Short- and Long-Term Influence of Brush Canopy Cover on Northern Bobwhite Demography in Southern Texas

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Abstract

Extensive research has been devoted to quantifying the habitat needs and selection of many wildlife species. However, how habitat selection affects the long-term demographic performance of a species largely has been ignored. We used northern bobwhite (*Colinus virginianus*) and brush canopy coverage—an important habitat component for quail—to evaluate the influence of habitat on short- and long-term demographic performance of this species. We used data from a 5-yr (2001–2005) radiotelemetry study of northern bobwhite in southern Texas to obtain estimates of bobwhite density, survival, and production on three study areas with 5%, 11%, and 32% brush canopy cover. Our objectives were to compare these demographic variables individually among brush canopy cover classes and then simulate their cumulative effect on demographic performance using a simulation model. All demographic parameters were similar among the three brush canopy cover classes. However, simulation modeling indicated that long-term demographic performance was greater on the 11% and 32% brush canopy cover classes. Simulated bobwhite populations were 2–3 times higher in these two cover classes than the 5% brush canopy cover class. In addition, the probability of population persistence was greater in the 11% (0.91) and 32% (1.00) brush canopy cover classes than the 5% cover class (0.54) using a quasi-extinction criterion of ≤ 40 birds (≤ 0.05 birds $\cdot$ ha^{-1}). Our study highlights the shortcoming of considering only short-term effects when comparing habitat given that short- and long-term effects of habitat on demographic performance can differ.

Key Words: canopy, *Colinus virginianus*, density, population extinction, quail, woody cover

INTRODUCTION

Previous research has been devoted to quantifying the habitat needs and selection of many wildlife species. However, how habitat use affects the long-term demographic performance of a species largely has been ignored (Franklin et al. 2000). Woody vegetation is an important component of northern bobwhite (*Colinus virginianus*) habitat. Bobwhites use woody vegetation for food (Jackson 1969; Lehmann 1984; Hernández and Guthery 2012), thermal cover (Forrester et al. 1998; Hiller and Guthery 2005), loafing cover (Johnson and Guthery 1988; Hernández and Guthery 2012), and escape cover from predators (Jackson 1969; Kopp et al. 1998; Hernández and Guthery 2012).

The amount of brush canopy cover needed by bobwhites has been previously estimated by various researchers (Schroeder 1985; Johnson and Guthery 1988; Bidwell et al. 1991; Rice et al. 1993; Kopp et al. 1998; Guthery et al. 2000a). However, recommendations for the amount of woody cover have varied greatly ranging from a low of ~5% (Guthery 1986) to a high of 85% (Guthery et al. 2000a). These broad estimates could be due to slack in bobwhite habitat (Guthery 1999), inconsistencies in methodology, or differences in scale of measurement (i.e., point of use vs. pasture). Kopp et al. (1998) reported that bobwhites preferred patches with 20–60% brush canopy cover at points of use (i.e., flushing and landing points) whereas other researchers made recommendations (1–5% brush canopy cover) at the pasture scale (Jackson 1969; Lehmann 1984; Guthery 1986). Such wide range of brush canopy cover values has made brush management for bobwhites a somewhat contentious issue.

Most of the estimates above are based on the presence (Forrester et al. 1998, Kopp et al. 1998) or density (Rice et al. 1993) of bobwhites. How habitat selection affects bobwhite population persistence has not been considered. Production and survival (i.e., fitness) in bobwhite populations are important parameters leading to increases and viability in those populations (Guthery et al. 2000b; Sandercock et al. 2008). Therefore,

it is important to determine the influence of habitat on bobwhite population viability.

Our objective was to compare bobwhite population performance (density, productivity, survival, and persistence) among three study sites with varying amounts of brush canopy cover on a short-term (i.e., 6-yr) scale. We also compared the cumulative, long-term (i.e., 100-yr) demographic performance of bobwhite populations in these different cover classes using a simulation model to evaluate the hypothesis that brush canopy cover might have differing short-term and long-term impacts on bobwhite populations. We used the terms short-term and long-term to reflect annual and century time scales, respectively.

METHODS

Study Area

Our study area was located on the Encino Division of King Ranch (42,448 ha), Brooks County, Texas, which lies in the eastern portion of the Rio Grande Plains ecoregion (Gould 1975). The study area consisted of three experimental units (North Viboras=1,966 ha; La Loba=1,379 ha; and Cuates=1,240 ha) that were spaced 5–8 km apart and were spatially independent respective to bobwhite populations (i.e., bobwhites did not travel between experimental units). Experimental units were arranged north to south with a decreasing percentage of brush canopy cover present at each experimental unit (North Viboras=32%; La Loba=11%; Cuates=5%). Sites were representative of the range of brush canopy cover and landscape habitat variability present on the study area (Rader et al. 2007). All three experimental units were under the same land management regime. Because only one experimental unit occurred in each brush canopy cover class, the study was pseudoreplicated, and inferences are limited to the study area. However, the concepts derived from model simulations remain robust.

Vegetation in the Rio Grande Plains ecoregion is characterized as a mixed-brush community (Scifres 1980). Vegetation specific to the study area consisted predominantly of honey mesquite (*Prosopis glandulosa* Torr.), huisache (*Acacia farnesiana* [L.] Willd.), granjeno (*Celtis ehrenbergiana* [Klotzsch] Liebm.), live oak (*Quercus virginiana* Mill.), and prickly pear cactus (*Opuntia engelmannii* Salm-Dyck ex Engelm. var. *lindheimeri* [Engelm.] Parfitt & Pinkava; Hernández et al. 2002). Predominant forbs included croton (*Croton* spp.), sunflower (*Helianthus annuus* L.), dayflower (*Commelina erecta* L.), and partridge pea (*Chamaecrista fasciculata* [Michx.] Greene; Hernández et al. 2002). Common grasses included little bluestem (*Schizachyrium scoparium* [Michx.] Nash), paspalum (*Paspalum* spp.), three awn (*Aristida* spp.), gulf cordgrass (*Spartina spartinae* [Trin.] Merr. ex Hitchc.), King Ranch bluestem (*Bothriochloa ischaemum* [L.] Keng), Kleberg bluestem (*Dichanthium annulatum* [Forssk.] Stapf), sandbur (*Cenchrus spinifex* Cav.), red lovegrass (*Eragrostis secundiflora* J. Presl), and buffelgrass (*Pennisetum ciliare* [L.] Link; Hernández et al. 2002).

Climatic conditions are classified as semiarid, subhumid and are characterized by a high rate of evaporation (Williamson 1983). The months of June and September generally receive the greatest amount of precipitation. Monthly precipitation ranges 1.4–13.0 cm with a mean annual rainfall of 65.4 cm (Williamson 1983). Annual rainfall during our study was 54.9 cm (2001), 62.4 cm (2002), 97.4 cm (2003), 69.4 cm (2004), 31.9 (2005), and 71.5 (2006; rainfall data from Falfurrias, Texas Weather Station, NOAA 2007).

Field Data

Density. Rusk et al. (2007) and Schnupp et al. (2013) evaluated survey methods for estimating bobwhite density on our study area during 2005–2008, using distance sampling (Buckland et al. 2001). Transects were developed in ArcMap and uploaded onto field computers so survey effort and detections could be monitored in the field to determine if the necessary sample size (i.e., > 60 detections) and effort (i.e., 91 km of effort) was accrued. The number and length of transects varied per pasture because of the shape of the pasture perimeter. Transects were traversed during the first and/or last 3 h of daylight. Transects were flown at a height of 7 m and a velocity of 37 km · hr^{-1} using a Robinson R44 (Robinson Helicopter Company, Torrance, CA). Pilots utilized an Envizio plus lightbar (Raven Industries, Sioux Falls, SD) to navigate transects. The recorded perpendicular distances were analyzed with Program DISTANCE 5.0 (Thomas et al. 2004). The best detection function was chosen based on Akaike's Information Criterion (AIC) values and goodness of fit using Chi-square analysis (Buckland et al. 2001). Surveys were conducted by randomly selecting the starting transect and flying the subsequent transect that was 400 m away. We continued with this scheme in a sequential manner until all transects were traversed. We used density estimates derived from helicopter transects for autumn (October–December 2005–2008; Rusk et al. 2007; Schnupp et al. 2013) to evaluate the performance of our simulation model.

Productivity. We captured bobwhites using standard funnel traps (Stoddard 1931) and night netting (Labisky 1968) throughout the study period (2000–2005). Individuals were classified by sex and age (Rosene 1969) and leg-banded. Bobwhites weighing over 150 g were fitted with a 5–6 g neck-loop radio transmitter (Shields et al. 1982; American Wildlife Enterprises, Tallahassee, FL). Bobwhites were monitored three times · wk^{-1} throughout the year, which was partitioned into four seasons based on bobwhite life history: breeding (spring; 1 March–31 May), nesting (summer; 1 June–31 August), covey prefrost (autumn; 1 September–30 November), and covey postfrost (winter; 1 December–28 February). Capture, handling, and marking of northern bobwhites were within the guidelines of the Texas A&M University–Kingsville Animal Care and Use Committee (Permit No. 2003-3-3).

We used radio-marked bobwhites to estimate the proportion of hens that entered the nesting season (15 April) and attempted to nest, regardless of the nest fate and regardless if the hen survived the nesting season. This sample therefore included hens that entered the nesting season but died before having a nesting opportunity or before a nest could be found. We also used these hens to determine the number of nesting attempts per hen. We assumed nesting when we obtained consecutive locations of a radio-marked bird at the same point

and located nests by homing. When a nest was found, we documented clutch size and continued monitoring until nesting was terminated (i.e., abandoned, depredated, or hatched).

We defined productivity (*Prod*) as the number of chicks produced during the spring and/or the summer nesting season. Productivity was calculated deterministically as:

$$Prod = Breed \times Clutch \times NestSurv$$
$$\times NestAttempt \times PropNest \qquad [1]$$

where *Breed* is the number of adult females entering the spring breeding season; *Clutch* is the clutch size; *NestSurv* is the estimate of daily nest survival (0.9593) from Rader et al. (2007), raised to the 23rd power to estimate nest survival for the 23-d incubation period; *NestAttempt* is the number of nesting attempts per adult female that enter the nesting season and nested during that nesting season (spring and summer, regardless of whether they survived the nesting season); and *PropNest* is the proportion of adult female bobwhites that enter the nesting season and nest during the spring and/or the summer nesting seasons, regardless of whether they survived the nesting season.

Survival. Survival rates were calculated using the Kaplan–Meier estimator (Kaplan and Meier 1958) and staggered-entry approach (Pollock et al. 1989a, 1989b) to estimate seasonal survival. We assumed that birds were randomly sampled, survival times for individuals were independent, left-censored individuals (staggered entry) had survival distributions similar to previously marked individuals, and causes for censoring (i.e., radio failure) were independent of the birds' fate. We only included bobwhites surviving > 14 d after radio-marking to minimize trapping or handling bias on survival probabilities (Pollock et al. 1989a, 1989b; White and Garrott 1990).

Simulation Model

We used the population model developed by DeMaso et al. (2011, 2013) to evaluate the long-term (i.e., 100-yr) effect of brush canopy cover on bobwhite population performance. The model is described in detail by DeMaso (2008), and DeMaso et al. (2011, 2013). Briefly, the population model is a stochastic, sex- and age-structured model based on difference equations, with stochastic variables drawn from normal and Weibull distributions. The population model was developed for bobwhites in southern Texas using data from our long-term radiotelemetry study and programmed using STELLA 9.0.2 software (ISEE Systems, Incorporated, Lebanon, NH).

The model represents production and survival of adult and juvenile, female and male bobwhites and is partitioned into four, 3-mo seasons corresponding to the seasons defined above for radio-monitoring (i.e., breeding, nesting, covey prefrost, and covey postfrost). The model represents the flow of material (i.e., individual bobwhites) through a system (e.g., a bobwhite population on 800 ha) for 100 yr (DeMaso et al. 2011). The general flow of material through the model begins with the production of chicks during spring and summer. Spring and summer juvenile mortality relates specifically to chicks during their first months of life and the juveniles (older chicks) that enter the adult cohort during spring of the following year.

Chicks are divided equally into female and male segments of the population and each segment has a juvenile and adult age class. Losses due to seasonal mortality are removed from each segment of the population. The number of adults alive at the end of winter becomes the breeding population (DeMaso et al. 2011). Density-dependent reproduction and overwinter mortality are functions of total adults in the breeding population and total winter population, respectively. The model was validated with an independent data set. For additional details, we refer the readers to DeMaso (2008), and DeMaso et al. (2011, 2013).

Statistical Analyses

We compared demographic parameters among brush canopy cover classes using 95% confidence intervals for univariate comparisons (Johnson 1999). We also compared among brush canopy cover classes using a deterministic estimation of chick production that was calculated using an initial breeding population of 100 birds, constant nest survival rate of 0.3845 (Rader et al. 2007), and the pooled mean values of the demographic variables. We evaluated the cumulative, long-term influence of brush canopy cover on demographic performance by estimating the probability of population persistence using a quasi-extinction criterion of < 0.05 bobwhites $\cdot$ ha^{-1} (≤ 40 bobwhites for our study area). This criterion was based on minimum spring densities reported in the literature (Spears 1991). This criterion is below the 0.25 bobwhites $\cdot$ ha^{-1} considered to be indicative of very poor bobwhite populations (Guthery 1986)

RESULTS

Short-term Demographic Comparisons

All demographic parameters were similar among the three brush canopy cover classes. These included the mean proportion of females attempting to nest (Table 1), the mean number of nesting attempts per female (Table 1), clutch size (Table 2), seasonal survival (Table 3), and autumn densities (Table 4). The deterministic estimation of chick production resulted in the production of 309, 241, and 314 chicks for the 5%, 11%, and 32% brush canopy cover classes, respectively. Brush canopy cover therefore did not appear to influence short-term demographic performance.

Long-term Demographic Performance

Simulation modeling indicated that chick production, autumn population, and spring population were lower on the 5% brush canopy cover treatment than on the other two treatments, which were similar (Table 5). Chick production at the 11% and 32% brush canopy cover classes was nearly double the chick production at the 5% brush canopy cover class. The autumn population (Fig. 1) and spring population (Fig. 2) long-term trends in the 11% and 32% brush canopy cover classes also were two to three times higher than in the 5% brush canopy cover class. Simulated winter age ratios were higher on the 32% brush canopy cover treatment and lower, but similar on the other two treatments (Table 5). The probability of autumn population persistence was greater in the 11% (0.91) and 32%

Table 1. The proportion of female northern bobwhites that were alive and entered the nesting season on 15 April that attempted to nest, the proportion that did not attempt to nest, and the number of nesting attempts per hen regardless if they survived the nesting season, 2001–2005, Brooks County, Texas, USA.

	Brush canopy cover								
	5%			11%			32%		
Year	Nesting	Not nesting[1]	Nests · hen^{-1}	Nesting	Not nesting[1]	Nests · hen^{-1}	Nesting	Not nesting[1]	Nests · hen^{-1}
2001	0.54	0.46	1.4	0.71	0.29	1.3	0.63	0.37	1.4
2002	0.77	0.23	1.7	1.00	0.00	2.0	0.50	0.50	3.0
2003	0.56	0.44	1.9	0.60	0.40	1.3	0.80	0.20	2.5
2004	0.75	0.25	1.7	0.77	0.23	1.3	0.56	0.44	2.0
2005	0.50	0.50	1.2	0.71	0.29	1.0	0.44	0.56	1.5
Pooled	0.60	0.40	1.6	0.71	0.29	1.3	0.57	0.43	1.9

[1]Includes hens that entered the nesting season on 15 April, but might have died before they attempted to nest.

(1.00) brush canopy cover classes than in the 5% brush canopy cover class (0.54) using a quasi-extinction criterion of ≤ 40 birds (≤ 0.05 birds · ha^{-1}).

DISCUSSION

The influence of brush canopy cover on bobwhite populations differed by time scale in our study. Brush canopy cover (5–32%) had no influence on bobwhite population performance on in the short term; however, the probability of population persistence increased with brush canopy cover in the long term. Interactive effects between slack in bobwhite habitat (Guthery 1999) and weather might explain this contrasting influence of brush canopy cover through time.

Guthery (1999) proposed that "slack" occurred in bobwhite habitat, that is, that different habitat configurations could result in equally suitable space for bobwhites. Guthery (1999) identified three sources giving rise to slack, one of which was the interchangeability of functions provided by woody and herbaceous cover. This interchangeability permits canopy cover of woody and herbaceous plants to vary among landscapes with usable space remaining constant. If slack occurs in bobwhite habitat, then varying amounts of brush canopy cover (within a suitable range) would have no influence on bobwhite populations. This prediction was supported by our study on a short time scale.

An interesting finding is that the prediction was not supported on a longer time scale. None of the demographic parameters differed among the three brush canopy cover classes when compared individually in the short term, but a long-term, cumulative effect was detected. Bobwhite abundance and probability of population persistence increased with increasing brush canopy cover. The strong influence of weather on bobwhite populations might explain why slack did not result in comparable population performance on a longer time scale.

Bobwhite populations on southwestern rangelands are strongly influenced by rainfall, increasing during periods of abundant rainfall and decreasing during drought (Kiel 1976; Hernández et al. 2005; Tri et al. 2013). This influence of rainfall can be so great that it can override the influence of habitat on bobwhite populations, at least on an annual time frame. Brazil et al. (2012) provided evidence toward this phenomenon. They documented that the amount of nesting cover accounted for about 67% of the variation in bobwhite productivity during a wet year but had little predictive power (<1%) during a dry year. Given the high interannual variability of rainfall in southern Texas (Norwine and Bingham 1986) and the apparent, relative strength of habitat–bobwhite relationships as a function of rainfall, bobwhite population performance should be more influenced by current rainfall rather than habitat on an annual time scale. In contrast, the influence of habitat on bobwhite population performance might be better captured on a longer time scale because a longer time period would dampen the high interannual variability and capture average population performance. This could explain our contrasting results.

Regardless of the cause, the salient point is that brush canopy cover had a different influence on bobwhite populations

Table 2. Sample size (*n*), mean northern bobwhite clutch size ($\bar{x}$), standard error (SE), minimum (Min), and maximum (Max) by brush canopy cover class and year, 2001–2005, Brooks County, Texas, USA.

	Brush canopy cover														
	5%					11%					32%				
Year	*n*	$\bar{x}$	SE	Min	Max	*n*	$\bar{x}$	SE	Min	Max	*n*	$\bar{x}$	SE	Min	Max
2001	14	12.4	0.6	9	17	18	11.5	1.0	1	19	12	12.9	1.0	8	19
2002	12	13.0	0.6	10	16	6	11.0	0.9	8	14	6	10.8	0.8	7	13
2003	24	12.3	0.5	8	19	16	11.3	0.5	8	16	23	12.4	0.5	9	18
2004	22	12.4	0.7	5	20	16	11.9	0.4	9	15	17	11.2	1.0	1	22
2005	12	11.4	0.6	9	16	9	11.7	0.7	9	16	15	11.1	0.5	9	17
Pooled	84	12.3	0.3	5	20	65	11.5	0.3	1	19	73	11.8	0.4	1	22

Table 3. Sample sizes[1] (n), empirical estimates of mean northern bobwhite seasonal survival ($\hat{s}$), standard error (SE), minimum (Min), and maximum (Max) by brush canopy cover for spring (1 March–31 May), summer (1 June–31 August), autumn (1 Sepember–30 November), and winter (1 December–28 February) by age and sex during 2001–2005, Brooks County, Texas, USA.

| | | | | | Brush canopy cover | | | | | | | | | | | | | |
| | | | | 5% | | | | | 11% | | | | | 32% | | | |
Sex	Age	Season	n	$\hat{s}$	SE	Min	Max	n	$\hat{s}$	SE	Min	Max	n	$\hat{s}$	SE	Min	Max
Female	Adult	Spring	5	0.506	0.072	0.357	1.000	5	0.654	0.106	0.360	1.000	5	0.472	0.100	0.200	0.706
		Summer	5	0.512	0.051	0.356	0.667	5	0.723	0.029	0.661	0.800	5	0.600	0.132	0.292	1.000
		Autumn	5	0.744	0.103	0.484	1.000	5	0.666	0.100	0.432	1.000	5	0.751	0.053	0.550	0.856
		Winter	5	0.622	0.116	0.267	1.000	5	0.784	0.103	0.540	1.000	5	0.618	0.159	0.250	1.000
	Juvenile	Spring	1	0.625	—	0.625	0.625	—	—	—	—	—	—	—	—	—	—
		Summer	1	0.750	—	0.750	0.750	1	0.818	—	0.818	0.818	1	0.167	—	0.167	0.167
		Autumn	1	1.000	—	1.000	1.000	2	0.917	—	0.833	1.000	1	1.000	—	1.000	1.000
		Winter	4	0.833	0.096	0.667	1.000	4	0.249	0.111	0.000	0.539	4	0.856	0.144	0.424	1.000
Male	Adult	Spring	5	0.680	0.084	0.504	1.000	5	0.611	0.071	0.430	0.851	5	0.557	0.090	0.305	0.758
		Summer	5	0.660	0.045	0.548	0.786	5	0.597	0.048	0.473	0.727	5	0.501	0.099	0.200	0.818
		Autumn	5	0.798	0.034	0.714	0.900	5	0.838	0.062	0.635	1.000	5	0.802	0.071	0.571	1.000
		Winter	4	0.659	0.122	0.468	1.000	5	0.515	0.107	0.148	0.800	5	0.465	0.144	0.000	0.875
	Juvenile	Spring	1	0.500	—	0.500	0.500	—	—	—	—	—	1	0.595	—	0.595	0.595
		Summer	1	0.714	—	0.714	0.714	2	0.357	—	0.000	0.714	2	0.714	0.286	0.429	1.000
		Autumn	2	0.900	0.100	0.800	1.000	2	0.360	0.100	0.800	1.000	3	1.000	0.000	1.000	1.000
		Winter	3	0.488	0.244	0.000	0.750	3	0.293	0.244	0.714	0.750	4	0.688	0.138	0.333	1.000

[1]The number of seasonal estimates for an age- and sex-class category, not the number of radio-marked bobwhites on which sex- and age-class survival estimates were based.

dependent upon time. This finding is important because most wildlife management decisions are based on short-term effects of habitat. If short-term and long-term effects of habitat have differing effects on demographic performance, then potential negative effects of erroneous management decisions might not be noticed until years later. Our study indicates that managers can manage properties similar to our study area with about 10–30% brush canopy cover at the pasture scale without fear of harming bobwhite populations. One caveat is that we only had brush canopy cover treatments at the lower end of the brush canopy cover range utilized by bobwhites. Bobwhites will utilize brush canopy cover of ~5% (Guthery 1986) to ~80% (Schroeder 1985; Kopp et al. 1998). A broader range of cover classes would have allowed for wider inferences, but such a study was not logistically feasible in our study area.

An unresolved issue in bobwhite habitat management is whether populations respond to habitat quality or usable space (Masters et al. 2009). The habitat-quality paradigm suggests that populations will increase with increasing quality attributes such as food or plant diversity. However, Guthery (1997) argued that quantity of usable space was the principal determinant of population persistence and density. He defined usable space as space compatible with the physical, behavioral, and physiological adaptations of bobwhites. Space was either usable or not usable with no component of quality. In space–time saturation of usable space, density on an area would fluctuate due to stochastic events such as weather, but not habitat quality. Increasing habitat "quality" in space–time saturation would not result in increased densities. Guthery's (1997) hypothesis therefore would predict that demographic parameters would not vary within the bounds of habitat suitability.

Our data provide an indirect test of Guthery's (1997) usable space hypothesis. We know our study area is usable for bobwhites. Bobwhite populations have persisted at moderate to high densities on this large, contiguous landscape for at least the past 70 yr (Lehmann 1984). Thus, Guthery's (1997) hypothesis would be supported if demographic parameters did not vary among brush canopy cover classes, a prediction supported by our short-term findings. The long-term simula-

Table 4. Sample size (n), northern bobwhite density ($\hat{D}$; birds · ha^{-1}), and standard error (SE) estimated using helicopter surveys with distance sampling methodology during autumn (October–December), 2005–2008, Brooks County, Texas, USA.

| | | | Brush canopy cover | | | | | | |
| | 5% | | | 11% | | | 32% | | |
Year	n	$\hat{D}$	SE	n	$\hat{D}$	SE	n	$\hat{D}$	SE
2005	40	2.44	0.54	36	2.19	0.49	30	1.75	0.55
2006	16	0.67	0.31	9	0.42	0.29	14	0.51	0.35
2007	60	1.01	0.18	112	1.86	0.28	30	1.31	0.50
2008	33	0.31	0.12	39	0.64	0.16	12	0.18	0.11

Table 5. Number of replicate simulations (*n*), mean ($\bar{x}$), standard error (SE), minimum (Min), and maximum (Max) of northern bobwhite chick production, autumn density (birds $\cdot$ ha^{-1}), autumn population, spring population, and winter age ratio (juveniles:adult) by brush canopy cover class derived from a simulation model of a northern bobwhite population, Brooks County, Texas, USA.

| | | Brush canopy cover | | | | | | | | | | | |
| | | 5% | | | | 11% | | | | 32% | | | |
Parameter	*n*	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max
Chicks produced	120	404.6	33.7	0.6	1,728.1	940.5	64.2	0.0	3,666.6	1,100.0	62.5	7.3	3,338.6
Autumn density	120	0.68	0.05	0.00	2.60	0.70	0.03	0.02	1.79	0.8	0.04	0.1	2.4
Autumn population	120	565.3	44.1	0.1	2,020.3	1,320.7	76.1	17.3	3,904.7	1,400.3	59.7	400.6	3,283.1
Spring population	120	464.0	36.9	0.1	1,553.8	1,185.5	61.2	128.7	3,251.0	1,340.9	70.8	244.7	5,366.4
Winter age ratio	120	2.8	0.19	0.0	14.5	2.3	0.16	0.0	8.0	4.9	0.39	<0.1	25.3

tions, however, did not support this prediction. Population size and probability of persistence of simulated populations increased with increasing brush canopy cover. A prediction arising from the habitat-quality hypothesis is that productivity, survival, and density would be optimum at some point within the bounds of habitat selection. We documented that chick production at 11% and 32% brush canopy cover classes was nearly double the chick production at 5% brush canopy cover class. Therefore, these findings appear to lend support that there could still be a component of habitat quality even within the context of usable space as defined by Guthery (1997).

IMPLICATIONS

We documented that the influence of brush canopy cover on bobwhite populations differed between short and long time

scales. This is an important finding both from a managerial and theoretical perspective. Managerially, the finding is significant because land managers often make decisions based on habitat research of short duration, which could lead to ineffectual or incorrect decisions in the long term. Our study suggests that managers wanting to maximize autumn bobwhite populations on areas similar to our study area should manage for a minimum of 10–30% brush canopy cover at the pasture scale. Theoretically, the finding is relevant because current habitat-management paradigms for bobwhites involve two contrasting concepts: usable space and habitat quality. We found evidence for both hypotheses depending on the short-term and long-term influence of brush canopy cover. Understanding how time can interact and affect the theoretical framework of these hypotheses is important for advancing habitat theory for northern bobwhite.
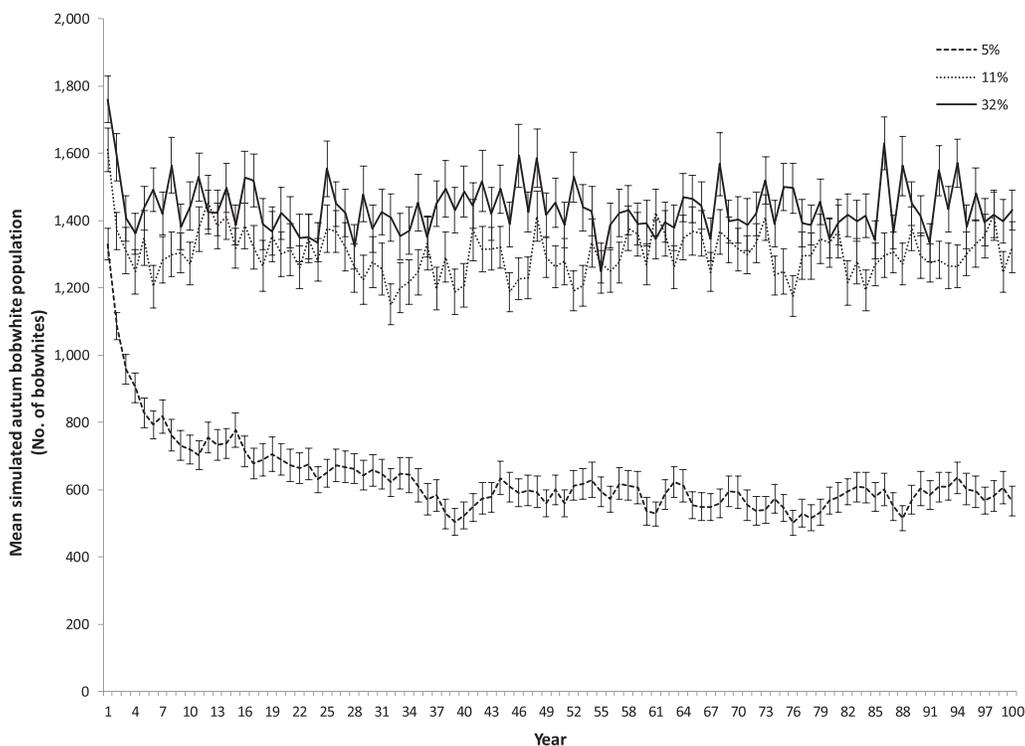

Figure 1. Simulated long-term trend mean ± standard error ($\bar{x} \pm$ SE) for autumn bobwhite populations in areas with 5%, 11%, and 32% brush canopy coverage, Brooks County, Texas, USA.
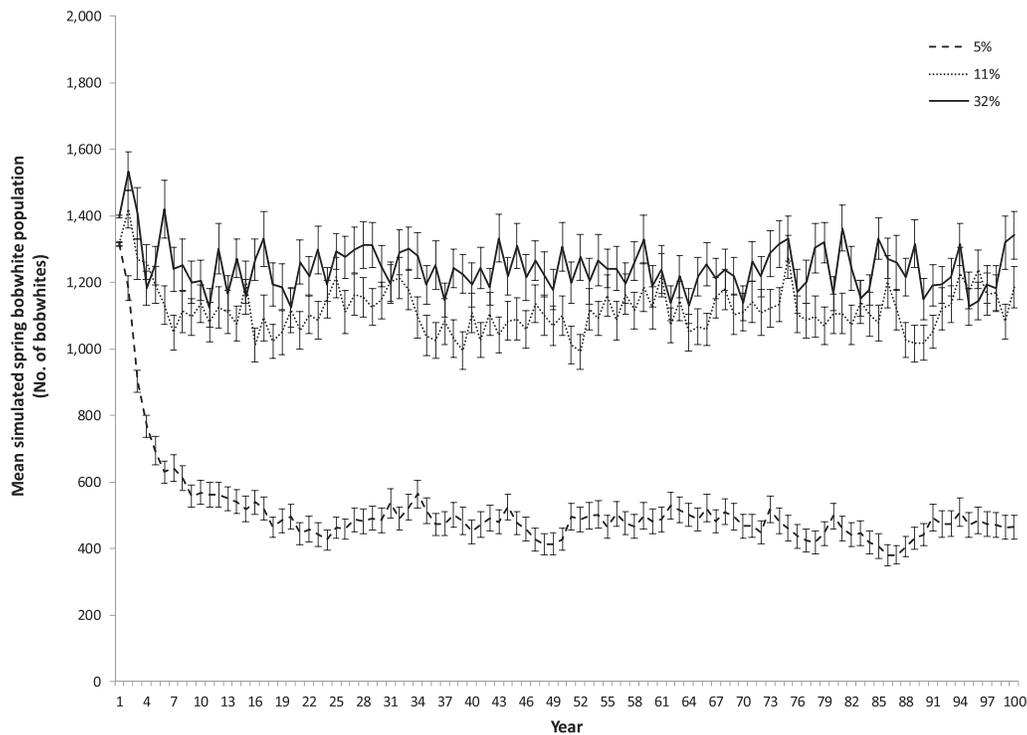
Figure 2. Simulated long-term trend mean ± standard error ($\bar{x}$ ± SE) for spring bobwhite populations in areas with 5%, 11%, and 32% brush canopy coverage, Brooks County, Texas, USA.

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