ 1 egg hatched) or non-successful nests (0 eggs hatched). Because birds were trapped throughout the breeding season, we were unable to determine if newly captured birds had nested previously. As a result, the number of bobwhite nests may have been underestimated.

Data Analyses

To evaluate effect of dispersal on survival and nesting success, we classified bobwhites into 2 groups (dispersers or non-dispersers). Because bobwhite home ranges generally cover < 1,000 m (Wiseman and Lewis 1981, Smith et al. 1982), we classified non-dispersal movements as < 1,000 m. Bobwhite dispersers were classified by movements > 2 home-range diameters (Turchin 1998) or movements > 2,000 m. Bobwhite movements were defined by straight-line distances between the 1st and 3rd locations of every set of 3 daily locations. All movement data were tested for homogeneity of variances (Levenes test; Steel and Torrie 1980) and were square-root transformed prior to analyses. To compare differences between age classes, we classified all juveniles as those born during the current breeding season. On January 1, all young-of-the-year were classified as adults.

We tested for age and sex effects on movement distances for dispersers and non-dispersers using analysis of variance (PROC GLM; SAS Institute Inc. 1996). Survival rates were calculated over the 30-day period immediately following the dispersal event. We compared survival rates (PROC LIFETEST, SAS Institute Inc. 1996; Allison 1995) between dispersers and non-dispersers using the Kaplan-Meier procedure (Kaplan and Meier 1958). To remove any bias associated with when individual quail dispersed throughout the year, survival rates were compared for groups of birds with similar seasonal dates of dispersal and non-dispersal movements.

Because some long-distance movements may require > 3 days to accomplish, we recorded movements between the 1st and last set of locations within a 30-day period. As a result, we were able to document dispersal distances between 2,000−40,000 m. We examined fitness consequences of making those 30-day long-distance movements using stepwise forward logistic regression model (PROC LOGISTIC; SAS Institute Inc. 1996) to predict relationships between dispersal distance with mortality and nesting success. Suitability of those models were tested using the Hosmer-Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 1989), where $P > 0.05$ indicated a suitable fit.

RESULTS

Captures and Dispersal Movements

We monitored an average of about 40 birds/month. Over the entire study, 17% (n = 162) of birds were never observed moving long distances and were classified as non-dispersers (< 1,000 m distance movement). About 41% (n = 393) of radio-marked birds were classified as dispersers because they moved a distance of > 2,000 m from their original place of capture. The other 42% (n = 402) of radio-marked birds moved a distance between 1,000–2,000 m, but those were not considered as dispersers based on our criteria. We postulated that those movements might have reflected seasonal range shifts unrelated to dispersal or may have been exploratory trips to neighboring areas. We documented bobwhite dispersal throughout the year. Percentage of all radio-marked birds that dispersed within a given month ranged from 2% to 42%, with highest dispersal activities in April and August (Figure 1).

Survival

Dispersers.–Dispersal distances varied widely among dispersers, and 68% of the dispersers moved between 2,000–3,000 m during a 3-day dispersal event. Females (n = 177) were less likely to disperse > 2,000 m than males ($n = 216$; $\chi^2 = 3.87$, $P = 0.049$). Mean dispersal distance was 3,048 m ± 195 m for males and 3,161 m ± 217 m for females and did not differ significantly ($F = 0.15$, $d.f. = 1$, $P = 0.699$). Juveniles (n =

185) were just as likely to disperse as adults ($n = 208$; $\chi^2 = 1.35$, *d.f.* = 1, $P = 0.246$). However, juvenile bobwhite dispersal distances (3,411 m ± 258) were greater than those of adult bobwhite (2,821 m ± 148 m; $F = 4.16$, $P = 0.042$).

Survival rates (days post movement) of all bobwhite dispersers did not differ between males ($\hat{s} = 0.81$, *95% C.I.* = 0.76 − 0.86) and females ($\hat{s} = 0.69$, *95% C.I.* = 0.63 − 0.76) or between adults ($\hat{s} = 0.76$, *95% C.I.* = 0.70 − 0.82) and juveniles ($\hat{s} = 0.66$, *95% C.I.* = 0.59 − 0.73). Survival functions of bobwhite dispersers were similar between sex ($\chi^2 = 0.23$, *d.f.* = 1, $P = 0.630$) but differed between age group ($\chi^2 = 4.95$, *d.f.* = 1, $P = 0.026$). Survival rates of dispersing juveniles did not differ between males ($\hat{s} = 0.69$, *95% C.I.*= 0.60 − 0.78) and females ($\hat{s} = 0.63$, *95% C.I.*= 0.52 − 0.73), and survival functions were similar ($\chi^2 = 0.34$, *d.f.* = 1, $P = 0.562$) between sexes. Survival rates of dispersing adults did not differ between males ($\hat{s} = 0.77$, *95% C.I.*= 0.70 − 0.85) and females ($\hat{s} = 0.75$, *95% C.I.*= 0.67 − 0.84), and survival functions were similar ($\chi^2 = 0.01$, *d.f.* = 1, $P = 0.937$) between sexes. We further examined the effect of dispersal movements on survival by assessing the relationship between probability of mortality (P_m) and dispersal distance. Although not statistically significant, probability of mortality progressively increased with dispersal distance ($\chi^2 = 3.28$, *d.f.* = 1, $P = 0.070$; Figure 2).

Non-dispersers.--Non-dispersal movements of males ($\bar{x} = 189$ m ± 16.8 m) did not differ from females ($\bar{x} = 176$ m ± 13.4; $F = 0.32$, *d.f.* = 1, $P = 0.572$). Non-dispersal movements of adults ($\bar{x} = 188$ m, ± 21.0) did not differ from those of juveniles ($\bar{x} = 179$ m, ± 12.0; $P = 0.698$). Non-dispersal survival rates were similar for males ($\hat{s} = 0.43$, 95% C.I. = 0.33 − 0.53) and females ($\hat{s} = 0.58$, 95% C.I. = 0.47 − 0.70), but survival functions differed between sexes ($\chi^2 = 4.11$, *d.f.* = 1, $P = 0.043$). Survival rates also did not differ between adults ($\hat{S} = 0.50$, 95% C.I. = 0.39−0.63) and juveniles ($\hat{S} = 0.49$, 95% C.I. = 0.39−0.59) and survival functions of non-dispersers did not differ between age groups ($\chi^2 = 0.08$, *d.f.* = 1, $P = 0.783$).

Dispersers vs. Non-dispersers.–Because survival rates of dispersers and non-dispersers did not differ between age groups or sexes, we pooled our data to make comparisons between these 2 groups. Dispersing bobwhites had a survival rate ($\hat{S} = 0.72$, 95% C.I. = 0.67−0.76) nearly 1.5-times greater than that of non-dispersers ($\hat{S} = 0.50$, 95% *C.I.* = 0.42−0.58; Figure 3). Survival functions between dispersers and non-dispersers were different ($\chi^2 = 21.77$, *d.f.* = *1*, $P < 0.001$; Figure 3).

Nesting Success

Dispersers vs. Non-dispersers.--Throughout the breeding seasons (May-September 1991-1996), we radio collared 339 birds, of which 109 (32.2 %) initiated a nest. Dispersers ($n = 68$) initiated more nests than non-dispersers ($n = 41$; $\chi^2 = 6.69$, *d.f.* = 1, $P = 0.010$). However, number of successful nests between bobwhite dispersers ($n = 34$) and non-dispersers ($n = 26$) did not differ ($\chi^2 = 1.07$, *d.f.* = 1, $P = 0.302$). Dispersal distances did not differ between successful ($\bar{x} = 2{,}707$ m ± 190 m) and non-successful ($\bar{x} = 2{,}831$ m ± 214 m; $F = 0.19$, *d.f.* = 1, $P = 0.665$) nesters.

To determine effects of dispersal on excess energy reserves required for nesting, we performed a univariate logistic regression between probability of nest success (P_{ns}) and number of days after dispersal but prior to nest initiation. There was no relationship between nesting success ($\chi^2 = 0.73$, *d. f.* = 1, $P = 0.395$), suggesting that spring dispersal had a negligible effect on energy reserves required for bobwhites to successfully initiate a nest. We also found no relationships between P_{ns} and dispersal distance ($\chi^2 = 0.19$, *d.f.* = 1, $P = 0.661$).

DISCUSSION

Female-biased dispersal is a general phenomenon in many gallinaceous birds (Clarke et al. 1997), and other taxonomic groups (Greenwood 1980). Jamieson and Zwickel (1983) documented that mean dispersal distances of juvenile female blue grouse (*Dendragapus obscurus*) were nearly twice as far as those of juvenile males. Female-biased dispersal also was documented in juvenile ruffed grouse (*Bonasa umbellus*) where female dispersal distances were twice as great as male dispersal distances (Small and Rusch 1989). Female sage grouse (*Centrocercus urophasianus*) also disperse farther than males, but the proportions of male and female dispersers did not differ (Dunn and Braun 1985). Resource defense mating systems typically favor female-biased dispersal because males, unlike females, benefit from guarding familiar vital resources (Greenwood 1980, Wolff and Plissner 1998). As a result, females would benefit by dispersing because females choose mates that have defended the best resources (Clark et al. 1997). Contrary to studies of other gallinaceous birds, our results suggest that dispersal events of northern bobwhite are male-biased, because males were more likely to disperse > 2,000 m than females. However, dispersal distances were nearly identical between male and female dispersers.

Juvenile dispersal is a common trait in many avian species (Clarke et al. 1997). We found that juvenile dispersal distances were greater than adult dispersal distances but survival rates did not differ with age ($\chi^2 = 0.07$, $P = 0.780$), suggesting that mortality costs associated with increased juvenile dispersal distance was negligible. The inbreeding avoidance hypothesis states that juveniles disperse from their natal site to prevent breeding with relatives (Waser et al. 1986, Negro et al. 1997). Although adults were just as likely to disperse as juveniles, a greater number of birds chose to disperse (41%) than to remain philopatric (17%), which partially supports the inbreeding avoidance hypothesis. However, contrary to this hypothesis adults receive equal benefits from dispersal.

While dispersal may be a necessary phenomenon for inbreeding avoidance, range extension, and regulation of population densities for many species, there may be negative consequences of dispersal on individual fitness. Bensch et al. (1998) documented that dispersing great reed warblers (*Acrocephalus arundinaceus*) had lower life-time fitness than their philopatric counterparts. Johnson and Gaines (1990) documented that increased movement activities associated with long-distance dispersal can increase mortality by decreasing predator avoidance, and Dias and Blondel (1996) suggest that dispersing individuals may be less adapted to their new environments. However, our data suggest that bobwhites benefit from dispersal through greater survival. Johnson and Gaines (1987) found similar results and documented higher survival and reproductive activity for dispersing prairie voles (*Microtus ochrogaster*) than for non-dispersers. Bensch et al. (1998) reported similar life spans for dispersing and philopatric female great reed warblers. Furthermore, species of grouse did not suffer greater mortality during dispersal than more philopatric individuals (Beaudette and Keppie 1992, Small et al.

1993). Higher rates of survival for dispersers suggests that they are in better condition and consequently are more likely to escape predators and may be leaving unfavorable conditions for more suitable habitat. In areas where competition for vital resources (space and food) is increased due to high bobwhite density, dispersers may move into more favorable habitats where competition is diminished (Hamilton and May 1977).

Howard (1960) proposed that bobwhite dispersal may be an innate phenomenon. He hypothesized that inherited traits may compel individuals to disperse beyond confines of their parental home range. Because a greater proportion of both adult and juvenile bobwhites dispersed than remained philopatric, we suggest that bobwhite dispersal may be an evolutionary trait driven by a genetic stimulus motivating dispersal that ensures survival for the species. Gaines in fitness through higher probability of survival lends support for the emigrant fitness hypothesis proposed by Anderson (1989).

Probability of mortality and fitness costs associated with bobwhite dispersal are critical factors in the phenomenon of bobwhite dispersal. Although bobwhite that dispersed realized a greater survival advantage than non-dispersers, our evidence suggests that extremely long-distance dispersal may be costly, as evident by increased probability of mortality. Therefore, at some threshold distance, costs associated with increasing dispersal may eventually outweigh advantages.

Our data also suggest that bobwhite nest success is unrelated to dispersal distance. Bensch et al. (1998) found similar results for female great reed warblers (*Acrocephalus arundinaceus*). However, they found that immigrant (dispersing) male great reed warblers had lower numbers of fledglings and offspring recruits than did their philopatric counterparts. Because bobwhites appear to benefit from dispersal through greater survival, we postulate that dispersing bobwhites have greater energy reserves. These reserves would not only increase their chances of survival during dispersal but may also provide reserves required for nest initiation, as evident by greater nest initiation among dispersing bobwhite. Pattenden and Boag (1989) suggested that prenesting endogenous reserves can influence early nesting mallards (*Anas platyrynchos*). Bobwhites in poor condition may not be capable of dispersing or have enough energy reserves required for nest initiation. Giuliano et al. (1996) found that protein and energy deficiencies can lead to decreased body weight and egg production that ultimately cause reproductive failure in northern bobwhite. Although we lack data on bobwhite condition, we speculate that dispersing bobwhite had greater body weights and were in better condition prior to nesting than non-dispersers. Additionally, birds that dispersed initiated more nests because they generally had greater energy reserves required for egg production. Although nest success did not differ between dispersers and non-dispersers, dispersers may have a fitness advantage because they have a higher probability of survival and initiate more nests.

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Figure 1. Number and percentage of radio collared bobwhite dispersers during 1991-1996 on Packsaddle Wildlife Management Area, Ellis County, Oklahoma.

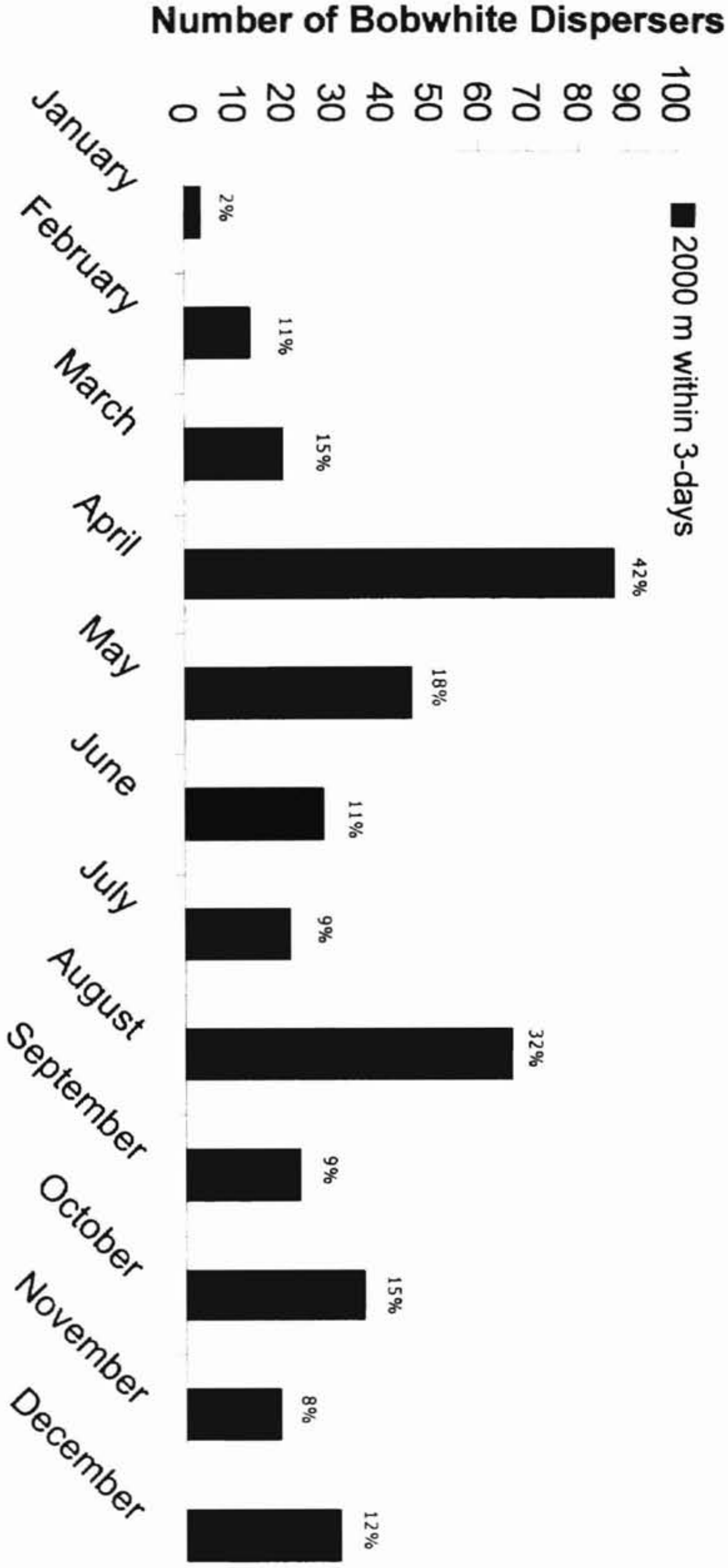
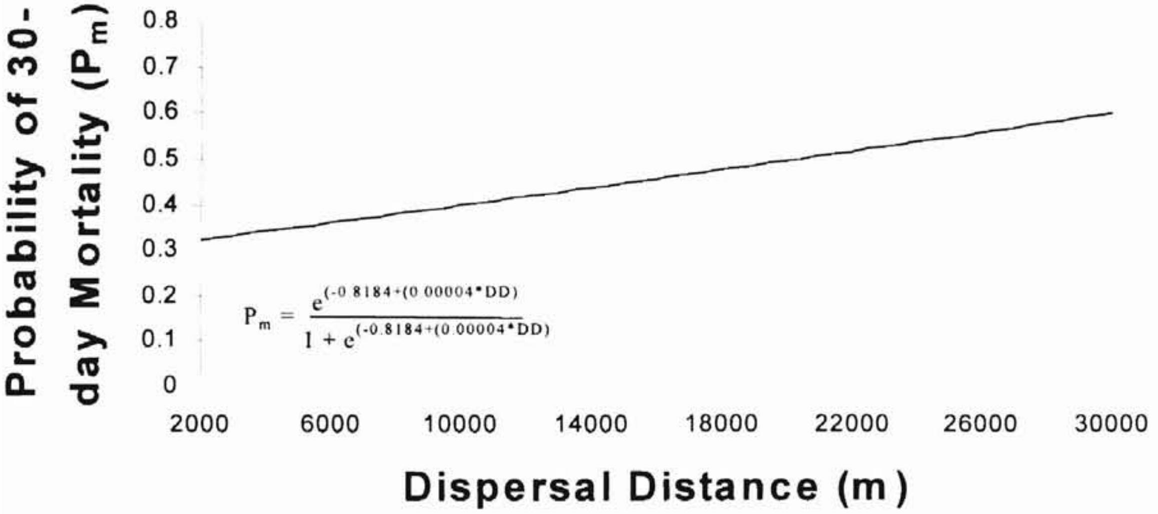

Number of Bobwhite Dispersers
100
90
80
70
60
50
40
30
20
10
0
■ 2000 m within 3-days
January
February
March
April
May
June
July
August
September
October
November
December
2%
11%
15%
42%
18%
11%
9%
32%
9%
15%
8%
12%

Figure 2. Relationships between dispersal distance and probability of mortality to 30 days post dispersal and numbers of radio collared bobwhite at Packsaddle Wildlife Management Area, Ellis County, Oklahoma. Values calculated from probability equations derived from univariate logistic-regression models ($P < 0.05$).


Probability of 30-day Mortality (P_m)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
$P_m = \frac{e^{(-0.8184+(0.00004*DD))}}{1+e^{(-0.8184+(0.00004*DD))}}$
2000
6000
10000
14000
18000
22000
26000
30000
Dispersal Distance (m)

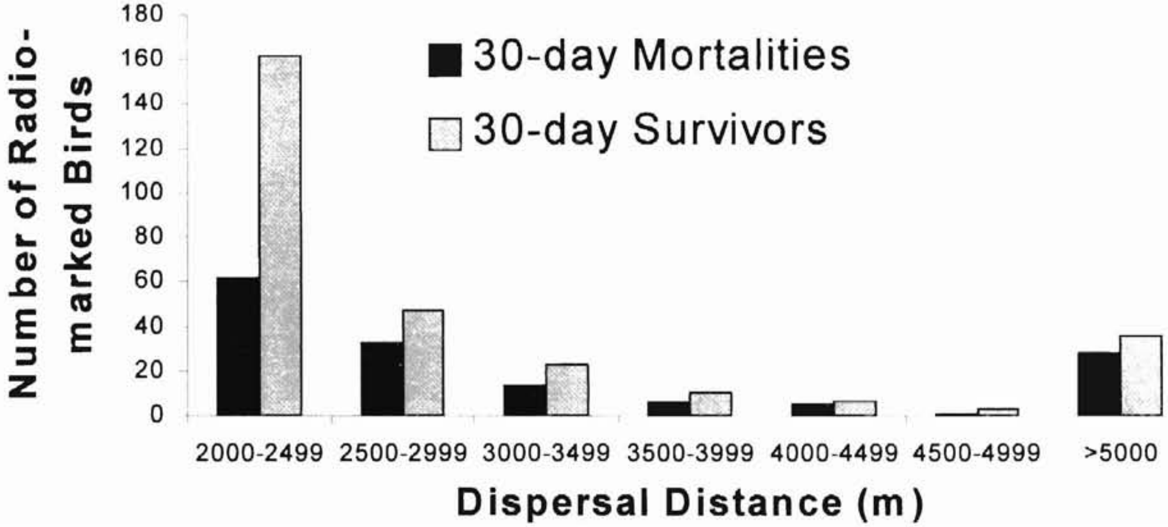
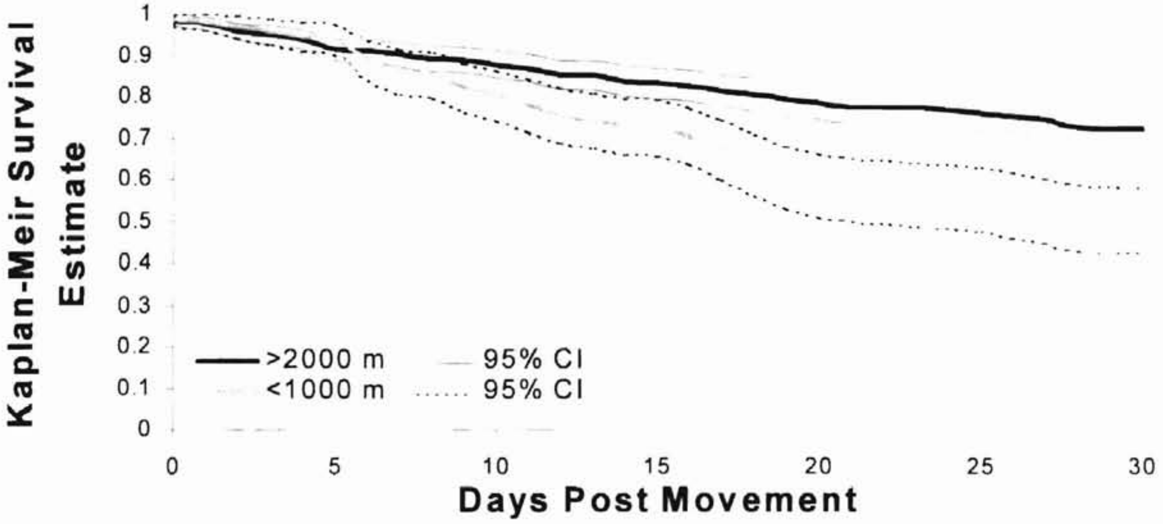
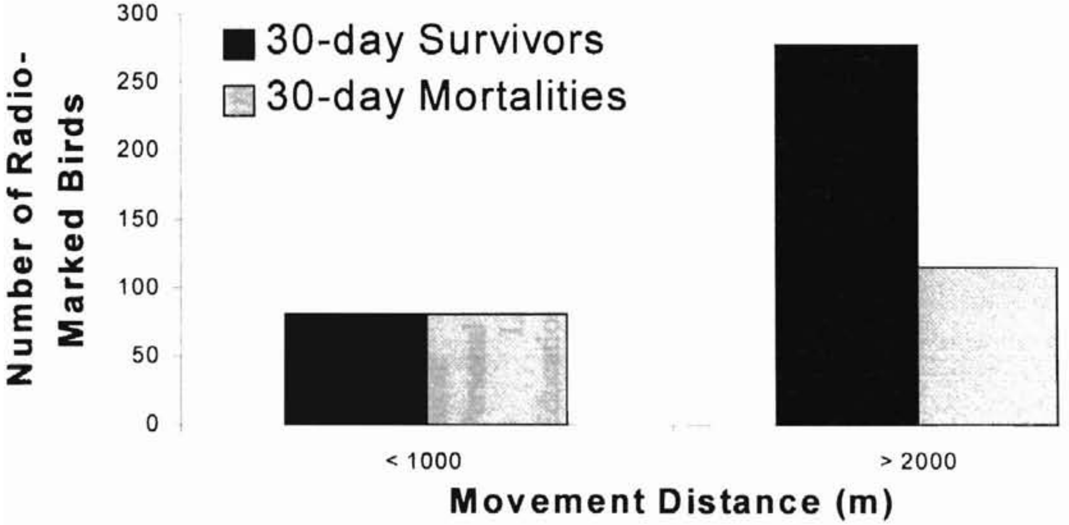

Number of Radio-marked Birds
180
160
140
120
100
80
60
40
20
0
■ 30-day Mortalities
□ 30-day Survivors
2000-2499
2500-2999
3000-3499
3500-3999
4000-4499
4500-4999
>5000
Dispersal Distance (m)

Figure 3. Kaplan-Meier survival functions (estimated from days post dispersal) and numbers of radio collared bobwhite during 1991-1996 at Packsaddle Wildlife Management Area, Ellis County, Oklahoma.


Kaplan-Meir Survival Estimate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30
Days Post Movement
>2000 m
<1000 m
95% CI
95% CI


Number of Radio-Marked Birds
300
250
200
150
100
50
0
30-day Survivors
30-day Mortalities
< 1000
> 2000
Movement Distance (m)

VITA

Darrell Townsend II

Candidate for the Degree of

Master of Science

Thesis: IMPROVING MANAGEMENT FOR NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*): RE-EVALUATION OF MOVEMENTS, NESTING HABITAT AND FEEDING ECOLOGY

Major Field: Wildlife and Fisheries Ecology

Biographical:

Personal Data: Born in Laurel, Mississippi, July 15, 1972, the son of Darrell and Linda Townsend.

Education: Received Bachelor of Science Degree in Wildlife and Fisheries Ecology from Oklahoma State University, in December 1995; completed requirements for Master of Science degree at Oklahoma State University in May 2000.

Professional Organizations: The Wildlife Society, Society for Range Management