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A SIMULATION MODEL OF SUSTAINED-YIELD HARVEST FOR NORTHERN BOBWHITE IN SOUTH TEXAS

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ABSTRACT

Recommended sustainable harvest rates for northern bobwhite (*Colinus virginianus*) vary greatly and range from 25% to 70% of the prehunt population. Because northern bobwhite populations have declined across their geographic range, determining sustainable harvest levels is critical for effective management. Our objectives were to use simulation modeling to identify sustainable rates of bobwhite harvest, probability of population persistence, and minimum viable population estimates. We also conducted a sensitivity analysis to evaluate the impacts of harvest on northern bobwhite populations in Texas, USA. We constructed a simulation model using Program STELLA 9.0 for a hypothetical northern bobwhite population on 800 ha in the South Texas Plains USA and modeled population dynamics to 100 years over a range of harvest rates (0–40%). A 20% harvest rate produced the greatest average yields (mean \pm standard error = 231 \pm 10 bobwhites harvested/year). Given a quasi-extinction

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criterion of ≤ 40 bobwhites (≤ 0.05 bobwhite/ha), a 30% harvest rate resulted in a high probability of quasi-extinction (PE = 0.75) within 47.8 ± 2.3 years. A 40% harvest rate was not sustainable (PE = 1.0), with quasi-extinction occurring within 15.5 ± 2.6 years. Harvesting northern bobwhite populations in the South Texas Plains at rates of 20–25% of the prehunt population should maximize long-term harvest while minimizing the probability of population extinction. Spring densities of 0.60–0.80 bobwhite/ha may represent minimum viable spring densities for northern bobwhite populations in the South Texas Plains as these are the densities associated with sustainable 20–25% harvest rates. Harvest rates $>30\%$ are likely to be excessive with respect to long-term population persistence for northern bobwhite populations in the South Texas Plains.

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Key words: *Colinus virginianus*, northern bobwhite, population dynamics, simulation modeling, sustained-yield harvest, Texas

Sustained-yield harvest is a recommended but untested management philosophy for northern bobwhite (*Colinus virginianus*; hereafter, bobwhite(s); Roseberry 1982). Recommended rates for sustainable harvest of northern bobwhite range from 25% to 70% of the prehunt population (Stoddard 1931, Rosene 1969, Vance and Ellis 1972, Roseberry 1979, Lehmann 1984). Identifying the appropriate harvest rate for bobwhites is important because harvest is considered to be partially additive to natural mortality (Roseberry 1979, Roseberry and Klimstra 1984, Guthery 2002, Yeiser et al. 2021) and therefore hunting can lead to excessive harvest pressure, overharvest, and unsustainable survival rates (Brennan and Jacobson 1992, Rolland et al. 2010). A possible reason for the wide variation in recommended harvest rates is that study-specific conditions (e.g., interactions between density-dependent and density-independent phenomena, population trends, and landscape context) are dynamic, and bobwhites exist in a diverse array of habitat types which occur in varying degrees of availability across the landscape. Bobwhite populations are declining across most of their geographic range (Brennan 1991, Williams et al. 2004a). However, where habitat exists, population trends are often stable or increasing (Veech 2006). Fragmented habitats are likely to be associated with declining populations (Veech 2006), and declining populations are more sensitive to changes in survival rates than stable or increasing populations (Sandercock et al. 2008, DeMaso et al. 2011).

Minimum viable spring density is the minimum density necessary to produce a population that persists over time. Given highly variable bobwhite abundance in semiarid environments (Kiel 1976) and the importance of reproduction in compensating for additive harvest mortality under sustained-yield harvest (Roseberry 1979, Roseberry and Klimstra 1984), it is intuitive that the target spring density should be greater than or equal to minimum viable spring density, as this value represents the threshold beyond which harvest would be detrimental to population persistence. Current knowledge of desired spring density is speculative (DeMaso 1999, Peterson 1999), or estimates are based on maximum percent summer gain, which assumes density-dependent production (Guthery 2002).

Systems modeling and analysis provide a tool for addressing problems within complex systems and allow investigators to examine the interplay among factors that impact system dynamics (Grant et al. 1997, Sage et al. 2003). A systems modeling approach to problem solving fosters recognition of potential causal relationships within complex systems that may otherwise remain unidentified. Furthermore, such an approach permits the testing of predictive ecological theory through inductive and deductive reasoning (Grant et al. 1997:6–7). Systems and simulation modeling can be used as a tool for studying avian ecology and population dynamics (e.g., Martinez et al. 2005, Tichit et al. 2007), including research specific to Galliformes (Potts et al. 1984; Rader et al. 2011; DeMaso et al. 2011, 2013). Simulation models have been applied to evaluate the impacts of harvest on bobwhite (Roseberry 1979), wild turkey (*Meleagris gallopavo*; Lobdell et al. 1972, Suchy et al. 1983, Rolley et al. 1998, Schwertner 2005, McGhee et al. 2008), and gray partridge (*Perdix perdix*; Potts 1986). Simulation models where values can be adjusted based on available estimates of population parameters (e.g., survival and mortality rates, production, and dispersal rates) can be a powerful tool for evaluating the effects of harvest on populations and providing harvest recommendations to managers.

Bobwhite populations are declining throughout the majority of their range, and quantifying sustainable harvest rates represents an important component of effective management. Applying a systems approach to bobwhite population dynamics in Texas, USA requires knowledge of the factors that directly impact bobwhite population parameters. The objectives of this study were to 1) construct a data-based systems model of bobwhite population dynamics using a dynamic modeling approach, 2) determine optimal harvest rates and minimum viable spring densities of northern bobwhite via stochastic simulations, and 3) conduct a sensitivity analysis designed to evaluate the impacts of model parameters on abundance of the winter (hunted) population. We defined optimal harvest rates as those that maximize probability of long-term population persistence within the context of sustained-yield harvest while optimizing yield (number of bobwhites harvested per year) and hence hunting opportunity. Based on the results of Guthery et al. (2000) our research hypotheses were that 1)

bobwhite harvest rates of 25–30% of the prehunt population would represent sustainable rates of harvest for bobwhites in the South Texas Plains and produce the largest average yield, and 2) harvest rates >30% would reduce the probability of population persistence below 95% over 100 years.

STUDY AREA

We collected field data for this research in the South Texas Plains Ecoregion of Texas (Gould 1975). The South Texas Plains experiences high annual and seasonal variability in rainfall amount and distribution, and quail populations therein exhibit irruptive population behavior (Lehmann 1984). Historical accounts of the region vary greatly (e.g., barren desert or lush grassland) depending on the rainfall conditions at the time (Lehmann 1984).

The study area was located on private rangeland in Brooks County, Texas within a landscape composed predominantly of suitable quail habitat. Fieldwork was located primarily on 3 core areas distributed north to south and separated by approximately 5 km. The northernmost area (North Viboras) was 1,966 ha, the center area (La Loba) was 1,379 ha, and the southernmost area (Cuates) was 1,240 ha. Land uses on the study area included wildlife management for commercial hunting (primarily bobwhite and white-tailed deer [*Odocoileus virginianus*]) and cattle production, as well as oil and gas production. Bobwhite hunting on the study sites was conducted by following dogs from vehicles. Average annual rainfall was 617 mm (NOAA National Climatic Data Center 2008). Mean winter (Nov–Mar) temperature was 16.7° C and summer (Apr–Aug) temperature was 30.0° C (NOAA National Climatic Data Center 2008). Soils were primarily sands (USDA Natural Resources Conservation Service 2008).

The plant community was a mixed-brush community characteristic of the South Texas Plains (McLendon 1991). Common brush and cactus species included mesquite, huisache (*Acacia farnesiana*), granjeno (*Celtis pallida*), brasil (*Condalia hookeri*), and Texas prickly pear (*Opuntia lindheimeri*; Hernández et al. 2002). Common forbs included doveweed (*Croton* spp.) and sunflower (*Helianthus* spp.; Hernández et al. 2002). Common grasses were seacoast bluestem (*Schizachyrium scoparium*), gulf cordgrass (*Spartina spartinae*), sandbur (*Cenchrus incertus*), and purple threeawn (*Aristida purpurea*; Hernández et al. 2002).

METHODS

Demographic Data

We used data from the South Texas Quail Research Project, a long-term telemetry study in the South Texas Plains (DeMaso 2008) to develop a simulation model of the impacts of harvest on bobwhite population dynamics. Radio-telemetry data collected from 2000–2005 provided information on

reproductive ecology of bobwhites which were used to estimate parameters impacting bobwhite reproduction (Rader et al. 2007, DeMaso et al. 2011). Bobwhites were captured, handled, and marked within the guidelines of the Texas A&M University-Kingsville Animal Care and Use Committee (Approval No. 2003-3-3). DeMaso (2008) provides details regarding demographic parameter estimation from radio-marked bobwhites and independent parameter estimates.

Density

We used density (number of bobwhites/ha) estimates provided by Schnupp et al. (2013) for spring density, and estimates from Rusk et al. (2007) and Schnupp (2009) for fall density. Both Rusk et al. (2007) and Schnupp (2009) used helicopter-based distance sampling (Buckland et al. 2001) to estimate bobwhite density. Predetermined transects were traversed at a height of 7–10 m above ground level and velocity of 37 km/hour in a Robinson R-44 helicopter (Robinson Helicopter Co., Torrance, CA, USA). Rusk et al. (2007) and Schnupp (2009) provide details on estimation of density using Program Distance (Thomas et al. 2004).

Harvest and Age Ratios

We compiled harvest data from a commercial hunting camp on our study site for use as a comparison to our simulated harvest data. Harvest rates were estimated in the field on 2 pastures during the 2007–2008 and 2008–2009 hunting season (Sands 2010). Additionally, harvest data (birds harvested per pasture and age of harvested birds) were collected from 1983–2008 and used to estimate juvenile:adult age ratios. Bobwhites were identified as juvenile or adult by inspection of the primary coverts (Leopold 1939).

Model Development

Conceptual overview.—We constructed a stochastic, age- and sex-specific population model that estimated probability of population persistence under harvest rates ranging from 0–40% (Figure 1). The model followed the general approach of DeMaso et al. (2011) and Rader et al. (2011), where bobwhites were produced during the spring and summer and removed as a result of natural mortality during each season. The model represented a bobwhite population on a hypothetical property of 800 ha. Our model consisted of stocks (chicks, juveniles, and adult bobwhites), flows (transfer of chicks, juveniles, and adult bobwhites into or out of the model), and auxiliary variables (e.g., survival rates, reproduction) that influenced flows. We conceptualized (Figure 1) and programmed our model using STELLA version 9.0 (ISEE Systems, Lebanon, NH, USA).

We simulated the dynamics of the population and evaluated its probability of persistence in the presence of harvest over a 100-year period. Stochasticity was invoked during each 100-year simulation by randomly selecting values for production and survival from empirically determined Weibull probability distributions generated within SAS 9.1 (SAS Institute Inc.,

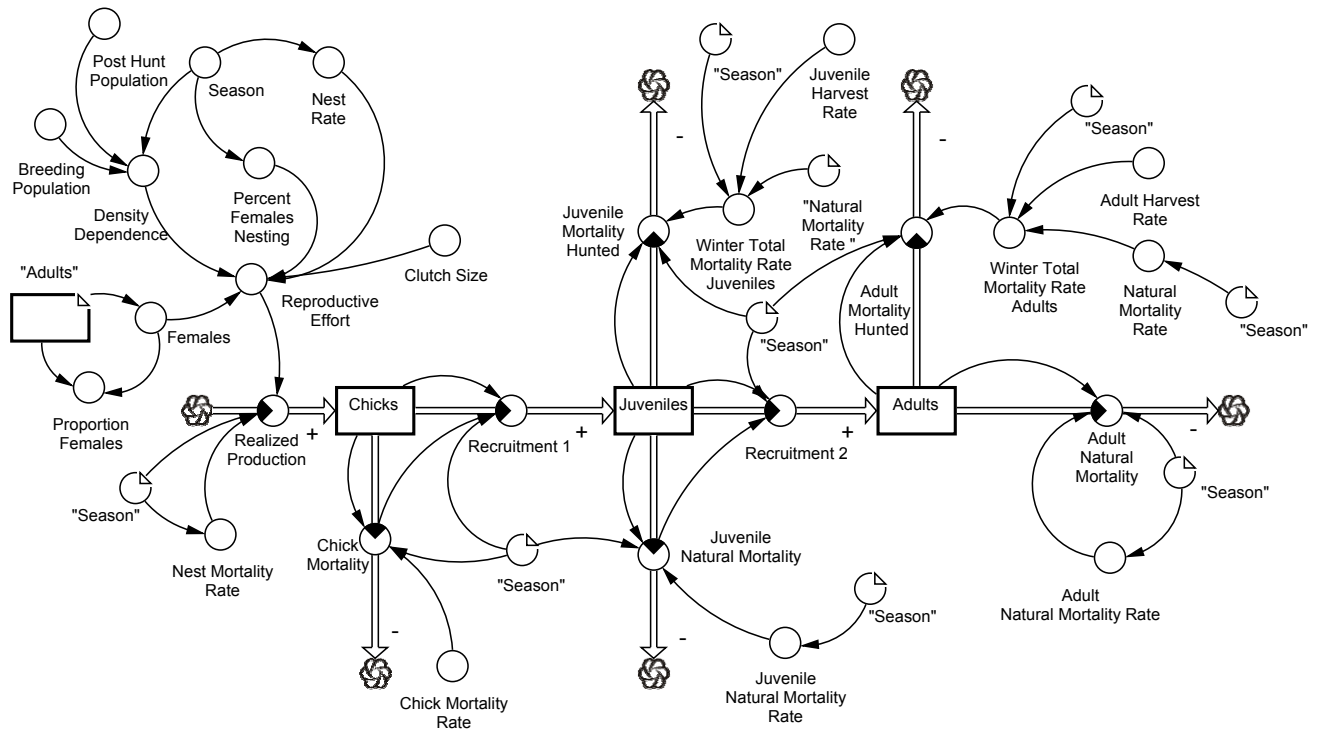


Fig. 1. A conceptual model of factors impacting northern bobwhite (*Colinus virginianus*) population dynamics in the South Texas Plains, USA. Boxes are state variables which represent stocks of northern bobwhites at different age classes (chicks, juveniles, and adults). Circles represent driving variables, auxiliary variables, or constants (e.g., natural mortality rates, density-dependence, harvest rates). Large arrows with centered circles represent flows. Flows transfer material into (+) or out of (-) state variables (e.g., production and mortality).

Cary, NC, USA). When Weibull parameters could not be estimated, we used normal distributions for stochastic variables (DeMaso et al. 2011).

Preliminary simulations.—Our reference value for determining population changes was 200 individuals in the simulated winter or spring populations, and change of 40 individuals in harvest at a significance level of $\alpha = 0.05$ with a probability of $P = 0.80$ that the difference would be detected if it existed (Grant et al. 1997). We estimated the number of simulations to run (n) using the formula provided by Sokal and Rohlf (1969:247) and Grant et al. (1997:61–64). We conducted 50 preliminary stochastic baseline simulations to obtain variance estimates for the following parameters: winter (hunted) population, spring (posthunt) population, and harvest. We used this information to calculate the required number of simulations. Preliminary simulations were conducted with a 20% harvest rate, and each model variable evaluated was simulated independently. Based on these calculations, we conducted 165 simulations for each level of harvest (0–40%) because it was the largest number of simulations considered necessary to achieve our objectives for model power (DeMaso et al. 2011).

Model Description and Specification

The model operated on a seasonal (quarterly) time step (Δt) of 3 months, where season 1 = spring (1 Mar–31 May), 2 = summer (1 Jun–31 Aug), 3 = fall (1 Sep–30 Nov), and 4 = winter (1 Dec–28 Feb), and was based on empirically derived

relationships and hypothesized links between population parameters and population dynamics (Figure 1; Appendices A, B). The model assumed that the 800-ha area was composed of 100% usable space (Guthery 1997) and that either no immigration or emigration occurred or immigration and emigration were equal.

Production.—Bobwhites in the South Texas Plains do not exhibit age-specific reproduction (Hernández et al. 2007a). The model considered all females entering the breeding period to have the same probability of initiating a nest. Banding records from the South Texas Plains indicate that approximately 45% of the spring adult bobwhite population was composed of females (Caesar Kleberg Wildlife Research Institute Quail Research Program unpublished data). We calculated the number of females in the breeding population ($Females_t$) each season by drawing from a normal distribution at time t with a mean value of 0.45 ± 1 standard deviation of the mean (Table 1). Values for percent females nesting ($PropNest_t$), clutch size ($ClutchSize_t$), and number of nests per hen ($NestRate_t$) were drawn each year from the Weibull distributions developed and used by DeMaso et al. (2011; Tables 1, 2). Density-dependent reproduction ($DDependence_t$) was incorporated by using a theoretical weak linear relationship described by Guthery et al. (2000) and developed and used by DeMaso et al. (2011): $DDependence = -0.00038386 \times \text{breeding population} + 0.95250$ (Table 2). Reproductive effort ($RepEffort_t$) was calculated as $ClutchSize_t \times Females_t \times NestRate_t \times DDependence_t$.

Table 1. Values of constants and parameters describing statistical distributions for stochastic variables in the population simulation model for northern bobwhites (*Colinus virginianus*) in the South Texas Plains, USA, during fall, winter, spring, and summer seasons. Parameters β , α , and γ represent the shape, scale, and location parameters of the Weibull distribution, and the parameters \bar{x} and σ represent the mean and standard deviation of the normal distribution. Both Weibull and normal distributions were truncated at 0.0 and the highest estimate from telemetry data, and values of parameters controlling reproduction were equal to zero except during spring and summer seasons (DeMaso et al. 2011). See text for details.

Parameter	Season ^a	Distribution	Value	β	α	γ	\bar{x}	σ
Production								
<i>DDependence</i>	1, 2		-0.004					
<i>ClutchSize_t</i>	1, 2	Weibull		14.306	4.988	0.000		
<i>Females_t</i>	1, 2	Normal					0.450	0.050
<i>NestRate_t</i>	1, 2	Weibull		0.766	1.361	0.975		
<i>PropNest_t</i>	1, 2	Weibull		25.289	1.569	42.827		
Mortality								
<i>ChickMortRate_t</i>	2, 3	Normal					0.4761	0.160
<i>JuvNatMortRate_t</i>	1, 2, 3, 4	Normal					0.2599	0.091
<i>AdultNatMortRate_t</i>	1, 2, 3, 4	Normal					0.2599	0.091
Harvest								
<i>JuvHarvestRate_t</i>	4	Constant	0–40% ^b					
<i>AdultHarvestRate_t</i>	4	Constant	0–40% ^b					

^a 1 = spring (breeding), 2 = summer, 3 = fall, 4 = winter (hunted)

^b Harvest was simulated at 0%, 10%, 15%, 20%, 25%, 30%, 40%, but remained constant during each set of simulations.

Table 2. Sample size (n), mean (\bar{x}), and 95% confidence interval (95% CI) for 7 model parameters used in the northern bobwhite (*Colinus virginianus*) sustained-yield harvest population model sensitivity analysis.

Category	Parameter	n	Descriptive parameter values	
			\bar{x}	95% CI
Productivity				
	<i>DDependence_t</i> ^a		-0.0004	
	<i>NestMort_t</i> ^b	109	0.6150	0.491–0.710
	<i>NestRate_t</i> ^c	15	1.7000	1.400–2.000
	<i>PropNest_t</i> ^c	15	0.6560	0.574–0.739
Mortality				
	<i>ChickMort_t</i> ^d	119	0.4761	
	<i>JuvNatMortRate_t</i> ^e	50	0.2599	
	<i>AdultNatMortRate_t</i> ^e	50	0.2599	

^a Slope of the theoretical, linear relationship between reproduction and spring and summer populations determined by DeMaso et al. (2011). No estimate of variance is associated with the intercept and slope of the regression line.

^b Estimate derived from data in Rader et al. (2007) for 23-day incubation period.

^c Estimate derived by DeMaso et al. (2011) based on empirical data from study site.

^d Estimate derived from data in Lusk et al. (2005).

^e Estimate based on 30% annual survival estimate for bobwhites in the South Texas Plains, USA (Hernández et al. 2007a, Sands et al. unpublished data)

Nest success was based on the daily nest survival rate (0.9593) estimated by Rader et al. (2007). We calculated the probability of nests surviving the incubation period (23 days) where survival = $0.9593^{23} = 0.3845$. Nest mortality (*NestMort_t*) = 0.6155 or $1 - \text{nest survival}$. We drew nest survival rates from a normal distribution ± 1 standard deviation of the mean. Realized reproduction (*RealReprod_t*) was calculated as the (*RepEffort_t*) – (*RepEffort_t* \times *NestMort_t*). *RealReprod_t* became the number of chicks (*Chicks_t*) hatched into the population each spring and summer.

Natural mortality.—Chick mortality was calculated using the 150-day survival rate based on the daily survival rate (0.9957) from Lusk et al. (2005). Chick survival = $0.9957^{150} = 0.5229$. Chick mortality rate (*ChickMortRate_t*) = 0.4771 or $1 - \text{chick survival}$. This rate was also used by DeMaso et al. (2011) to estimate chick survival during summer. We drew chick mortality rates from a normal distribution, ± 1 standard deviation of the mean, and calculated chick mortality (*ChickMort_t*) as *ChickMortRate_t* \times *Chicks_t*. We calculated recruitment of Chicks to juveniles (*Recruitment1*)

using $Chicks_t - ChickMort_t$. Individuals remaining after this calculation were classified as juveniles (*Juveniles*).

We calculated natural mortality of adults and juveniles based on an annual survival estimate of 30% (Hernández et al. 2007b). Each seasonal mortality rate (juvenile natural mortality rates: $JuvNatMortRate_t$ and adult natural mortality rates: $AdultNatMortRate_t$) was drawn from a normal distribution ± 1 standard deviation of the mean (Table 1). Natural juvenile mortality ($JuvNatMort_t$) was calculated as $Juveniles_t \times JuvNatMortRate_t$ and juvenile mortality during the hunting season was calculated as $Juveniles_t \times JuvHuntedMortRate_t$ (see following “Harvest” section). Recruitment of Juveniles to adults ($Recruitment_2$) was calculated as $Juveniles_t - JuvNatMort_t$ or $Juveniles_t - JuvHuntedMort_t$ (see “Harvest” section). Individuals remaining after this calculation were classified as adults ($Adults_t$). We calculated retention of adults from season to season as $Adults_t - AdultNatMort_t$ or $Adults_t - AdultHuntedMort_t$ (see “Harvest” section).

Harvest.—The model included harvest effects to evaluate the impacts of harvest within a sustained-yield harvest context. The winter population was subject to harvest (H) and natural mortality rate with the survivors constituting the breeding population. The impact of H on bobwhite mortality was modeled using the additive mortality model (Ricker 1958, Roseberry 1979, Guthery 2002):

$$Q_a = H_o + V_o - H_o V_o$$

where,

Q_a =total mortality rate from start to end of hunting season

H_o =harvest rate in a population with no natural mortality

V_o =natural mortality in the absence of harvest

The additive harvest model predicts that increasing the rate of harvest will increase the overall mortality rate (Q_a) within a population during the period of harvest, but that this increase does not result in 1:1 additivity because it accounts for natural mortality (V_o) that occurs within the population during the time of harvest (Roseberry 1979, Guthery 2002). We assumed that H_o was equal to a harvest rate H in a population that was experiencing natural mortality. H has been considered a sufficient approximation of H_o by other researchers (Roseberry 1981, Guthery 2002).

We calculated mortality of juveniles and adults during the hunting season as $JuvHuntedMort_t$ and $AdultHuntedMort_t$, where $JuvHuntedMort_t = Juveniles_t \times JuvHuntedMortRate_t$. $JuvTotalMortRate_t$ was the total mortality rate for juveniles during the winter (hunted population) and was calculated as $JuvHuntedMortRate_t = (JuvHarvestRate_t + JuvNatMortRate_t) - (JuvHarvestRate_t \times JuvNatMortRate_t)$. $AdultHuntedMortRate_t$ was the total mortality rate for adults during winter (hunted population) and was calculated as $AdultHuntedMortRate_t = (AdultHarvestRate_t + AdultNatMortRate_t) - (AdultHarvestRate_t \times AdultNatMortRate_t)$. $JuvHarvestRate_t$ was the percentage of juveniles harvested each hunting season. $AdultHarvestRate_t$ was the percentage of adults harvested each hunting season. Finally,

we calculated the number of bobwhites harvested each year ($Yield_t$) as $JuvHarvestRate_t \times Juveniles_t + AdultHarvestRate_t \times Adults_t$. We recognize that juvenile and adult bobwhites may be harvested at different rates during hunting season (Pollock et al. 1989, Shupe et al. 1990, Roseberry and Klimstra 1992). However, because bobwhites do not exhibit age-specific reproduction (Hernández et al. 2007a), and the determination of either age class cannot be made prior to harvest (e.g., hunters cannot distinguish adult birds from juveniles at flushing), we considered it justifiable to model these age classes with equal harvest rates. Essentially, we were more concerned with modeling the abundance of bobwhites from year to year and the number of bobwhites harvested than we were with modeling which demographic class (age and sex) to which each bobwhite in the population belonged.

We constructed a model that would optimize the yield from bobwhite hunting in the South Texas Plains while minimizing probability of population extinction. Guthery et al. (2000) suggested that bobwhites in southern latitudes (e.g., South Texas Plains) could sustain harvest rates $\leq 30\%$ and that 30–40% harvest rates would be excessive. Preliminary simulations indicated that 30–40% harvest could potentially impact population persistence, while harvest rates $\leq 10\%$ had no impact on persistence. Therefore, we ran 7 scenarios of 100-year simulations: 1) a baseline model (i.e., 0% harvest), 2) 10% harvest, 3) 15% harvest, 4) 20% harvest, 5) 25% harvest, 6) 30% harvest, and 7) 40% harvest.

Model Evaluation and Application

Simulated dynamics.—We evaluated the model by 1) visually inspecting model output for evidence of “boom and bust” dynamics characteristic of the South Texas Plains; 2) comparing the trend (slope \pm standard error [SE], 95% confidence interval [CI]) with an independent population index (i.e., August roadside counts conducted by Texas Parks and Wildlife Department [TPWD]); and 3) comparing our results with the observed estimates from our study site (Table 3). We estimated the winter (hunted) population and density, spring (posthunt) population and density, the total harvest (100-year total), population quasi-extinction (≤ 0.05 bobwhite/ha; DeMaso et al. 2011), mean harvest/year, finite rate of increase (λ), and proportion of density-based poor hunting conditions (winter population ≤ 0.60 bobwhite/ha; DeMaso et al. 2011) for each harvest scenario.

Model sensitivity.—We conducted a sensitivity analysis by using a deterministic version of the model. We made the model deterministic by assigning mean empirical values (DeMaso et al. 2011, Hernández unpublished data) to stochastic parameters (e.g., *PropNest*) and changing the value of one parameter by a consistent percentage. This was repeated for each variable used in the sensitivity analysis (Table 2). Mean variation of our stochastic parameters was approximately 17%; therefore, we varied each parameter in the sensitivity analysis by $\pm 17\%$ while holding the other parameters constant at their mean values.

Table 3. Comparisons between simulated and field estimated (observed) values of 5 population parameters of northern bobwhite (*Colinus virginianus*) populations in the South Texas Plains, USA. Simulated values are based on 165 stochastic baseline (0% harvest) runs; observed values are from the study area in Brooks County, Texas, 2001–2008.

Parameter	Simulated					Observed				
	<i>n</i>	\bar{x}	95% C	Min	Max	<i>n</i>	\bar{x}	95% CI	Min	Max
Spring density (bobwhites/ha) ^a	165	1.46	1.39–1.54	0.62	3.13	6	0.66	0.38–0.93	0.18	1.17
Winter density (bobwhites/ha) ^b	165	1.99	1.89–2.09	0.67	4.16	9	1.92	1.59–2.25	1.12	2.80
Juvenile:adult age ratio ^c	165	2.74	2.47–3.01	0.03	13.95	26	2.83	2.38–3.27	1.06	5.10
Finite rate of increase (λ) ^d	165	1.09	1.03–1.15	0.31	2.45	3	0.94	0.62–1.27	0.64	1.21

^a Observed estimates from Schnupp (2009).

^b Observed estimates from Rusk et al. (2007) and Schnupp (2009).

^c Observed estimates from hunter-harvested wings on study site, 1983–2008 (R. Howard, San Tomas Hunting Camp, personal communication).

^d Observed estimates calculated from Rusk et al. (2007) and Schnupp (2009) density estimates.

Bobwhite populations in the South Texas Plains are greatly impacted by production (Guthery et al. 2000, DeMaso et al. 2011). The simulation model constructed by DeMaso et al. (2011) was driven mostly by changes in nesting attempts per hen, nest survival, proportion of hens nesting, sex ratio at hatch, and density-dependent reproduction. We did not consider sex ratio at hatch as a model parameter, but we did evaluate the impacts of *NestMort*, *NestRate*, *PropNest*, and *DDependence* on the winter (hunted) population.

Sandercock et al. (2008) found that chick and adult survival parameters explained the greatest amount of variance in the λ of bobwhite populations. Thus, in addition to the production parameters, we tested the seasonal impacts of varying *JuvNatMortRate_p* and *AdultNatMortRate_t* on the winter population. It was not necessary to evaluate the impacts on spring population or yield as these parameters are correlated with the winter population (i.e., results would have been nearly identical).

Applied harvest management scenario.—Bobwhite managers in the South Texas Plains often discontinue harvest when they consider fall-winter populations too low to be safely harvested (e.g., 0.25 bobwhite/ha). We wanted to evaluate the effects of discontinuing harvest during population lows. Therefore, we conducted a series of simulations ($n = 191$) where no harvest was conducted ($Q_a = 0$) if the winter (season 4) density was <0.25 bobwhite/ha (200 birds). Otherwise, the population was harvested at rates of 20–30%. We determined the number of simulations necessary for this scenario using the methodology described earlier. Based on these results we ran 191 simulations of the harvest discontinuation scenario at 20%, 25%, and 30% harvest rates, and evaluated the impacts of these rates on winter and spring populations, probability of population persistence, yield, and frequency of hunting stoppage.

RESULTS

Model Dynamics

Visual inspection of our baseline model (Figure 2) indicated the dynamic “boom and bust” behavior typical of South Texas Plains bobwhite populations. Our baseline model was consistent (95% CIs overlapped) with 3 of 4 observed parameters (winter density adult:juvenile age ratio, and finite rate of increase) at our study site. Finite rate of increase from simulations indicated a 9% annual increase, whereas the observed estimate indicated a 6% annual decrease at our study site (Table 3). However, CIs of these estimates overlapped. Population trends (slope \pm SE, 95% CI) based on TPWD survey data and model data were different. The TPWD data indicated a declining trend (-0.72 ± 0.22 , 95% CI = $-1.16 - -0.28$), while our model output indicated a stable to slightly increasing trend (0.93 ± 0.94 , 95% CI = $-0.93 - 2.79$). Our model remained generally consistent (e.g., 95% CIs overlapping with 3 of 4 observed parameters) as harvest increased from 0–15% (Table 3, Appendix C). Beyond 20% harvest rates, 95% CIs of model predictions overlapped only with spring density (20% harvest, 25% harvest) and finite rate of increase (20% harvest, 25% harvest, 30% harvest, and 40% harvest; Appendix C).

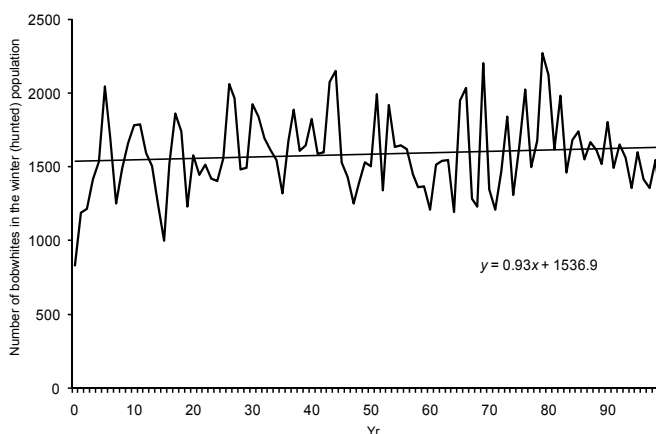


Fig. 2. Population projection and trend based on the mean of 5 randomly selected baseline (0% harvest) winter northern bobwhite (*Colinus virginianus*) populations simulated over a 100-year period.

Harvest Rates, Yield, and Population Persistence

Increasing harvest rates resulted in 11–94% decreases in mean winter (hunted) populations from the baseline population (Figure 3), and 21–95% decreases in mean spring (breeding) populations (Figure 4) as harvest increased from 0% to 40%. Our model indicated that bobwhite harvest rates $\leq 20\%$ did not impact probability of quasi-extinction [P (quasi-extinction) ≤ 0.95] (Table 4). A 20% harvest rate resulted in a 7% probability of quasi-extinction within an average (\pm SE) of 53.0 ± 7.8 years, a 30% harvest rate resulted in a 75% quasi-extinction probability within an average 47.8 ± 2.3 years, and a 40% harvest rate resulted in population quasi-extinction in 100% of simulations within an average of 15.5 ± 2.6 years (Table 4).

Harvest rates of 20% and 25% produced the greatest annual yield ($\bar{x} \pm$ SE: 231 ± 10 and 219 ± 11 bobwhites harvested/year, respectively), which also produced the greatest

total harvest over the 100-year simulation (Table 5). Since the model included a density-dependent production component, age ratios (juveniles:adults) increased by 15–54% as harvest rates increased from 0–30%; however, this relationship collapsed at a 40% harvest rate due to the high frequency of quasi-extinction. Mean spring densities at 20% and 25% harvest rates were 0.78 bobwhite/ha (95% CI: 0.71–0.84) and 0.60 bobwhite/ha (95% CI: 0.55–0.65), respectively (Appendix C).

Proportion of simulations with density-based poor hunting conditions (<0.6 bobwhite/ha) increased from 111% to 184% as the annual harvest rate increased from 10 to 40% (Table 6), but density-based poor hunting conditions occurred at all levels of harvest (0–40%). As harvest increased from 15% to 25%, the mean number of years with poor harvest conditions increased from 5.53 ± 0.45 (95% CI: 4.65–6.41) to 26.41 ± 1.08 (95% CI: 24.29–28.53), a 378% increase per 100 years (Table 6).

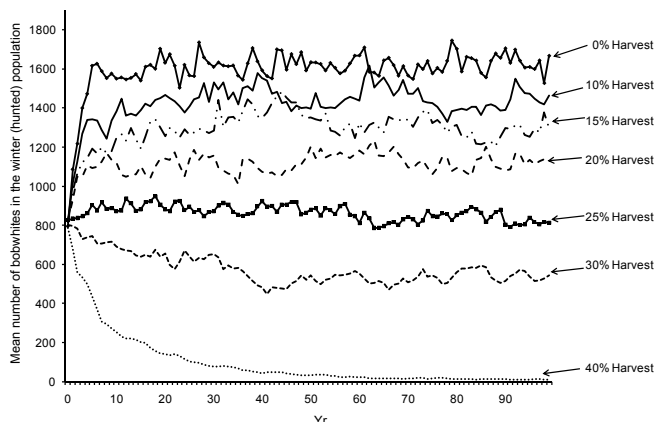


Fig. 3. Trends in simulated mean winter (hunted) northern bobwhite (*Colinus virginianus*) populations on an 800-ha area based on 165 simulations at 0%, 10%, 20%, 25%, 30%, and 40% harvest rates in the South Texas Plains, USA.

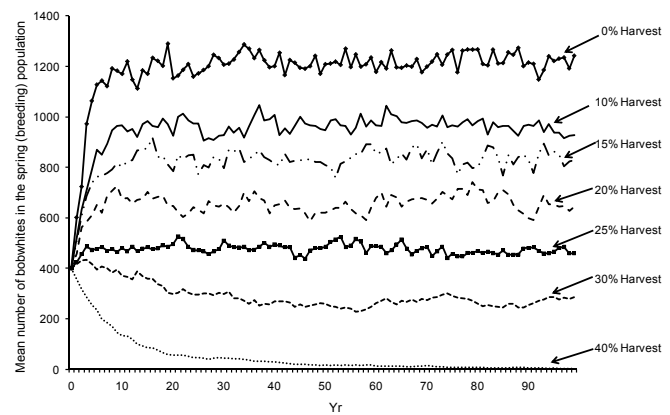


Fig. 4. Trends in simulated mean spring (breeding) northern bobwhite (*Colinus virginianus*) populations on an 800-ha area based on 165 simulations at 0%, 10%, 20%, 25%, 30%, and 40% harvest rates in the South Texas Plains, USA.

Table 4. Relationship between percent harvest, abundance (winter and spring), probability of population persistence (P), and time to quasi-extinction^a in a simulated northern bobwhite (*Colinus virginianus*) population in the South Texas Plains, USA ($n = 165$, 100-year simulations).

Harvest	Seasonal abundance								P	Population persistence			
	Winter population ^b				Spring population ^c					Time to quasi-extinction (years)			
	$\bar{x} \pm$ SE	95% CI	Min	Max	$\bar{x} \pm$ SE	95% CI	Min	Max		$\bar{x} \pm$ SE	95% CI	Min	Max
0%	1,509 \pm 41	1,509–1,671	539	3,328	1,170 \pm 30	1,112–1,229	497	2,501	1.00	–	–	–	–
10%	1,402 \pm 51	1,302–1,503	320	3,781	952 \pm 32	889–1,015	123	2,419	1.00	–	–	–	–
15%	1,347 \pm 47	1,255–1,438	301	3,921	820 \pm 33	755–886	107	2,304	1.00	–	–	–	–
20%	1,148 \pm 45	1,059–1,237	260	3,163	621 \pm 26	570–671	110	1,679	0.93	53.0 \pm 7.8	37.6–68.2	10.5	92.5
25%	863 \pm 41	784–943	43	3,185	480 \pm 22	437–523	25	1,428	0.75	56.5 \pm 4.0	48.6–64.3	16.3	99.5
30%	522 \pm 35	453–591	13	2,525	260 \pm 18	225–297	4	1,395	0.25	47.8 \pm 2.3	43.3–52.3	4.5	97.5
40%	34 \pm 7	20–48	0	844	16 \pm 2	12–20	0	159	0.00	15.5 \pm 2.6	10.4–20.6	3.5	53.3

^a Quasi-extinction occurs when the population declines to ≤ 40 bobwhites (≤ 0.05 bobwhite/ha; DeMaso et al. 2011).

^b Winter population (season 4) is the population subject to hunter harvest.

^c Spring population (season 1) is the population immediately following hunting season and represents the initial breeding population for the next year.

Table 5. Simulated yield (mean \bar{x} , standard error [SE], 95% confidence interval [CI], range, mean 100-year total yield) from a northern bobwhite (*Colinus virginianus*) population at 6 different rates of harvest in the South Texas Plains, USA ($n = 165$ simulations).

Harvest Rate	Average annual yield				Mean total yield (100 years)			
	$\bar{x} \pm \text{SE}$	95% CI	Min	Max	$\bar{x} \pm \text{SE}$	95% CI	Min	Max
10%	153 \pm 5	143–164	22	357	14,428 \pm 95	14,242–14,613	10,779	17,111
15%	189 \pm 7	176–201	47	472	19,188 \pm 154	18,885–19,490	14,484	24,333
20%	231 \pm 10	211–252	43	888	22,461 \pm 278	21,917–23,005	13,876	31,502
25%	219 \pm 11	198–248	15	696	22,269 \pm 342	21,599–22,938	9,692	32,032
30%	158 \pm 10	137–179	2	737	16,822 \pm 414	16,009–17,636	4,122	29,113
40%	18 \pm 5	8–27	0	719	4,192 \pm 236	3,730–4,654	519	17,671

Table 6. Proportion of simulations with density-based poor hunting conditions (≤ 0.60 bird/ha in the winter population; DeMaso et al. 2011) and mean number of years with density-based poor hunting conditions per 100-year simulation at 7 different rates of harvest in the South Texas Plains ($n = 165$).

Harvest rate	Simulations with poor hunting conditions	Years with poor hunting conditions			
		$\bar{x} \pm \text{SE}$	95% CI	Min	Max
0%	35.2%	0.72 \pm 0.11	0.51–0.92	0	6
10%	74.5%	2.78 \pm 0.24	2.31–3.24	0	15
15%	87.2%	5.53 \pm 0.45	4.65–6.41	0	39
20%	97.6%	12.12 \pm 0.69	10.80–13.53	0	47
25%	100.0%	26.41 \pm 1.08	24.29–28.53	2	72
30%	100.0%	52.67 \pm 1.44	49.85–58.49	11	97
40%	100.0%	93.90 \pm 0.46	92.99–94.81	67	100

Model Sensitivity

Changes in reproductive parameters had the greatest impacts on simulated winter (hunted) populations (Table 7). Specifically nest mortality ($NestMort_t$) had the largest impact on the winter population. A 17% increase in nest mortality resulted in a 93% decrease in the winter population (Table 7). The proportion of hens nesting ($PropNest_t$) and the number of nests per hen ($NestRate_t$) had the same impact on fall populations. Increasing either of these parameters by 17% resulted in a 37% population increase. Reducing either variable by 17% resulted in a 52% population decrease. Reducing density-dependence ($DDependence_t$) in reproduction by 17% resulted in a 20% population increase, and increasing density-dependence in reproduction by 17% resulted in a 14% decrease in the population.

With the exception of chick mortality ($ChickMort_t$), mortality parameters had a comparatively low impact on the winter population. Reducing chick mortality by 17% resulted in a 34% population increase, and increasing chick mortality by 17% resulted in a 47% population decrease (Table 7). Increasing spring adult mortality ($AdultNatMortRat_1$) by 17% resulted in an 11% population decrease (Table 7). Increasing or reducing the remaining mortality rates of adults and juveniles resulted in <10% population increases or declines (Table 7).

Despite relatively high sensitivity of our deterministic model, our stochastic model was generally consistent

(95% CIs overlapping in 4 of 5 parameters) with observed parameters as harvest rates ranged from 0–25%, and appeared to be robust to changes in harvest rates $\leq 25\%$ with respect to observed data. Given that estimated harvest rates on our study area averaged $15.6 \pm 7.2\%$ per year (Sands 2010), it should not necessarily be expected that model predicted population parameters would remain consistent with field estimates at relatively high (30% and 40%) harvest rates.

Model Applications: Harvest in an Applied Context

Our harvest management scenario indicated that when hunting was discontinued at 0.25 bird/ha, probability of population persistence increased for 20%, 25%, and 30% harvests (Table 8). However, despite decreased probability of quasi-extinction at 30% harvest rates, 20% and 25% harvest rates resulted in 21% and 23% greater annual yields of bobwhites, respectively (Table 9). Mean spring densities at 20% and 25% harvest rates were 0.81 (95% CI: 0.75–0.87) and 0.66 (95% CI: 0.61–0.72), respectively. This scenario also indicated harvest rates of 30% resulted in increased frequency of hunting season closure and reduced average yields compared to harvest rates <30% (Table 10). In 30% harvest simulations, hunting seasons were closed at least once in 96.3% of simulations, with a mean of 6.6 ± 0.3 seasons (Table 10).

Table 7. Northern bobwhite (*Colinus virginianus*) sensitivity analysis of 11 model parameters varied by $\pm 17\%$, based on variation associated with empirical parameter estimates (if there was a measure of variation associated with the estimate), and the absolute difference between the winter (hunted) population, at -17% and $+17\%$, and their percent difference from the baseline (mean values for all model parameters): winter population (1,351 bobwhites).

Category	Parameter	Variation	Winter (hunted) population difference		
			Value	Absolute difference	% Difference
Productivity					
<i>DDependence_t</i>		+17%	1,155	472	-14.51
		-17%	1,627		
<i>NestMort_t</i>		+17%	90	2,001	-93.34
		-17%	2,091		
<i>NestRate_t</i>		+17%	1,854	1,213	37.23
		-17%	641		
<i>PropNest_t</i>		+17%	1,854	1,213	37.23
		-17%	641		
Mortality					
<i>ChickMort_t</i>		+17%	717	1,098	-46.93
		-17%	1,815		
<i>JuvNatMortRate₃</i>		+17%	1,249	196	-7.55
		-17%	1,445		
<i>JuvNatMortRate₄</i>		+17%	1,269	155	-6.07
		-17%	1,424		
<i>AdultNatMortRate₁</i>		+17%	1,201	281	-11.10
		-17%	1,482		
<i>AdultNatMortRate₂</i>		+17%	1,285	131	-4.89
		-17%	1,416		
<i>AdultNatMortRate₃</i>		+17%	1,285	131	-4.89
		-17%	1,416		
<i>AdultNatMortRate₄</i>		+17%	1,226	230	-9.25
		-17%	1,456		

Table 8. Relationship between percent harvest, abundance (winter and spring), probability of population persistence (P), and time to quasi-extinction^a in a simulated northern bobwhite (*Colinus virginianus*) population at 3 different rates of harvest in the South Texas Plains, USA ($n = 191$, 100-year simulations) when harvest is discontinued when winter populations are ≤ 0.25 birds/ha (200 birds).

Harvest	Seasonal abundance								P	Population persistence			
	Winter population ^b				Spring population ^c					Time to extinction (years)			
	$\bar{x} \pm SE$	95% CI	Min	Max	$\bar{x} \pm SE$	95% CI	Min	Max		$\bar{x} \pm SE$	95% CI	Min	Max
20%	1,114 \pm 40	1,034–1,194	204	2,770	651 \pm 24	604–698	98	2,121	0.99	51.0 \pm 0.0	– 51.0	51.0	
25%	911 \pm 38	836–986	126	3,220	531 \pm 24	484–577	82	1,791	0.97	47.5 \pm 8.6	30.6–64.4	26.5 77.5	
30%	584 \pm 27	530–638	116	2,200	321 \pm 15	291–351	69	1,043	0.94	37.5 \pm 8.1	21.6–53.5	6.8 88.5	

^a Quasi-extinction occurs when the population decline to ≤ 40 bobwhites (≤ 0.05 bobwhite/ha; DeMaso et al. 2011).

^b Winter population (season 4) is the population subject to hunter harvest.

^c Spring population (season 1) is the population immediately following hunting season and represents the initial breeding population for the next year.

Table 9. Simulated yield (mean [\bar{x}], standard error [SE], 95% confidence interval [CI], range, mean 100-year total yield) from a northern bobwhite population at 3 different rates in the South Texas Plains, USA ($n = 191$ simulations) when harvest is discontinued when winter populations are ≤ 0.25 bird/ha (200 birds).

Harvest rate	Average annual yield				Mean total yield (100 years)			
	$\bar{x} \pm SE$	95% CI	Min	Max	$\bar{x} \pm SE$	95% CI	Min	Max
20%	232 \pm 9	214–249	0	681	22,393 \pm 223	21,956–22,829	13,145	29,770
25%	228 \pm 11	207–250	0	994	22,106 \pm 280	21,557–22,564	11,581	32,509
30%	188 \pm 11	166–209	0	1,071	19,716 \pm 308	19,113–20,319	11,659	35,697

Table 10. Proportion of simulations with ≥ 1 year harvest ending density ≤ 0.25 bobwhite/ha and mean number of years with a harvest ending per 100-year simulation at 3 different harvest rates in the South Texas Plains, USA ($n = 165$ simulations) when winter populations are ≤ 0.25 bird/ha (200 bobwhites).

Harvest rate	Simulations with ≥ 1 year ending	Mean number of years with ending			
		$\pm SE$	95% CI	Min	Max
20%	29.3%	0.68 \pm 0.11	0.47–0.88	0	9
25%	70.7%	2.35 \pm 0.19	1.98–2.71	0	13
30%	96.3%	6.61 \pm 0.31	5.99–7.22	0	21

DISCUSSION

Sustainable Harvest Rates and Spring Population Goals

Sustainable harvest rates.—Harvesting bobwhite populations in the South Texas Plains at rates of $\leq 20\%$ of the prehunt population may maximize long-term harvest while minimizing the probability of population extinction, at least on areas that represent fully usable habitat space and in populations that tend to be stable to increasing from year to year (as was the case for our simulated population). Additionally, our model indicated that harvest rates $>30\%$ would significantly decrease the probability of long-term population persistence, and that 40% harvest rates would result in population extinction. This represents sustainable harvest rates that are lower than those reported from other regions of the bobwhite range (e.g., Vance and Ellis 1972, Roseberry 1979).

Vance and Ellis (1972) suggested that harvest rates as high as 60–80% of the hunted population had no detrimental impact on bobwhite abundance. Based on our results and those of Roseberry (1979), we question these estimates in the absence of significant immigration that perhaps masked detrimental effects of these harvest rates. Simulations based on a 24-year dataset (Roseberry and Klimstra 1972) of demographic data from southern Illinois, USA (Roseberry 1979) indicated that harvest rates $\geq 50\%$ of the population severely impacted the ability of bobwhite populations to compensate for losses from hunting. These harvest rates required exponential increases in summer gains to maintain stable population densities. However, harvest rates of 40–45% appeared to be acceptable for maintaining suitable densities in Illinois (Roseberry 1979).

Scale of hunting (i.e., property size) influences sustainable yields. For example, Guthery et al. (2000) reported that probability of persistence did not reach 0.95 for populations subject to summer catastrophes (e.g., severe droughts) and experiencing 40% harvest until demographic capacities exceeded 10,000. The density required to sustain a 40% harvest may be reasonable for a large property (e.g., $\geq 10,000$ ha; 1 bobwhite/ha) but not for our hypothetical property (800 ha; 12.5 bobwhites/ha). It should be noted that given our model conditions (800-ha area, 0% immigration), 40% harvest rates were never sustainable over a 100-year simulation.

Spring population goals.—In arid and semiarid regions, New World quail population dynamics are influenced by weather (Heffelfinger et al. 1999, Hernández et al. 2005). Influences of rainfall and temperature are likely to obscure effects of density-dependent population mechanisms, and may result in weak density-dependent population growth. Using harvest rates to achieve spring (breeding) population goals is a longstanding component of sustained-yield harvest theory (Roseberry 1982). Our data indicate that spring densities of 0.60–0.80 bobwhite/ha are associated with harvest rates that optimize harvest and reduce probability of population extinction (20% and 25% harvest rates). The probability of extinction further declines when harvest is discontinued during years of poor production. To this end, the range of 0.60–0.80 bobwhite/ha represents a minimum viable spring density for bobwhites in the South Texas Plains. Mean field estimates of spring densities on our study sites were 0.66 bobwhite/ha (95% CI: 0.38–0.93), which may indicate that some bobwhite populations in this region currently occur near this density at the beginning of the breeding period.

The simulation model developed by Yeiser et al. (2021) based on data from bobwhites in the Red Hills region of the

Gulf Coastal Plain, USA, indicated that density-dependence was unlikely to fully compensate for harvest mortality even when density-dependence was relatively strong. In regions where density-dependent effects may be relatively weak relative to the impact of weather conditions (Sands 2010), the predictability of reproduction based on spring density may become even more tenuous. In declining bobwhite populations, hunting pressure may actually increase (Brennan and Jacobson 1992), and harvest can become an increasingly additive and unsustainable component of mortality (Rolland et al. 2010). In declining populations, sustainable harvest rates may be lower than the 15–25% range suggested by our model.

A more conservative and perhaps more appropriate approach to harvest management in these situations is to determine a long-term sustainable harvest rate (e.g., 15%), prescribe a harvest based on the prehunt population (e.g., 150 of 1,000 birds), and discontinue harvest when prehunt density is $<0.25/\text{ha}$. Weak density-dependence in the South Texas Plains populations of bobwhites decreases the benefits of harvesting in excess of 25% to reach the minimum viable spring density. This is because a positive density-dependent response in reproduction, as a result of reduced abundance, is likely to be less pronounced than in other regions. Successful implementation of either strategy depends on precise (e.g., $\pm 5\%$ of the true population) estimates of the hunted population.

Managing Hunting to Facilitate Sustainable Harvests

Timing of harvest.—Bobwhite harvest is considered additive to natural mortality (Roseberry and Klimstra 1984, Williams et al. 2004b), and timing of harvest impacts the degree of additive mortality that results from harvest (Kokko and Lindström 1998, Kokko 2001). The majority of harvest in the South Texas Plains occurs from December to February. Presumably, harvesting during the late winter (Jan–Feb) produces more additive mortality than if the majority of harvest occurred from October to December. Bobwhite hunting conditions are often less than optimal (i.e., temperatures $>30^\circ\text{C}$; abundant, green cover conditions prior to a winter frost) during the early portions of legal hunting season in the South Texas Plains, and many hunters prefer to hunt late in the season. Given this, it is important to choose harvest rates that will not result in excessive additivity. Our model indicates that harvest rates $<20\%$ should be sustainable on a long-term basis.

Hunting pressure.—Hardin et al. (2005) recognized that hunting pressure and harvest could be managed by altering hunting behaviors within the context of hunter-covey interface theory (Radomski and Guthery 2000, Guthery 2002). Once a winter hunted population is estimated and a harvest prescription assigned, the level of daily harvest can be determined: daily harvest \times number of days hunted = prescribed yield. Daily harvest can be controlled by regulating number of birds killed per covey (both bagged and wounded) or velocity (km/hour) of hunting parties, or both (Hardin et al. 2005). Conducting hunts at low velocities has potential

to reduce daily harvest without reducing total hunting time (Hardin et al. 2005), which could impact hunter satisfaction.

Connecting Harvest Management to Habitat Management

The widespread decline of the bobwhite in the United States is primarily the result of broadscale habitat loss and degradation (Brennan 1991, 1999). Management of bobwhite habitat and harvest has traditionally been conducted at improper scales, which may have exacerbated this decline (Williams et al. 2004a), especially considering that unsustainable harvest rates and harvest pressure exist in locations where populations are declining (Brennan and Jacobson 1992, Rolland et al. 2010). Researchers who study migratory game birds have recognized that connecting population goals based on harvest and habitat management objectives would improve conservation of these species (Runge et al. 2006, Rappole et al. 2008). The reason for this is that where habitat is lost, sustainable annual yields decrease (Runge et al. 2006). Conversely, expansion of habitat increases the level of sustainable annual yields and improves hunting opportunity (Runge et al. 2006).

A parallel situation exists within the bobwhite management paradigm. For instance, in the South Texas Plains, a reduction in necessary habitat components (e.g., abundance of available nesting cover) resulted in simulated bobwhite populations decreasing by 75% from baseline conditions (Rader et al. 2011). Our model indicates that reducing the hunted population by 33% would result in a 28% decrease in mean annual harvest yield. Thus, it appears that the effect of maintaining usable bobwhite habitat space (Guthery 1997) on bobwhite population production, yield, and ultimately population viability is palpable. Given that rangewide bobwhite population recovery requires a landscape-scale approach to habitat management and a regional or local approach to harvest management (Peterson 2001, Williams et al. 2004a), bobwhite conservation would be best suited by unifying population recovery goals with habitat and harvest objectives.

MANAGEMENT IMPLICATIONS

Harvesting bobwhite populations in the South Texas Plains at rates of 20–25% of the prehunt population (based on accurate population estimates) may maximize long-term harvest while minimizing the probability of population extinction. Harvest rates $>30\%$ are excessive with respect to long-term population persistence. For high probability of population persistence and optimal yield, managers should harvest 15–20% of winter bobwhite populations and discontinue harvest when winter populations are ≤ 0.25 bird/ha. Managers must realize that even in the presence of optimal habitat and conservative harvest (15–25% mean annual harvest), density-based poor hunting conditions will occur in 5–25% of hunting seasons. However, maximizing usable habitat area within a landscape has the potential to increase annual yield of bobwhites.

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APPENDIX A.

Parameter and variable definitions used to simulate bobwhite harvest in the South Texas Plains.

Parameter or variable	Definition
$Adults_t$	Adult northern bobwhite (individuals ≥ 1 year old).
$AdultHarvestRate_4$	Proportion of adult northern bobwhites removed from the population by hunting during season 4.
$AdultHuntedMort_4$	Total mortality of adults during season 4.
$AdultHuntedMortRate_4$	Total mortality rate of adults during season 4 as calculated by the additive harvest model (see text).
$AdultNatMortRate_t$	The natural mortality rate of adults in seasons 1–4.
Area	Geographic area of interest in the model (800 ha).
$Chicks_t$	Number of eggs successfully hatched.
$ChickMort_t$	Number of chicks dying during season 2 and season 3.
$ChickMortRate_t$	Proportion of chicks dying during season 2 and season 3.
$ClutchSize_t$	Clutch size for northern bobwhites during the breeding season (season 1 and season 2).
Δt	Represents the time step of the model. Time step from t to $t + 1$ (3 months or 1 season).
$Density_t$	Number of northern bobwhites/ha.
$DDependence_4$	Density-dependent reproduction, a density-dependent feedback loop that scales the relationship between the breeding population (season 1 and season 2). Study site-specific values were derived by DeMaso et al. (2011).
$Juveniles_t$	The number of chicks surviving to become juveniles in season 3 and season 4.
$JuvHarvestRate_4$	The proportion of juveniles removed from the population by hunting during season 4.
$JuvHuntedMortRate_4$	The total mortality rate of juveniles during season 4 as calculated by the additive harvest model (see text).
$JuvHuntedMort_4$	Total juvenile mortality during season 4.
$JuvNatMort_t$	Natural mortality rate of juveniles during season 3 and season 4.
$Females_t$	Number of females in the population during a given season.
$NestRate_t$	Number of nests initiated per female during the breeding season (season 2 and season 3).
$PropNest_t$	Proportion of females in the population nesting during the breeding season (season 2 and season 3).
$RealReprod_t$	Number of chicks (Chickst) hatched into the population each spring and summer (season 2 and season 3).
$Recruitment1$	Number of chicks becoming juveniles in season 2 and season 3.
$Recruitment2$	Number of juveniles becoming adults in season 3 and season 4.
$RepEffort_t$	Number of eggs produced each breeding period.
$Season_{1-4}$	Counter that represents 4 periods in a year as they relate to northern bobwhite phenology in the South Texas Plains: 1 = spring (1 Mar–31 May); 2 = summer (1 Jun–31 Aug); 3 = fall (1 Sep–30 Nov); 4 = winter (1 Dec–28 Feb).
$Yield_4$	The number of northern bobwhite harvested during winter (season 4).

APPENDIX B.

Difference equations used in STELLA 9.0 to parameterize and run harvest simulation model.

Hunter_Harvest =

Adults(t) = Adults(t - dt) + (Recruitment_2 - Adult_Mortality_Hunted - Adult_Mortality_Natural) * dt

INIT Adults = 200

INFLOWS:

Recruitment_2 = If (Season = 3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0

OUTFLOWS:

Adult_Mortality_Hunted = If (Season = 4) then (Adults*Winter_Total__Mortality__Rate_Adults) else 0

Adult_Mortality_Natural = If (Season = 1) or (Season = 2) or (Season = 3) then (Adults*Post_Hunt_through_Breeding__Mortality_Rate) else 0

Juveniles(t) = Juveniles(t - dt) + (Recruitment_1 - Recruitment_2 - Juvenile__Mortality__Hunted - Juvenile__Mortality__Natural) * dt

INIT Juveniles = 0

INFLOWS:

Recruitment_1 = If (Season = 2) then (Chicks-Chick__Mortality) else if (Season = 3) then (Chicks-Chick__Mortality) else 0

OUTFLOWS:

Recruitment_2 = If (Season = 3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0

Juvenile__Mortality__Hunted = if (Season = 4) then ((Juveniles*Juvenile_Total_Mortality_Rate__Winter)) else 0

Juvenile__Mortality__Natural = If (Season = 3) then (Juveniles * Juvenile_Mortality_Rate) else 0

Adults__Harvested = Adults*Harvest__Rate

Age_Ratio = If (Season = 3) then (Juveniles/Adults) else if (Season = 4) then (Juveniles/Adults) else 0

Harvest__Rate = If (Season = 4) then 0.4 else 0

Hunted__Density = If (Season = 4) then (Hunted__Population/Area) else 0

Juveniles__Harvested = Juveniles*Harvest__Rate

Northern_Bobwhite__Harvested = Adults__Harvested+Juveniles__Harvested

Season = Counter (1,5)

Productivity =

Bounded_Density_Dependence = If (Density__Dependence < 0) then 0 else (Density__Dependence) Clutch_Size = If (Season = 1) THEN (14.30617 * (-LN(RANDOM(0,1)))^(1/4.98768) + 0) ELSE

If (Season = 2) THEN (14.30617 * (-LN(RANDOM(0,1)))^(1/4.98768) + 0) ELSE 0

Eggs = Clutch_Size*Nests

Females = Adults*NORMAL(0.45, 0.05)

Nests = (Females*Nest__Rate*Percent_Females__Nesting)*Bounded_Density_Dependence

Nest__Rate = If (Season = 1) THEN (0.76644 * (-LN(RANDOM(0,1)))^(1/1.36121) + 0.97447) else if (Season = 2) THEN (0.76644 * (-LN(RANDOM(0,1)))^(1/1.36121) + 0.97447) ELSE 0

Percent_Females__Nesting = If (Season = 1) then ((25.28907 * (-LN(RANDOM(0,1)))^(1/1.56920) + 42.82725)/100) ELSE if (Season = 2) THEN ((25.28907 * (-LN(RANDOM(0,1)))^(1/1.56920) + 42.82725)/100) ELSE 0

Seasonal_Population_Parameters = Adults(t) = Adults(t - dt) + (Recruitment_2 - Adult_Mortality_Hunted - Adult_Mortality_Natural) * dt

INIT Adults = 400

INFLOWS:

Recruitment_2 = If (Season = 3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0

OUTFLOWS:

Adult_Mortality_Hunted = If (Season = 4) then (Adults*Winter_Total__Mortality__Rate_Adults) else 0

Adult_Mortality_Natural = If (Season = 1) or (Season = 2) or (Season = 3) then (Adults*Post_Hunt_through_Breeding__Mortality_Rate) else 0

Chicks(t) = Chicks(t - dt) + (Realized__Production - Recruitment_1 - Chick__Mortality) * dt

INIT Chicks = 0

INFLOWS:

Realized__Production = If (Season = 1) then (Reproductive_Effort)-(Reproductive_Effort*Nest_Mortality_Rate) else if (Season = 2) then (Reproductive_Effort)-(Reproductive_Effort*Nest_Mortality_Rate) else 0

Appendix B, continued

Difference equations used in STELLA 9.0 to parameterize and run harvest simulation model.

OUTFLOWS: Recruitment_1 = If (Season = 2) then (Chicks-Chick__Mortality) else if (Season = 3) then (Chicks-Chick__Mortality) else 0
 Chick__Mortality = If (Season = 2) then (Chick_Mortality_Rate*Chicks) else if (Season = 3) then (Chick_Mortality_Rate*Chicks) else 0
 Juveniles(t) = Juveniles(t - dt) + (Recruitment_1 - Recruitment_2 - Juvenile__Mortality__Hunted - Juvenile__Mortality__Natural) * dt
 INIT Juveniles = 0

INFLOWS:

Recruitment_1 = If (Season = 2) then (Chicks-Chick__Mortality) else if (Season = 3) then (Chicks-Chick__Mortality) else 0

OUTFLOWS:

Recruitment_2 = If (Season = 3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0
 Juvenile__Mortality__Hunted = if (Season = 4) then ((Juveniles*Juvenile_Total_Mortality_Rate__Winter)) else 0
 Juvenile__Mortality__Natural = If (Season = 3) then (Juveniles *Juvenile_Mortality_Rate) else 0

Area = 800
 Breeding_Density = If (Season = 2) then (Breeding__Population_Adults/Area) else 0
 Breeding__Population_Adults = If (Season = 2) then (Adults) else 0
 Density = Total__Population/Area
 Density__Adults_and_Juveniles = Population_Adults_and__Juveniles/Area
 Density_Acres = Density*0.4047
 Density_Adults_and_Juveniles_Acres = Density__Adults_and_Juveniles*0.4047
 Hunted__Population = If (Season = 4) then (Adults+Juveniles) else 0
 Hunted__Density = If (Season = 4) then (Hunted__Population/Area) else 0
 Population_Adults_and__Juveniles = Adults+Juveniles
 Post_Breeding_Density = If (Season = 3) then (Post_Breeding_Population/Area) else 0
 Post_Breeding_Population = If (Season = 3) then (Adults+Juveniles+Chicks) else 0
 Post_Hunt_Density = If (Season = 1) then (Post_Hunt__Population/Area) else 0
 Post_Hunt__Population = If (Season = 1) then (Adults) else 0
 Season = Counter (1,5)
 Total__Population = Adults+Juveniles+Chicks
 Chick_Mortality_Rate = If (Season = 2) then NORMAL (0.4761, 0.16) else if (Season = 3) then NORMAL (0.4761, 0.16) else 0
 Density__Dependence = If (Season = 1) Then (-0.00038386*Post_Hunt__Population + 0.95250) Else IF (Season = 2) Then (-0.00038386*Breeding__Population_Adults + 0.95250) else 0
 Juvenile_Mortality_Rate = If (Season = 3) then NORMAL (0.2599, 0.091) else 0
 Juvenile_Total_Mortality_Rate__Winter = If (Season = 4) then ((Harvest__Rate+Natural__Mortality)-(Harvest__Rate*Natural__Mortality)) else 0
 Natural__Mortality = If (Season = 4) then NORMAL (0.2599, 0.091) else 0
 Nest_Mortality_Rate = IF (Season= 1) then NORMAL(0.615, 0.07) else if (Season = 2) then NORMAL(0.615, 0.07) else 0
 Post_Hunt_through_Breeding__Mortality_Rate = If (Season = 1) then NORMAL (0.2599, 0.091) else If (Season = 2) then NORMAL (0.2599, 0.091) else if (Season = 3) then NORMAL (0.2599, 0.091) else 0
 Proportion_Females = If (adults = 0) then 0 else (Females/Adults)
 Reproductive_Effort = If (Season =1) then (Clutch_Size*Females*Percent_Females__Nesting*Nest__Rate)*Bounded_Density__Dependence else If (Season = 2) then (Clutch_Size*Females*Percent_Females__Nesting*Nest__Rate)*Bounded_Density__Dependence else 0
 Winter_Total__Mortality__Rate_Adults = If (Season = 4) then ((Harvest__Rate+Natural__Mortality)-(Harvest__Rate*Natural__Mortality)) else 0

APPENDIX C.

Simulated values of 4 bobwhite population parameters at 6 rates of harvest in the South Texas Plains.

Harvest Rate	Parameter	n	\bar{x}	95% CI	Min	Max
10%	Spring density (bobwhites/ha)	165	1.19	1.11–1.27	0.15	3.02
	Winter density (bobwhites/ha)	165	1.75	1.63–1.89	0.40	4.73
	Juvenile : adult age ratio	165	3.20	2.92–3.49	0.41	10.79
	Finite rate of increase (λ)	165	1.09	1.03–1.16	0.32	2.55
15%	Spring density (bobwhites/ha)	165	1.03	0.94–1.11	0.13	2.88
	Winter density (bobwhites/ha)	165	1.68	1.57–1.80	0.38	4.90
	Juvenile : adult age ratio	165	3.18	2.92–3.45	0.28	11.45
	Finite rate of increase (λ)	165	1.07	1.01–1.13	0.33	2.76
20%	Spring density (bobwhites/ha)	165	0.78	0.71–0.84	0.14	2.10
	Winter density (bobwhites/ha)	165	1.44	1.32–1.55	0.32	3.95
	Juvenile : adult age ratio	165	3.72	3.30–3.92	0.91	11.14
	Finite rate of increase (λ)	165	1.11	1.03–1.19	0.38	3.80
25%	Spring density (bobwhites/ha)	165	0.60	0.55–0.65	0.03	1.79
	Winter density (bobwhites/ha)	165	1.08	0.98–1.18	0.05	3.98
	Juvenile : adult age ratio	165	4.04	3.77–4.34	0.94	10.70
	Finite rate of increase (λ)	165	1.08	1.02–1.13	0.30	2.32
30%	Spring Density (bobwhites/ha)	165	0.33	0.28–0.37	<0.01	1.74
	Winter Density (bobwhites/ha)	165	0.65	0.57–0.74	0.02	3.16
	Juvenile : adult age ratio	165	4.11	3.80–4.41	0.91	11.6
	Finite rate of increase (λ)	165	1.10	1.03–1.17	0.27	3.43
40%	Spring density (bobwhites/ha)	165	0.02	0.01–0.03	0.00	0.20
	Winter density (bobwhites/ha)	165	0.04	0.02–0.06	0.00	1.06
	Juvenile : adult age ratio	165	4.98	4.59–5.38	1.33	18.57
	Finite rate of increase (λ)	165	0.94	0.90–0.98	0.41	2.26