EVALUATING THE HARVEST RATE RECOMMENDATION FOR NORTHERN BOBWHITES IN SOUTH TEXAS

D. Abraham Woodard[1, 2]
Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Boulevard, MSC 218, Kingsville, TX 78363, USA

Leonard A. Brennan
Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Boulevard, MSC 218, Kingsville, TX 78363, USA

Fidel Hernández
Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Boulevard, MSC 218, Kingsville, TX 78363, USA

Humberto L. Perotto-Baldivieso
Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Boulevard, MSC 218, Kingsville, TX 78363, USA

Neal Wilkins
East Foundation, 200 Concord Plaza Drive, Suite 410, San Antonio, TX 78216, USA

Andrea Montalvo
East Foundation, 310 East Galbraith Street, Hebbronville, TX 78361, USA

ABSTRACT

The current harvest rate recommendation for northern bobwhites (*Colinus virginianus*; hereafter, bobwhite) in South Texas, USA is 20% of the autumn population, including crippling loss. This recommendation is based on population simulations of empirical data. We completed the first field evaluation of the 20% harvest recommendation by comparing prehunting and posthunting bobwhite density estimates on a hunted and nonhunted site in South Texas during the 2018–2019, 2019–2020, and 2020–2021 statewide bobwhite hunting seasons in Jim Hogg County, Texas. We conducted line-transect distance sampling surveys on 4 occasions per year (early November, mid-December, late January, early March) from a helicopter platform and prescribed the 20% annual bobwhite harvest from the November density estimate. According to our bobwhite density estimates, we found that bobwhite mortality (e.g., population decline) varied seasonally between hunted (= 54% ± 3%) and nonhunted sites (= 46% ± 5%). Our spring density estimates on both sites (i.e., hunted vs. nonhunted) were similar through the first 2 years but diverged in 2020–2021, with bobwhite densities that were 129% higher on the nonhunted site. Comparing our annual spring density results to the means reported from population models (i.e., 100-year simulations) used to create the 20% harvest recommendation, we found that the mean spring density of the model simulations was higher than our mean field estimates on both our hunted (+59%) and nonhunted sites (+77%). We recommend a conservative approach to prescribing a bobwhite harvest in South Texas, such as using the lower 95% confidence interval of a bobwhite abundance estimate for calculating harvest prescriptions, due to variability within density estimates and bobwhite survival in semiarid ranges.

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[1] *E-mail: d.abrahamwoodard@gmail.com*
[2] *Present address: East Foundation, 310 East Galbraith Street, Hebbronville, TX 78361, USA*

Northern bobwhites (*Colinus virginianus*) have been studied intensively for a century (Sandercock et al. 2008). Despite such attention, populations have declined across their geographic ranges (Rosene 1969, Klimstra 1982, Brennan 1991). These population declines have been attributed to changes in land use (Klimstra 1982, Brennan 1991) and loss of usable space (Guthery 1997). However, questions regarding the effects of hunting and the sustainability of populations exposed to hunting remain unanswered (Brennan 1991, Brennan et al. 2014a).

Early research by Errington and Hamerstrom (1935) found a biological justification for northern bobwhite harvest through the compensatory relationship between natural mortality and hunting-related mortality that they deemed a "doomed surplus." This theory was supported by research for nearly 40 years (Guthery 2002), but later investigations revealed this historical theory to be potentially misleading (Roseberry and Klimstra 1984, Guthery 2002). The primary challenge is that northern bobwhite harvest tends to vary along a gradient between being entirely compensatory to natural mortality and entirely additive to natural mortality (Roseberry 1979, Roseberry and Klimstra 1984, Curtis et al. 1989, Pollock et al. 1989, Robinette and Doerr 1993, Dixon et al. 1996). This gradient is influenced by the rate and timing of harvest (Lehmann 1984, Roseberry and Klimstra 1984, Pollock et al. 1989, Robinette and Doerr 1993, Kokko 2001, Brennan et al. 2014*a*).

Rates of harvest imposed on bobwhite populations can also vary annually and regionally. Early researchers documented a relationship between population abundance and fluctuations in hunting pressure from year to year (Stoddard 1931, Vance and Ellis 1972). Peterson and Perez (2000) confirmed this relationship with national and statewide bobwhite survey data, considering it a "self-limiting" function of harvest. However, Guthery et al. (2004*b*) found that bobwhite hunter efficiency and average hunter skill can increase during population lows, which can have impacts on localized densities. State regulations regarding bobwhite harvest are constructed to allow maximum flexibility and opportunity, providing only a general framework (e.g., season dates, daily bag limits) for management decisions at fine scales (Cooke 2007). Changes to these regulations, such as reductions to bag limits and shorter season lengths, may have limited effects on local populations (Peterson and Perez 2000, Peterson 2001, Guthery et al. 2004*a*, Tomeček et al. 2015). Therefore, harvest itself must be managed at the individual property or pasture scale (Lehmann 1984, Williams et al. 2004, Sands et al. 2012, Tomeček et al. 2015).

To this day, there is still considerable uncertainty regarding recommended northern bobwhite harvest rates. Proposed northern bobwhite harvest rates have varied across the species' geographic range from 0% to 70% (Guthery et al. 2000). In the 1930s, Stoddard (1931) considered a harvest rate of less than 50% sustainable depending on environmental conditions and the control of predators. Likewise, Rosene (1969) recommended a maximum harvest of 45% for the southeastern United States. In Illinois, USA, Vance and Ellis (1972) argued that a 70% harvest compensates for natural mortality. However, according to northern bobwhite population simulations by Roseberry (1979), harvest beyond 40–45% of fall populations was detrimental to maintaining sustainable breeding populations, a result that was supported by subsequent work by Sands (2010) and Guthery et al. (2000).

Theoretically, a sustained yield harvest should be prescribed to meet a desired spring density that will maximize the rate of population gain from spring to fall through density-dependent production (Guthery 2002). In areas with highly variable and unpredictable weather patterns (e.g., South Texas, USA), underlying density-dependent processes act inconsistently through time and space (DeMaso et al. 2013), and more conservative approaches to harvest are thus recommended (Sands et al. 2013). Therefore, maintaining a viable northern bobwhite population should be the harvest management focus. A viable breeding density of bobwhites should persist after total fall-to-spring mortality, including harvest (Sands 2010, DeMaso et al. 2011).

The current harvest recommendation for South Texas is a 20% harvest, including factoring for crippling loss (Brennan et al. 2014*a*). This recommendation is based on simulated population responses to various harvest prescriptions and stochastic environmental conditions over a 100-year time frame (Guthery et al. 2000, Sands 2010). Population simulations have been useful in determining key variables that affect bobwhite population persistence (Roseberry 1979, Guthery et al. 2000, Sandercock et al. 2008, DeMaso et al. 2011, Rader et al. 2011, Sands et al. 2012, DeMaso et al. 2013). According to Sands (2010), a 20% annual harvest in South Texas achieved the highest yield with greater than 95% probability of population persistence over 100 years. Guthery et al. (2000) found similar results with their simulations, recommending a harvest rate of 20–25%. Reed et al. (1998), Guthery (2002), and Brennan (2002) recommended testing the results from such models in the field using empirical data.

Many researchers have called for studies regarding the effects of bobwhite harvest intensity and timing on subsequent breeding densities (Roseberry 1979, Brennan 1991, Burger et al. 1994, Peterson 1999, Peterson and Perez 2000, Rollins 2002). The controlled manipulation of bobwhite harvest intensity, timing, and distribution compared to carefully selected nonhunted control populations permits evaluations of harvest (Brennan 1991, Burger et al. 1994), but quantifying the effects requires a time series of fall density, spring density, natural mortality, and total harvest (Guthery 2002, Sands et al. 2013).

The aim of this study was to evaluate the effects and feasibility of implementing the sustainable harvest rate recommendation for bobwhite populations in South Texas and compare bobwhite density trends from field estimates of hunted and nonhunted study areas, as well as comparisons to outputs from model simulations. We used density estimates obtained from line-transect distance sampling from a helicopter platform, which is the recommended method for estimating bobwhite density in Texas rangelands (DeMaso et al. 2010) and is widely used across South Texas. We controlled bobwhite harvest timing, intensity, and spatial distribution while making monthly density estimates of hunted and nonhunted bobwhites to compare seasonal population trends and mortality. We hypothesized that a 20% harvest is attainable using standard South Texas hunting practices at densities <1.0 bobwhite/hectare. Second, we hypothesized that hunting-related mortality consisting of 16% retrieved and 4% assigned crippling loss based on the fall abundance estimate would result in mean spring breeding densities within 95% confidence intervals (CIs) of both a nonhunted site with a similar fall density and the mean of spring density from simulations by Sands (2010).

STUDY AREA

The study took place on two ranches located in Jim Hogg County, Texas (Figure 1). The ranches are approximately 35 km south of Hebbronville, Texas, within the South Texas Plains Ecoregion (Gould 1975). The ranches are owned and operated by the East Foundation, established in 2007 from the estate of Robert C. East. The hunted site was the entire Buena Vista Ranch, with a total of 6,118 hectares. Our designated nonhunted area consisted of 3 separate sites (1,265 hectares, 1,593 hectares, and 1,518 hectares) totaling 4,376 hectares within the San Antonio Viejo Ranch (60,290 ha). We adopted these sites from Bruno (2018), which served as refence areas for a long-term quail and grazing study. Bruno (2018) selected multiple sites to mitigate any unforeseeable circumstance where a single area would no longer serve as a control (e.g., wildfire). Quail hunting was prohibited within the San Antonio Viejo Ranch; any potential quail hunting or baiting that may have occurred near the nonhunted sites would have been on adjacent property not owned by the East Foundation. The distance between hunted and nonhunted areas was 19 km. The primary land use for both ranches has been cattle production for over 100 years.

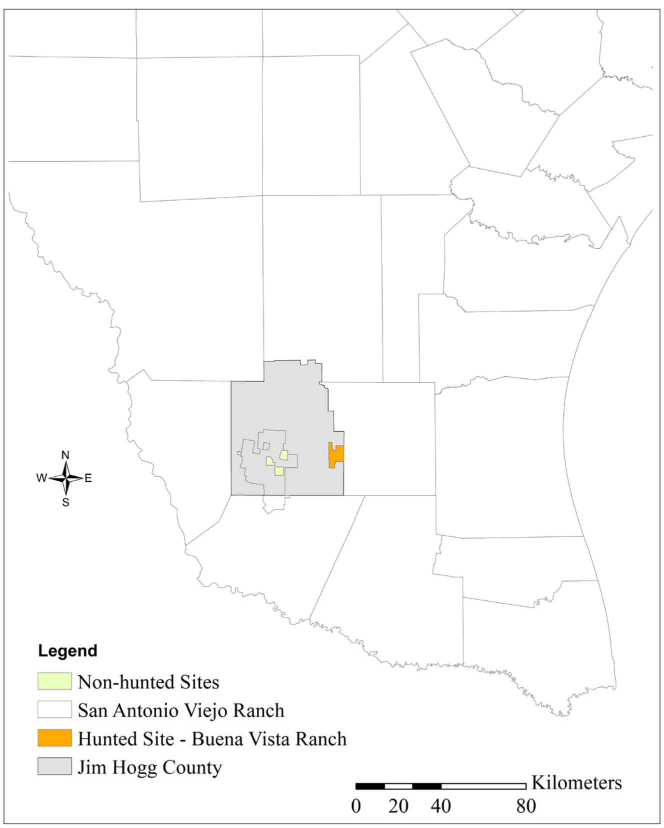

Fig. 1. Locations of hunted (Buena Vista Ranch) and nonhunted sites (3 reference pastures within the San Antonio Viejo Ranch) in Jim Hogg County, Texas, USA.

According to Sanders et al. (1974), the mean annual rainfall for Jim Hogg County is 47 cm. The annual rainfall on the hunted site was 92.2 cm in 2018, 50.1 cm in 2019, and 74.3 cm in 2020. The annual rainfall on the nonhunted area was 72.1 cm in 2018, 39.9 cm in 2019, and 79.3 cm in 2020. The mean daily temperature is 23° C, with a summer average of 30.5° C and a winter average of 15° C (Sanders et al. 1974). Predominant soil on both sites ranged from deep fine sands to sandy loams (Sanders et al. 1974, Gould 1975). Dominant woody vegetation consisted of honey mesquite (*Prosopis glandulosa*), brasil (*Candalia hookeri*), granjeno (*Celtis pallida*), and catclaw acacia (*Acacia greggi*). The herbaceous plant community was dominated by seacoast bluestem (*Schuzachyrium scoparium* var. *littorale*), Lehman love grass (*Eragrostis lehmanniana*), purple threeawn (*Aristida purpurea*), Texas broomweed (*Gutierrezia texana*), and croton (*Croton* spp.).

METHODS

Abundance Estimates and Population Trends

We estimated bobwhite abundance for our study sites using line-transect distance sampling from a helicopter platform. We contracted a Robinson R44 helicopter (Robinson Helicopter Co., Torrance, CA, USA) and pilot for each survey. We created the survey transects using ArcMap 10.8.0 (Esri, Inc., Redlands, CA, USA), spacing transects 200 meters apart to simulate 100% coverage (Figure 2). We oriented the transects on the hunted site from north and south to account for the geographical shape of the property boundary, while the transects on the nonhunted site were oriented east and west, as established during the long-term monitoring project on this area that began in 2014 (Bruno 2018). Pilots followed transect routes loaded into Garmin Nuvi 52LM (Garmin Corp., Lenexa, KS, USA) using Mapwell 11.0 software (BALARAD, Slovak Republic). We traversed every other transect until all transects were surveyed to reduce the probability of double counts (Rusk et al. 2007, Schnupp et al. 2013).

Following the protocols outlined by Schnupp et al. (2013) and DeMaso et al. (2010), we maintained 3 observers and 1 pilot, flying at average speeds of 37 km/hr and an altitude

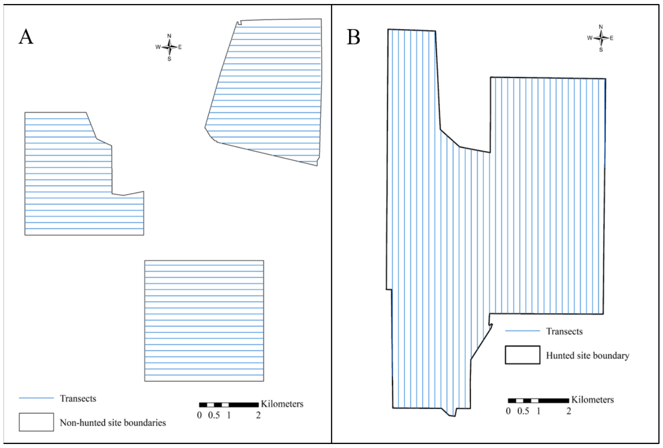

Fig. 2. Line transects for distance sampling from a helicopter platform on A) nonhunted and B) hunted sites in Jim Hogg County, Texas, USA.

of 7–10 meters. Northern bobwhite locations were obtained from laser range finders (Trimble Laser Ace 1000, Trimble Navigation Ltd., Sunnyvale, CA, USA) and stored on a Juno Handheld unit (Trimble 5 series, Trimble Navigation Ltd.). In December 2020, we incorporated a TruePulse 360r laser rangefinder (Laser Technology Inc., Centennial, CO, USA) after evaluating our equipment's accuracy from the helicopter platform (Montalvo et al. 2022: under review). During the survey, the front-seat observer detected coveys directly in front of the helicopter while the two rear-seat observers detected coveys to the left and right of the helicopter (DeMaso et al. 2010, Schnupp et al. 2013). Upon detecting a covey, the pilot held position by hovering (Schnupp et al. 2013) while the observer marked the location of the initial observation with a laser range finder and estimated the number of birds within the covey. Rear-seat observers would mark locations on their respective sides, and the front-seat observer operated the Juno. The pilot would signal a covey when detected, but was not considered an observer (Schnupp et al. 2013).

We conducted the first line-transect distance sampling survey in December of the 2017–2018 hunting season (28 Oct–25 Feb) to obtain baseline bobwhite densities prior to any harvest on study sites. During the subsequent years, the surveys reflected critical times associated with our evaluation of harvest and overwinter mortality of northern bobwhite populations (Rosene 1969:180, Lehmann 1984:306, Roseberry and Klimstra 1984:5, Burger et al. 1994, DeMaso et al. 2010). We conducted the pre-hunt survey at the onset of the statewide hunting season (i.e., early November) and a pre-breeding survey in early March (DeMaso et al. 2010, Brennan et al. 2014*a*), before covey breakup and reproductive efforts. We flew two additional surveys during the hunting season to compare mortality rates (i.e., harvest and natural mortality) between 3 designated periods representing the early, middle, and late months of the hunting seasons. Therefore, we conducted 4 flights/year on both hunted and nonhunted sites, occurring in early November, mid-December, late January, and early March.

Harvest Methods and Structure

We prescribed a northern bobwhite harvest of 20% to the hunted area as recommended by Brennan et al. (2014*a*), using the abundance estimates from the November surveys. The calculated prescription included both bobwhites retrieved and the estimated number of bobwhites shot but not retrieved (i.e., crippled [downed, legged, feathered]) while hunting. The projected figure of crippled bobwhites was according to Haines et al. (2009), who estimated losses to be on average 20% of the bobwhites brought to bag. Therefore, the 20% harvest recommendation represented a 16% retrieved and a 4% figure of crippling loss (i.e, harvest rate [20%] × crippling rate [20%] = 4%, or 25% of total harvest). However, researchers documented all hunter-covey interactions, including the detected number of crippled bobwhites harvested during each covey encounter. When the number of crippled bobwhites exceeded the 4% projection for the year, additional crippled bobwhites counted towards the total harvest.

We calculated harvest prescriptions for each pasture (i.e., 5 pastures ranging from 1,093 hectares to 3,077 hectares) to distribute harvest based on local density (Williams et al. 2004, Sands et al. 2012, Brennan et al. 2014*a*, Tomeček et al. 2015). Additionally, the pasture quotas were divided evenly across our early (early November–mid-December), middle (mid-December–late January), and late periods (late January–early March). However, the quota per period was considered a "target" for our hunting cooperators without penalty for falling short of the monthly quota.

The bobwhite hunting methods were standard for South Texas (Howard 2007). Hunters followed pointed dogs in modified hunting vehicles until a covey was pointed, where hunters approach the covey on foot (Hernández and Guthery 2012). Hunters were not allowed to use supplemental feed or bait along roadsides. However, they could pursue any covey found within the hunted area, without limits to the number of bobwhites harvested per covey or the number of pursuits following the covey rise. Therefore, we limited hunters only according to state game regulations and the total annual harvest prescription.

We recorded all hunting activities and harvest using detailed hunting logs (see Woodard et al. this volume). A trained observer would ride with the hunting party or follow the hunting party in a utility task vehicle (UTV), staying within a close proximity (i.e., <9 meters directly behind the hunting party). Observers documented each covey interaction, including an estimate of covey size, shots fired, bobwhites retrieved, and bobwhites crippled.

Age and Sex Ratios

We estimated the age and sex ratios of bobwhites on both the hunted and nonhunted sites. We determined age (i.e., juvenile or adult) and sex (i.e., male or female) according to Rosene (1969). When possible, we determined the estimated hatch date for juvenile bobwhites within our samples (Hernández and Guthery 2012). We determined sex and age ratios for our hunted site from the hunter-harvested bobwhites, and we obtained age and sex ratios on the nonhunted sites from trapped and released northern bobwhites. We used standard funnel traps (Stoddard 1931) baited with grain sorghum (*Sorghum bicolor*) for capture. We followed all animal care and use guidelines according to Institutional Animal Care and Use Committee approval number 2018-01-31-A3 and Texas Parks and Wildlife Department scientific research permit number SPR-0413-044.

ANALYSES

Abundance Estimates

We estimated bobwhite density for each helicopter survey using the length of transects, covey detections, covey sizes, and perpendicular distances within Program Distance version 7.2, release 1 (Thomas et al. 2010). We analyzed the bobwhite abundance from our November survey for each year and site using the Conventional Distance Sampling (CDS) engine within Program Distance to determine the annual bobwhite harvest quotas for that specific hunting season. Upon completion of the last survey of the year (i.e., March survey), we analyzed seasonal density trends per site using CDS with a pooled detection function, CDS stratified by month, and multiple covariate distance sampling (MCDS) with the month as a covariate within Program Distance (Marques et al. 2007). This approach allowed for improved precision of our time-series analysis and our original November density estimate (Marques et al. 2007, Buckland et al. 2015). We fit probability detection functions from perpendicular distance measurements and examined frequency histograms for outliers and truncation points (Buckland et al. 2001). We fit models to the detection function and assigned a key function (i.e., Half normal, Hazard, or Uniform) along with a series expansion term if required (i.e., Cosine, Simple polynomial, Hermite polynomial), evaluating each model based on the three goodness of fit tests (i.e., Cramer VonMises with cosine and uniform, Kolmogorov-Smirnov) and Akaike's Information Criterion (Buckland et al. 2001; see Appendices A, B, C, D).

Hunted vs. Nonhunted Comparisons

We compared densities between hunted and nonhunted sites using the Z-test for independent samples outlined in Buckland et al. (2001:eqn. 3.102). We estimated survival and mortality (i.e., population decline) across hunting seasons (i.e., fall–spring) and within seasons (i.e., early, middle, late periods of the hunting seasons) by measuring changes in density on both the hunted and nonhunted sites (Roseberry and Klimstra 1984, DeMaso et al. 2010). Under this approach, we assumed density changes represent mortality and a balance between immigration and emigration (i.e., immigration + emigration = 0). This assumption is supported by Teinert et al. (2013), who analyzed mark-recapture data of radio-collared bobwhites during the fall–spring periods in South Texas.

Specifically, we calculated the total mortality (i.e., percent decline; equation 2.1) from prehunting to posthunting (Nov–Mar; Roseberry and Klimstra 1984, DeMaso et al. 2010) and for each period (i.e., early, middle, late), along with the percentage of natural mortality (NM) not accounted for by harvest (K; Roseberry and Klimstra 1984). Total mortality (Q) of a study site during a period of interest can be described as the difference between the prehunting bobwhite abundance (N_i) and the posthunting abundance (N_{i+1}). Subsequently, we estimated percent mortality (M) or percent decline and percent mortality not accounted for by harvest using the following:

Equation 2.1 $M = Q/N_i$, or $M = (N_i – N_{i+1})/N_i$
Equation 2.2 $NM = M – (K/N_i)$, or $(Q – K)/N_i$

We used the additive model of harvest mortality to determine the nature of harvest (equation 3; Ricker 1958). Furthermore, we estimated the rate of bobwhites lost to bobwhites harvested (α–additivity, equation 4), the proportional reduction in post-hunt population (p_a, equation 5), and the proportional reduction in one fall population to the next (β–additivity, equation 6). The α–additivity was calculated for each period by dividing the difference in estimated abundances on the nonhunted sites (N_{po}) and the abundance estimate of the hunted site (N_{ph}) by the total harvest (K) for the period (Guthery 2002). Proportional reduction in post-hunt population due to harvest (p_a) was calculated for the periods (Guthery 2002), while the proportional reduction in one fall population ($N_{po\text{-}f}$) to the next (β–additivity) was calculated only annually (Guthery 2002).

Equation 3 $Q = V_0 + K_0 – V_0K_0$
Equation 4 $\alpha\text{–additivity} = (N_{po} – N_{ph})/K$
Equation 5 $p_a = (N_{po} – N_{ph})/N_{po}$
Equation 6 $\beta\text{–additivity} = [N_{po\text{-}f} + 1 – N_{ph\text{-}f} + 1\ ]/N_{po\text{-}f}$
where,
V_0= natural mortality in the absence of harvest mortality
K_0 = harvest mortality in the absence of natural mortality
K = harvest mortality in the presence of natural mortality
HR = harvest rate (periodic or seasonal)

We calculated percent summer gain (i.e., population increase from spring to fall) and adult summer mortality (ASM) annually for hunted and nonhunted areas. Percent summer gain (PSG) is derived from the proportional increase in net production of northern bobwhites from spring (N_b) to fall (N_f) using equation 7 (Roseberry and Klimstra 1984). Adult summer mortality is derived from the percent summer gain and the ratio of juveniles to adults (J:A) from our study sites (equation 8; Guthery 2002).

Equation 7 $PSG = [(N_f – N_b)/N_b] \times 100$
Equation 8 $ASM = 1 – (PSG +1)/(J{:}A + 1)$

RESULTS

Based on our November bobwhite abundance estimates, the 20% harvest prescription for the hunted site was 422 bobwhites during the 2018–2019 hunting season (27 Oct–24 Feb), 852 bobwhites during the 2019–2020 season (26 Oct–23 Feb), and 1,005 bobwhites during the 2020–2021 season (31 Oct–28 Feb; Table 1). The harvest prescription was reached for each of the 3 hunting seasons, requiring 59 bobwhite hunts (163.2 hours) in 2018–2019, 74 bobwhite hunts (254.4 hours) in 2019–2020, and 78 bobwhite hunts (250.5 hours) in 2020–2021 (Table 2). The number of crippled and lost bobwhites detected by hunting parties was above the 4% prescription (i.e., predicted crippling losses) during 2 years, representing 30% of overall harvest mortality in 2019–2020 and 35% of the overall harvest in 2020–2021.

Our bobwhite density estimates on both the hunted and nonhunted sites were similar during our baseline survey in December of the 2017–2018 hunting season (Table 3, Figure 3). In 2018–2019, we detected an increase in bobwhite density from November to December on both sites, along with evidence of a late-season hatch (Woodard et al. 2019). However, from December through March, bobwhite populations on both hunted and nonhunted sites had similar monthly trends and similar pre-breeding densities. During the 2019–2020 hunting season, we detected a sharp population decline on our nonhunted site between November and December. The spring breeding population (i.e., March) on our nonhunted site was 35% lower than our hunted site. During the 2020–2021 hunting season, our bobwhite density estimates were lower on the hunted site for each survey. Spring bobwhite density on our hunted site following the 2020–2021 hunting season was 55% lower than our nonhunted site. The mean spring density estimate across years and sites was 0.33 ± 0.003 bobwhites/hectare. Compared to simulations from Sands (2010), our observed spring densities were 59% (49–78%) lower than simulated densities on the hunted site and 77% (73–82%) lower on the nonhunted sites (Table 4).

The seasonal analysis conducted using MCDS improved the model fit of our detection functions and precision in density estimates for both sites, allowing us to reevaluate our annual (Table 5) and periodic (Table 6) harvest rates. According to our seasonal analysis, the realized harvest rate was 12% during the 2018–2019 hunting season, 17% in 2019–2020, and 22% in 2020–2021.

The mean seasonal mortality (i.e., population decline from November to March) was 54% (range = 32–77%) on our hunted site and 46% (range = 13–66%) on our nonhunted site (Table 7). Mortality per period (i.e., early, middle, late) varied between years and from site to site (Table 8). The greatest variation in mortality per period between the hunted and the nonhunted site occurred during the late period of 2020–2021, with total periodic mortality on the hunted site 10% greater than the nonhunted site (21% vs. 31%).

The estimated seasonal mortality varied from predictions using the additive harvest model. Mortality on our hunted site was greater than predicted in the 2018–2019 and 2020–2021 hunting seasons and less than the predicted mortality in the 2019–2020 season (Table 9). Mortality per period also varied between our observed rate and predicted. The additive model underpredicted mortality by as much as 16.4% and overpredicted mortality by up to 16.8% (Table 10). Our evaluations of the

Table 1. Annual harvest prescriptions for northern bobwhites (*Colinus virginianus*) on designated hunted site based on November abundance estimates calculated from line-transect distance sampling from a helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. The 20% harvest prescription represents a 16% retrieved and 4% crippling loss as recommended by Brennan et al. (2014*a*).

Year	Abundance (95% CI)	% CV	20% Harvest	Retrieved; crippled
2018–2019	2,100 (1,588–2,803)	14.5%	422	(338; 84)
2019–2020	4,262 (3,302–5,501)	13.0%	852	(682; 170)
2020–2021	5,026 (3,792–6,661)	14.4%	1,005	(804; 201)

Table 2. Summary of annual northern bobwhite (*Colinus virginianus*) hunting pressure and harvest according to designated periods: early (Nov–mid-Dec), middle (mid-Dec–late Jan), and late (late Jan–late Feb). The hunting parameters were collected during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

Year	Period	Hunts	Hunting hours	Total harvest	Retrieved; crippled
2018–2019	Early	10	24.9	30	(23; 7)
	Middle	33	91.6	269	(213; 56)
	Late	16	46.7	124	(102; 22)
	Total	59	163.2	423	(338; 85)
2019–2020	Early	23	70.8	201	(154; 47)
	Middle	35	124.7	413	(322; 91)
	Late	16	58.9	238	(182; 56)
	Total	74	254.4	852	(658; 194)
2020–2021	Early	24	73.7	201	(150; 51)
	Middle	37	118.4	548	(422; 126)
	Late	17	58.4	250	(170; 80)
	Total	78	250.5	999	(742; 257)

Table 3. Comparisons of northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% CIs, coefficients of variation [CVs]) between hunted and nonhunted sites obtained from line-transect distance sampling surveys via helicopter platform conducted in 1) early November, 2) mid-December, 3) late January, and 4) early March during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

		Hunted site		Nonhunted site				
Year	Survey	$\hat{D}$ (± 95% CI)	% CV	$\hat{D}$ (± 95% CI)	% CV	Difference ± SE[a]	z-score[a]	*P*-value[b]
2017–2018[c]	2	0.61 (0.46–0.81)	14.2%	0.62 (0.48–0.79)	12.5%	- 0.01 ± 0.12	0.06	0.952
2018–2019	1	0.45 (0.33–0.62)	15.6%	0.35(0.27–0.44)	12.3%	+ 0.11 ± .08	1.38	0.167
	2[d]	0.59 (0.43–0.80)	15.6%	0.45 (0.33–0.58)	14.5%	+ 0.14 ± 0.57	0.24	0.812
	3	0.48 (0.36–0.63)	13.8%	0.43 (0.29–0.53)	15.0%	+ 0.05 ± 0.08	0.56	0.575
	4	0.40 (0.30–0.53)	14.1%	0.39 (0.27–0.44)	12.3%	< 0.00 ± 0.09	0.04	0.964
2019–2020	1	0.84 (0.70–1.02)	9.6%	0.76 (0.46–1.24)	25.5%	+ 0.08 ± 0.19	0.43	0.664
	2	0.53 (0.43–0.66)	10.9%	0.39 (0.29–0.53)	15.5%	+ 0.14 ± 0.08	1.79	0.073
	3	0.50 (0.38–0.66)	13.9%	0.38 (0.28–0.50)	14.5%	+ 0.12 ± 0.09	1.43	0.153
	4	0.40 (0.31–0.51)	12.3%	0.26 (0.17–0.39)	21.2%	+ 0.14 ± 0.07	2.07	0.039
2020–2021	1	0.73 (0.61–0.88)	9.3%	0.93 (0.78–1.12)	9.2%	- 0.20 ± 0.10	1.90	0.057
	2	0.63 (0.53–0.76)	9.2%	0.84 (0.68–1.04)	10.9%	- 0.21 ± 0.11	1.97	0.048
	3	0.35 (0.29–0.42)	9.7%	0.45 (0.34–0.61)	15.0%	- 0.10 ± 0.06	1.66	0.097
	4	0.17 (0.12–0.22)	16.2%	0.38 (0.29–0.50)	13.5%	- 0.22 ± 0.05	3.97	< 0.001

[a] Standard error of the difference and z-score calculated according to Buckland et al. (2001).
[b] H_0: $D_1 – D_2$; or $D_1 – D_2 = 0$
[c] Single density estimates were completed during the 2017–2018 hunting season for baseline density comparisons.
[d] Survey 2 during the 2018–2019 hunting season was conducted on 1–2 February 2019.

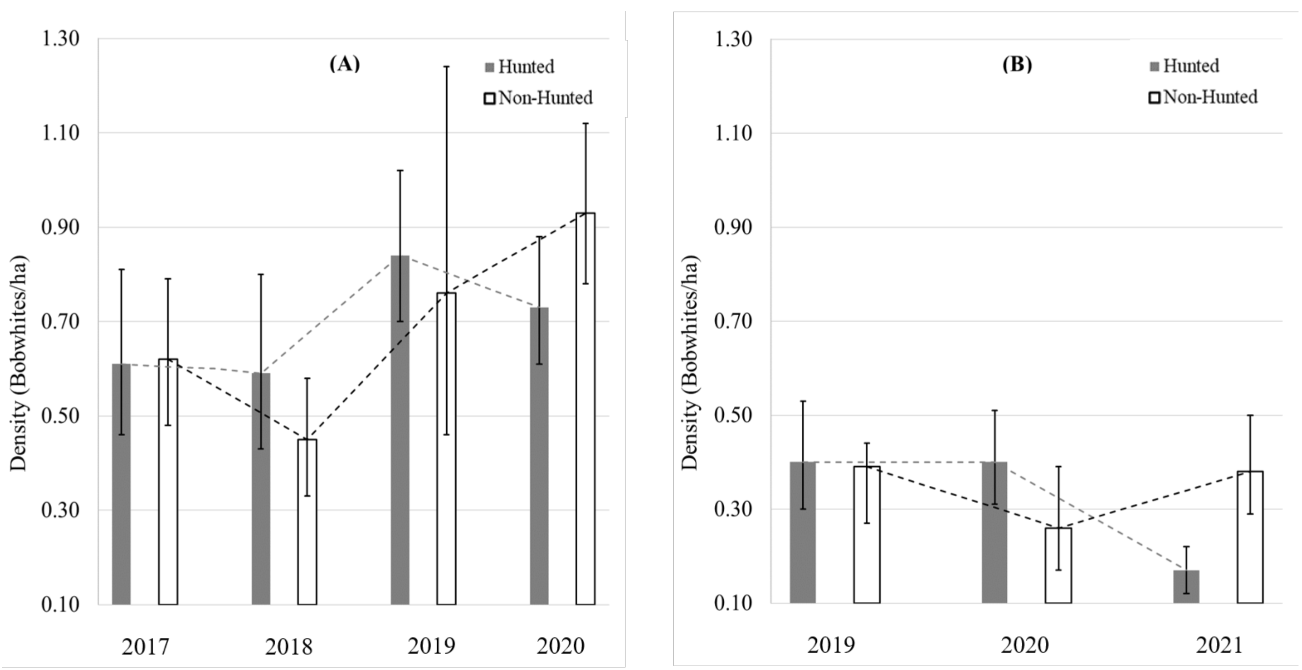

Fig. 3. Trends and comparisons of northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% confidence intervals) in A) fall and B) spring between hunted and nonhunted sites obtained from line-transect distance sampling surveys via helicopter platform in Jim Hogg County, Texas, USA. Fall density estimates were calculated from November (2019 and 2020) and December (2017 and 2018) bobwhite surveys. Spring density estimates were calculated from March surveys conducted in 2019, 2020, 2021.

Table 4. Comparisons of spring northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% CIs, coefficients of variation [CVs]) between field observations and means of 100-year simulations from stochastic model by Sands (2010). Observed density estimates obtained from line-transect distance sampling surveys via helicopter platform conducted in early March of 2019, 2020, and 2021 in Jim Hogg County, Texas, USA.

		Observed		Simulated		
Site	Year	$\hat{D}$ ± SE	(95% CI)	$\hat{D}$ ± SE	(95% CI)	Difference
Hunted	2018–2019	0.40 ± 0.07	(0.30–0.53)	0.78 ± 0.03	(0.71–0.84)	-0.38
Hunted	2019–2020	0.40 ± 0.04	(0.31–0.51)	0.78 ± 0.03	(0.71–0.84)	-0.38
Hunted	2020–2021	0.17 ± 0.02	(0.12–0.22)	0.78 ± 0.03	(0.71–0.84)	-0.61
Nonhunted	2018–2019	0.39 ± 0.06	(0.27–0.44)	1.46 ± 0.04	(1.39–1.54)	-1.07
Nonhunted	2019–2020	0.26 ± 0.05	(0.17–0.39)	1.46 ± 0.04	(1.39–1.54)	-1.20
Nonhunted	2020–2021	0.38 ± 0.05	(0.29–0.50)	1.46 ± 0.04	(1.39–1.54)	-1.08

Table 5. Comparisons of November northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% CIs, coefficients of variation [CVs]) using a conventional distance sampling (CDS) analysis (November only) and results from the seasonal analysis (i.e., 4 surveys per hunting season). Density estimates were obtained from sites obtained from line-transect distance sampling surveys via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons on the hunted and nonhunted sites in Jim Hogg County, Texas, USA. Seasonal analysis included conventional distance sampling with a pooled detection function, conventional distance sampling with a fully stratified detection function, and multiple-covariate distance sampling (see Appendix A and Appendix B).

		CDS analysis		Seasonal analysis				
Site	Year	($\hat{D}$ ± 95% CI)	% CV	($\hat{D}$ ± 95% CI)	% CV	Difference ± SE[a]	z-score[a]	P-value[b]
Hunted	2018–2019	0.34 (0.26–0.46)	14.8%	0.45 (0.33–0.62)	15.6%	- 0.11 ± 0.08	1.32	0.188
Hunted	2019–2020	0.70 (0.54–0.90)	13.0%	0.84 (0.70–1.02)	9.6%	- 0.15 ± 0.10	1.52	0.129
Hunted	2020–2021	0.82 (0.62–1.09)	14.4%	0.73 (0.61–0.88)	9.3%	+ 0.09 ± 0.13	0.66	0.510
Nonhunted	2018–2019	0.39 (0.29–0.53)	15.4%	0.35(0.27–0.44)	12.3%	+ 0.05 ± 0.07	0.64	0.525
Nonhunted	2019–2020	0.68 (0.44–1.04)	17.4%	0.76 (0.46–1.24)	25.5%	- 0.08 ± 0.22	0.36	0.721
Nonhunted	2020–2021	0.92 (0.76–1.11)	9.6%	0.93 (0.78–1.12)	9.2%	- 0.01 ± 0.15	0.08	0.940

[a] Standard error of the difference and z-score calculated according to Buckland et al. (2001).
[b] H_0: $D_1 – D_2$; or $D_1 – D_2 = 0$

Table 6. Comparisons of annual harvest rates and range (harvest rate × 95% CIs), according to November northern bobwhite (*Colinus virginianus*) abundance estimates ($\hat{D}$, 95% CIs) using a conventional distance sampling (CDS) analysis (November only) and results from the seasonal analysis (i.e., 4 surveys per hunting season) from line-transect distance sampling surveys via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons on the hunted and nonhunted sites in Jim Hogg County, Texas, USA.

		CDS analysis		Seasonal analysis	
Year	Harvest	Abundance (95% CI)	% Harvest	Abundance (95% CI)	% Harvest
2018–2019	423	2,100 (1,588–2,803)	20.0 (15.1–26.6)	3,594 (2,630–4,911)[a]	11.8 (8.6–16.1)
2019–2020	852	4,262 (3,302–5,501)	20.0 (15.5–25.8)	5,153 (4,264– 6,226)	16.5 (13.7–20.0)
2020–2021	999	5,026 (3,792–6,661)	19.9 (15.0–26.3)	4,484 (3,728–5,395)	22.3 (18.5–26.8)

[a] December abundance used for realized harvest due to the increase in density from early November to mid-December (Woodard et al. 2019).

Table 7. Seasonal mortality (M; %) comparisons of northern bobwhites (*Colinus virginianus*) between hunted and nonhunted sites and percentage of natural mortality not accounted for by harvest (% NM) during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Seasonal mortality represents the difference in density estimates from November to March according to line-transect distance sampling via helicopter platform. Range values represent differences between lower 95% CI, upper 95% CI, and max difference (lower 95% CI – upper 95% CI) from November to March.

	Nonhunted site		Hunted site		
Year	M	ranges	M	ranges	NM[a]
2018–2019[b]	13.0	(16.7, 23.6, 53.1)	32.4	(30.3, 34.4, 62.7)	20.6
2019–2020	65.6	(62.7, 68.3, 86.2)	52.9	(55.4, 50.3, 69.4)	36.4
2020–2021	59.0	(62.2, 55.4, 73.8)	77.4	(80.3, 74.7, 86.4)	55.1

[a] Percentage of natural mortality not accounted for by harvest (% NM) on hunted site = total mortality rate – harvest rate.
[b] Seasonal mortality was calculated using difference between mid-December (peak density) to March density estimates due to increase in density from early November to mid-December (Woodard et al. 2019).

Table 8. Periodic mortality (M, %) comparisons of northern bobwhites (*Colinus virginianus*) between hunted and nonhunted sites, and percentage of natural mortality not accounted for by harvest (% NM) during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Periodic mortality represents the difference in density estimates between 4 seasonal surveys (early November, mid-December, late January, and early March) according to line-transect distance sampling via helicopter platform representing early, middle, and late hunting season periods. Range values represent differences between lower 95% CI, upper 95% CI, and max difference (lower 95% CI – upper 95% CI) from between seasonal surveys.

		Nonhunted site		Hunted site		
Year	Period	M	Ranges	M	Ranges	NM[a]
2018–2019	Early[b]	-	-	-	-	-
	Middle	3.9	(10.3, 8.6, 49.5)	18.4	(15.3, 21.4, 54.6)	10.9
	Late	9.5	(7.2, 16.5, 48.7)	17.2	(17.8, 16.6, 52.5)	12.9
2019–2020	Early	48.8	(38.1, 57.7, 77.0)	36.8	(38.4, 35.1, 57.8)	30.6
	Middle	2.3	(0.4, 4.2, 45.9)	5.5	(11.0, 0.0, 42.2)	-7.9
	Late	31.2	(39.5, 21.7, 65.8)	21.2	(18.5, 23.7 ,53.0)	11.3
2020–2021	Early	9.7	(12.7, 6.7, 39.3)	14.0	(13.8, 14.2, 40.4)	8.8
	Middle	46.3	(50.4, 41.8, 67.8)	44.5	(45.0, 44.0, 61.9)	18.9
	Late	15.4	(12.8, 17.9, 51.7)	52.6	(58.4, 47.4, 71.6)	28.9

[a] NM (%) on hunted site = total mortality rate – harvest rate.
[b] Bobwhite mortality was not estimated during the early period of 2018–2019 due to an increase in overall density from early November to mid-December (Woodard et al. 2019).

rate of bobwhites lost to bobwhites harvested (α–additivity), the proportional reduction in post-hunt population (p_α), and the proportional reduction in one fall population to the next (β–additivity) proved unrealistic (i.e., >1, or < 0). These models required identical starting densities and did not function when mortality on the nonhunted site was higher than on the hunted sites (Guthery 2002; see Appendix E).

The mean percentage of females across both hunted and nonhunted sites was 47%, ranging from 44% to 51.9%. The percentage of juveniles on hunted and nonhunted sites was similar during the 2018–2019 and 2020–2021 hunting seasons (Table 11). During the 2019–2020 hunting season, the percentage of juveniles on the nonhunted site was 16% lower than the hunted site. The percent summer gain (PSG) was positive for each summer analyzed (2019 and 2020) on both the hunted and nonhunted sites (Table 12). The estimated ASM on the hunted site was 24% higher than the nonhunted site during summer 2019 and 42% higher in summer 2020.

Table 9. Seasonal mortality (M, %) estimates of northern bobwhites (*Colinus virginianus*) as predicted using the additive harvest model and the observed mortality. Observed seasonal mortality was calculated using the difference in density estimates from November to March according to line-transect distance sampling via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

	Predicted[a]	Observed[b]	
Year	M	M	Difference
2018–2019[c]	23.3	32.4	-9.1
2019–2020	71.3	52.9	18.4
2020–2021	68.1	77.4	-9.3

[a] Predicted mortality using the additive model of harvest mortality (equation 3; Ricker 1958): $Q_a = H_o + V_o + H_oV_o$.
[b] Observed mortality on the hunted site.
[c] Observed seasonal mortality was calculated using difference between mid-December (peak density) to March density estimates due to increase in density from early November to mid-December (Woodard et al. 2019).

Table 10. Periodic mortality (M, %) comparisons of northern bobwhites (*Colinus virginanus*) as predicted using the additive harvest model and the observed mortality during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Observed periodic mortality calculated using the difference in density estimates between 4 seasonal surveys (early November, mid-December, late January, and early March) according to line-transect distance sampling via helicopter platform representing early, middle, and late hunting season periods.

		Predicted[a]	Observed[b]	
Year	Period	M	M	Difference
2018–2019	Early[c]	-	-	-
	Middle	11.4	18.4	-7.0
	Late	13.3	17.2	-3.9
2019–2020	Early	52.0	36.8	15.2
	Middle	15.4	5.5	9.9
	Late	37.9	21.2	16.8
2020–2021	Early	14.4	14.0	0.5
	Middle	60.1	44.5	15.5
	Late	36.2	52.6	-16.4

[a] Predicted mortality using the additive model of harvest mortality (equation 2, Ricker 1958): $Q_a = H_o + V_o + H_oV_o$.
[b] Observed mortality on the hunted site.
[c] Bobwhite mortality was not estimated during the early period of 2018–2019 due to an increase in overall density from early November to mid-December (Woodard et al. 2019).

Table 11. Sex (M = male, F = female) and age (A = adult, J = juvenile) ratios of northern bobwhites (*Colinus virginianus*) from hunted and nonhunted sites during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Ratios were collected using hunter-harvested bobwhites along with trapped and released bobwhites.

				Sex			Age		
Year	Site	Method	*n*	M	F	% F	A	J	% J
2017–2018[a]	Hunted	Trap	133	72	61	45.9%	48	85	63.9%
	Nonhunted	-	-	-	-	-	-	-	-
2018–2019	Hunted	Harv	337[b]	185	149	44.6%	126	211	62.6%
	Nonhunted	Trap	61	31	30	49.2%	23	38	62.3%
2019–2020	Hunted	Harv	658	346	312	47.4%	193	465	70.7%
	Nonhunted	Trap	297[c]	163	129	44.2%	133	164	55.2%
2020–2021	Hunted	Harv	742[d]	388	353	47.6%	159	583	78.6%
	Hunted[e]	Trap	213[f]	104	90	46.4%	29	184	86.4%
	Nonhunted	Trap	245	117	126	51.9%	56	189	77.1%

[a] 2017–2018 was baseline year on hunted area, with hunting initiated during the 2018–2019 season.
[b] Three juveniles harvested of unknown sex.
[c] Five juveniles trapped and released of unknown sex.
[d] One juvenile harvested of unknown sex.
[e] Bobwhites were trapped and released on the hunted site in October 2020, prior to hunting season.
[f] Nineteen juveniles trapped and released of unknown sex.

DISCUSSION

Reaching the annual bobwhite harvest prescription was a matter of hunting efficiency and effort. For instance, covey encounter rates and harvest per covey varied between seasons and periods (see Woodard et al. this volume), but harvest prescriptions were reached by the addition of more hunts (i.e., effort). However, our harvest results revealed a potential discrepancy regarding total crippling loss. Our crippling rates (i.e., 20–26% of the total harvest, 25–35% of the retrieved harvest) were greater than reported by Rosene (1969) in Alabama, USA, Doster et al. (1982) in Florida, USA, and Roseberry and Klimstra (1984) in Illinois, USA. Haines et al. (2009) defined the total crippling loss as mortality in which 1) bobwhites are noticeably shot and downed, but not retrieved, 2) bobwhites are noticeably shot but not downed or retrieved (i.e., feathered), and 3) bobwhites are not noticeably shot or downed, but subsequently died from wounds undetected.

Table 12. Estimates of percent summer gain (PSG), adult summer mortality (ASM), and finite rate of increase (spring and fall) for northern bobwhites (*Colinus virginianus*) on hunted and nonhunted sites in Jim Hogg County, Texas, USA. Density was estimated using line-transect distance sampling via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons.

Site	Year	Spring $\hat{D}$	Fall $\hat{D}$	J:A[a]	PSG[b]	ASM[c]	λ[d] (spring)	λ[d] (fall)
Hunted	2017[e]	-	0.61	1.77	-	-	-	-
	2018[e]	-	0.59	1.67	-	-	-	0.96
	2019	0.40	0.84	2.41	112.1%	37.8%	-	1.43
	2020	0.40	0.73	3.67	84.8%	60.4%	1.00	0.87
	2021	0.17	-	-	-	-	0.42	-
Nonhunted	2017[e]	-	0.62	-	-	-	-	-
	2018[e]	-	0.45	1.65	-	-	-	0.73
	2019	0.39	0.76	1.23	92.8%	13.5%	-	1.68
	2020	0.26	0.93	3.37	257.7%	18.2%	0.66	1.23
	2021	0.38	-	-	-	-	1.47	-

[a] Juvenile to adult ratio.
[b] Percent summer gain = $(D_{fall} - D_{spring})/D_{spring}$; see Roseberry and Klimstra (1984).
[c] Adult summer mortality = 1 – (PSG +1)/(J:A + 1); see Guthery (2002:53).
[d] Finite rate of increase (λ) = Dt +1/Dt
[e] Bobwhite densities were not estimated in March 2017 or March 2018.

During this study, hunters reached or exceeded the assigned crippling rate assumed by Brennan et al. (2014*a*) in all 3 years, without factoring for any bobwhites that were not noticeably downed or feathered (i.e., undetected cripples; Haines et al. 2009). Therefore, an unknown amount of crippling loss remains unaccounted for in addition to our total harvest.

Another challenge we found was related to our estimates of bobwhite density. Distance sampling from a helicopter has been shown to be a reliable method for estimating bobwhite densities (Shupe et al. 1987, Rusk et al. 2007, DeMaso et al. 2010), but changes within populations occurring after the calculation of a harvest prescription along with the variation within individual estimates evidently influenced results. For instance, during the 2018–2019 hunting season, our seasonal abundance estimate for December was 30% higher than our November estimate, changing our harvest prescription from 20% of the fall population to only 12%. In fact, the November density estimates from each initial survey (i.e., single November surveys) were different from the estimates from our seasonal analyses, despite statistical similarities (e.g., z-score *P*-values). According to Guthery (1988), the acceptable variation within a density estimate for bobwhites with proper survey distance sampling design is anything with less than a 20% coefficient of variation (% CV). The level of uncertainty with density estimates is a fundamental issue regardless of the species being sampled. However, this level of uncertainty seems to be heightened when prescribing bobwhite harvests. Using the November abundance estimate from 2020–2021 (CV = 14.4%, 95% CI = 3,792–6,661) as an example, the 20% harvest prescription (i.e., 1,005 bobwhites) was potentially 15% or 27% of harvest rate (i.e., 20% × 95% CIs).

Our average overwinter mortality on the hunted site (54% ± 3%) and the nonhunted site (46% ± 5%) was similar to those reported by Robinette and Doerr 1993 and Guthery (2002:101), and with scaled quail (*Callipepla squamata*) in New Mexico, USA by Campbell et al. (1973). The variation of overwinter mortality within sites and the similarities of overwinter mortality between sites provide evidence that the nature of harvest is a gradient between compensatory and additive, as Roseberry (1979) and many others have suggested. Our spring density and mortality rate estimates were similar between the hunted and nonhunted sites during the first 2 hunting seasons but diverged during the 2020–2021 hunting season. We assume that this was potentially influenced by the combination of harvest and environmental conditions. South Texas was exposed to below-freezing conditions that lasted 13 February–20 February 2021, which are highly unusual circumstances for bobwhites in this region. Roseberry and Klimstra (1984:62) reported a 230% increase in daily mortality during intense winter storms in Illinois. Stanford (1972) also reported lower spring densities and lower reproductive efforts following severe winters in Missouri, USA. However, whether the freeze of February 2021 factored into the total mortality rate on our hunted site remains unknown.

Another discrepancy we found was between our observed spring densities and the spring density of simulated populations from Sands (2010). However, Sands (2010:Table 3) also reported discrepancies between simulated results and the spring densities of his field observations. The Sands (2010) population model and models by Guthery et al. (2000) and DeMaso et al. (2011) were constructed from a hypothetical population within 800 hectares of 100% usable space (Guthery 1997). We assumed that the amount of usable space within our study sites is less than 100% but represents bobwhite habitat in South Texas. Additionally, Sands (2010) constructed his model using a mean annual mortality of 70% (Hernández et al.

2007), estimating natural mortality per season (i.e., period 4) by drawing a random value from normal distribution (±1 SD = 10%) with a mean mortality rate of 26%. Our results indicate that 26% natural mortality (range = 16%–36%) may have underpredicted mortality during the winter period within both hunted and nonhunted simulations. Therefore, the densities and outcomes reported from simulated models by Sands (2010) and the 20% harvest rate recommended by Brennan et al. (2014*a*) may require additional analyses. More recently, Sisson et al. (2017) recommended a 15% harvest in the southeastern United States (Alabama, Florida, Georgia, South Carolina), a figure they believe limits the additive effects of both harvest and translocation.

In summary, our 3-year evaluation of a sustainable harvest has provided valuable insight regarding bobwhite populations during the hunting season on relatively large areas (i.e., >4,000 hectares). Additional research using multiple harvest rates over longer temporal scales and multiple study sites would improve our understanding of the underlying nature of harvest and the long-term sustainability of populations exposed to hunting pressure.

MANAGEMENT IMPLICATIONS

Our results suggest that prescribing a 20% harvest to an estimate of density requires consideration for the variation within a density estimate. This variation can have a considerable influence on the realized harvest rates and total mortality. We found that annual and periodic differences in overwinter mortality varied between hunted and nonhunted populations. Average spring densities across both sites were less than those from the model simulations by Sands (2010), on which the 20% harvest recommendation was based. Therefore, we recommend applying a conservative approach when calculating a harvest prescription, using a reduced harvest rate (e.g., 15%) or calculating harvest prescriptions using the lower confidence intervals of density estimates.

LITERATURE CITED

Brennan, L. A. 1991. How can we reverse the northern bobwhite population decline? Wildlife Society Bulletin 19:544–555.

Brennan, L. A. 2002. Closing remarks: pieces of the puzzle, circles in the stream. National Quail Symposium Proceedings 5:246–249.

Brennan, L. A., F. Hernández, E. D. Grahmann, F. C. Bryant, M. J. Schnupp, D. S. Delaney, and R. Howard. 2014*a*. Quail harvest guidelines for South Texas: concepts, philosophy, and applications. Technical Publication No. 3, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville.

Brennan, L. A., F. Hernández, and D. Williford. 2014*b*. Northern bobwhite (*Colinus virginianus*), version 2.0. *In* A. F. Poole, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Bruno, A. 2018. Northern bobwhite density estimates in relation to experimental grazing regimes. Dissertation, Texas A&M University-Kingsville, Kingsville, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.

Buckland, S. T., E. A. Rexstad, T. A. Marques, and C. S. Oedekoven. 2015. Distance sampling: methods and applications. First edition. Springer International Publishing, Switzerland.

Burger, L. W., E. W. Kurzejeski, L. D. Vangiler, T. V. Dailey, and J. H. Schulz. 1994. Effects of harvest on population dynamics of upland gamebirds: Are bobwhite the model? Transactions of the North American Wildlife and Natural Resource Conference 59:466–476.

Campbell, H., D. K. Martin, P. E. Ferkovich, and B. K. Harris. 1973. Effects of hunting and some other environmental factors on scaled quail in New Mexico. Wildlife Monographs 34.

Cooke, J. L. 2007. Quail regulations and the rule-making process in Texas. Pages 299–312 *in* L. A. Brennan, editor. Texas quails: ecology and management. Texas A&M University Press, College Station, USA.

Curtis, P. D., B. S. Mueller, P. D. Doerr, and C. R. Robinette. 1989. Seasonal survival of radio-marked northern bobwhite quail from hunted and nonhunted populations. Pages 263–275 *in* C. J. Amlaner, Jr., editor. Proceedings of the Tenth International Symposium on Biotelemetry. University of Arkansas Press, Fayetteville, USA.

DeMaso, S. J., W. E. Grant, F. Hernández, L. A. Brennan, N. J. Silvy, X. B. Wu, and F. C. Bryant. 2011. A population model to simulate northern bobwhite population dynamics in southern Texas. Journal of Wildlife Management 75: In Press.

DeMaso, S. J., J. P. Sand, L. A. Brennan, F. Hernández, and R. W. DeYoung. 2013. Simulating density-dependent relationships in South Texas bobwhite populations. Journal of Wildlife Management 77:24–32.

DeMaso, S. J., M. J. Schnupp, E. J. Redeker, L. A. Brennan, J. P. Sands, T. W. Teinert, A. M. Fedynich, F. C. Bryant, R. M. Perez, and D. Rollins. 2010. A practical and efficient helicopter survey technique to estimate bobwhite abundance on Texas rangelands. Technical Publication No. 2, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, USA.

Dixon, K. R., M. A. Horner, S. R. Anderson, W. D. Heniques, D. Durham, and R. J. Kendall. 1996. Northern bobwhite habitat use and survival on a South Carolina plantation during winter. Wildlife Society Bulletin 24:627–635.

Doster, G. L., W. R. Davidson, and W. M. Martin. 1982. Hunter success and crippling losses for bobwhite quail. National Quail Symposium Proceedings 2:45–47.

Errington, P. L., and F. N. Hamerstrom, Jr. 1935. Bob-white survival on experimentally shot and unshot areas. Iowa State College Journal of Science 9:625–639.

Gould, F. W. 1975. Texas plants—a checklist and ecological summary. Revised. Miscellaneous Publication 585, Texas Agricultural Experiment Station, College Station, USA.

Guthery, F. S. 1988. Line transect sampling of bobwhite density of rangeland: evaluation and recommendations. Wildlife Society Bulletin 16:193–203.

Guthery, F. S. 1997. A philosophy of habitat management for northern bobwhites. Journal of Wildlife Management 61:291−301.

Guthery, F. S. 2002. The technology of bobwhite management: the theory behind the practice. Iowa State Press, Ames, USA.

Guthery, F. S., A. K. Crews, J. J. Lusk, R. N. Chapman, and M. Sams. 2004*a*. Effects of bag limits on bobwhite hunters and harvest. Journal of Wildlife Management 68:1095–1103.

Guthery, F. S., M. J. Peterson, and R. R. George. 2000. Viability of northern bobwhite populations. Journal of Wildlife Management 64:646–662.

Guthery, F. S., M. J. Peterson, J. J. Lusk, M. J. Rabe, S. J. DeMaso, M. Sams, R. D. Applegate, and T. V. Dailey. 2004*b*. Multistate analysis of fixed, liberal regulations in quail harvest management. Journal of Wildlife Management 68:1104–1113.

Haines, A. M., F. Hernández, S. E. Henke, and R. L. Bingham. 2009. A review of crippling loss for northern bobwhites. National Quail Symposium Proceedings 6:420–425.

Hernández, F., and F. S. Guthery. 2012. Beef brush and bobwhites: quail management in cattle country. Texas A&M University Press, College Station, USA.

Hernández, F., R. M. Perez, and F. S. Guthery. 2007. Bobwhites on the South Texas Plains. Pages 273–298 *in* L. A. Brennan, editor. Texas quails: ecology and management. Texas A&M University Press, College Station, USA.

Howard, R. 2007. Operating a South Texas quail hunting camp. Pages 336–362 *in* L. A. Brennan, editor. Texas quails: ecology and management. Texas A&M University Press, College Station, USA.

Klimstra, W. D. 1982. Bobwhite quail and changing land use. National Quail Symposium Proceedings 2:1–5.

Kokko, H. 2001. Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. Wildlife Biology 7:141–150.

Lehmann, V. W. 1984. Bobwhites in the Rio Grande Plain of Texas. Texas A&M University Press, College Station, USA.

Marques, T.A., L. Thomas, S. G. Fancy, and S. T. Buckland. 2007. Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124:1229–1243.

Montalvo, A., D. A. Woodard, and L. A. Brennan. 2022. Evaluating distance sampling measurements using laser rangefinders from a helicopter platform. East Foundation Management Bulletin. Under review.

Peterson, M. J. 1999. Quail harvest management in Texas: a rational approach. Pages 124–133 *in* K. A. Cearly, editor. Preserving Texas' quail hunting heritage into the 21st century. Texas Agricultural Extension Service, Texas A&M University, College Station, USA.

Peterson, M. J. 2001. Northern bobwhite and scaled quail abundance and hunting regulation: a Texas example. Journal of Wildlife Management 65:828–837.

Peterson, M. J., and R. M. Perez. 2000. Is quail hunting self regulatory? Northern bobwhite and scaled quail abundance and quail hunting in Texas. National Quail Symposium Proceedings 4:85–91.

Pollock, K. H., C. T. Moore, W. R. Davidson, F. E. Kellogg, and G. L. Doster. 1989. Survival rates of bobwhite quail based on band recovery analyses. Journal of Wildlife Management 53:1–6.

Rader, M. J., L. A. Brennan, K. A. Brazil, F. Hernández, and N. J. Silvy. 2011. Simulating northern bobwhite population responses to nest predation, nesting habitat, and weather in South Texas. Journal of Wildlife Management 75:61–70.

Reed, J. M., D. Murphy, and P. F. Brussard. 1998. The efficacy of population viability analysis. Wildlife Society Bulletin 26:244–251.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bulletin 19, Fisheries Research Board of Canada, Ottawa, Ontario, Canada.

Robinette, C. F., and P. D. Doerr. 1993. Survival of northern bobwhite on hunted and nonhunted study areas in the North Carolina sandhills. National Quail Symposium Proceedings 3:74–78.

Rollins, D. 2002. Sustaining the 'quail wave' in the southern Great Plains. National Quail Symposium Proceedings 5:48–56.

Roseberry, J. L. 1979. Bobwhite population responses to exploitation: real and simulated. Journal of Wildlife Management 43:385–305.

Roseberry, J. L., and W. D. Klimstra. 1984. Population ecology of the bobwhite. Southern Illinois University Press, Carbondale, USA.

Rosene, W. 1969. The bobwhite quail: its life and management. Rutgers University Press, New Brunswick, New Jersey, USA.

Rusk, J. P., F. Hernández, J. A. Arredondo, F. C. Bryant, D. G. Hewitt, E. J. Redeker, L. A. Brennan, and R. L. Bingham. 2007. An evaluation of survey methods for estimating northern bobwhite abundance in southern Texas. Journal of Wildlife Management 71:1336−1343.

Sandercock, B. K., W. E. Jensen, C. K. Williams, and R. D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. Journal of Wildlife Management 72:970–982.

Sanders, R. R., C. M. Thompson, D. Williams, and J. L. Jacobs. 1974. Soil survey of Jim Hogg County, Texas. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C.

Sands, J. P. 2010. Testing sustained-yield harvest theory to regulate northern bobwhite hunting. Dissertation, Texas A&M University-Kingsville, Kingsville, USA.

Sands, J. P., S. J. DeMaso, L. A. Brennan, D. L. Williford, R. W. DeYoung, E. M. Wehland, F. Hernández, and K. S. Miller. 2012. Application of metapopulation theory to northern bobwhite conservation. National Quail Symposium Proceedings 7:108.

Sands, J. P., M. J. Schnupp, T. W. Teinert, S. J. DeMaso, F. Hernández, L. A. Brennan, D. Rollins, and R. M. Perez. 2013. Tests of an additive harvest mortality model for northern bobwhite (*Colinus virginianus*) harvest management in Texas, USA. Wildlife Biology 19:12–18.

Schnupp, M. J., F. Hernández, E. J. Redeker, F. C. Bryant, J. P. Rusk, S. J. DeMaso, J. P. Sands, T. W. Teinert, L. A. Brennan, D. Rollins, and R. M. Perez. 2013. An electronic system to collect distance-sampling data during helicopter surveys of northern bobwhite. Wildlife Society Bulletin 37:236−245.

Shupe, T. E., F. S. Guthery, and S. L. Beasom. 1987. Use of helicopters to survey northern bobwhite populations on rangeland. Wildlife Society Bulletin 15:458−462.

Sisson, D. C., T. M. Terhune II, W. E. Palmer, and R. E. Thackston. 2017. Contributions of translocation to northern bobwhite population recovery. National Quail Symposium Proceedings 8:151–159.

Stanford, J. A. 1972. Bobwhite quail population dynamics: relationships of weather, nesting, production, patterns, fall population characteristics, and harvest in Missouri quail. National Quail Symposium Proceedings 1:115–139.

Stoddard, H. L. 1931. The bobwhite quail: its habits, preservation and increase. Charles Scribner's Sons, New York, New York, USA.

Teinert, T. W., L. A. Brennan, F. Hernández, S. J. DeMaso, J. P. Sands, D. Rollins, M. J. Schnupp, and R. M. Perez. 2013. Overwinter survival of northern bobwhites in nonhunted areas in the Rolling Plains and South Texas Plains of Texas. Bulletin of the Texas Ornithological Society 46:22–29.

Thomas, L., S. T. Buckland, E. A. Rexsad, J. L. Laake, S. Strindberg, S. L. Hedly, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5−14.

Tomeček, J. M., B. L. Pierce, and M. J. Peterson. 2015. Quail abundance, hunter effort, and harvest of two Texas quail species: implications for hunting management. Wildlife Biology 21:303–311.

Vance, D. R. and J. A. Ellis. 1972. Bobwhite populations and hunting on Illinois public hunting areas. National Quail Symposium Proceedings 1:165–174.

Williams, C. K., F. S. Guthery, R. D. Applegate, and M. J. Peterson. 2004. The northern bobwhite: scaling our management for the twenty-first century: Wildlife Society Bulletin 32:861–869.

Woodard, D. A., A. Montalvo, L. A. Brennan, F. Hernández, H. L. Perotto-Baldivieso, and N. Wilkins. 2019. Documenting a late season quail hatch. East Foundation Management Bulletin 1:1–4.

APPENDIX A. Model selection and results from season analysis (November, December, January, March) using conventional distance sampling with a pooled detection function, conventional distance sampling with a stratified detection function, and multiple covariate distance sampling with month as covariate for line-transect distance sampling surveys via helicopter platform on the hunted site during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and three goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S = Kolmogorov-Smirnov.

Year	Analysis[a]	Covariate[b]	Key function[c]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2018–2019	MCDS	Date	HR	5	0.00	2,549.10	0.60	0.60	0.55
	CDS	Stratified f(0)	HN+cos	5	0.87	2,549.97	-	-	-
	MCDS	Date	HN	4	2.13	2,551.23	0.70	0.60	0.51
	CDS	Stratified f(0)	HN+hp	4	2.17	2551.27	-	-	-
	CDS	Stratified f(0)	HR+sp	8	3.47	2552.57	-	-	-
	CDS	-	HN+cos	2	3.61	2552.71	0.90	1.00	0.95
	CDS	Stratified f(0)	UN+cos	5	3.74	2552.84	-	-	-
	CDS	-	HN+hp	1	3.90	2553.00	0.70	0.60	0.73
	CDS	-	HR+sp	2	4.12	2553.22	1.00	1.00	0.98
	CDS	-	UN+cos	2	5.18	2554.28	1.00	1.00	0.87
	CDS	-	HR+sp	3	0.49	5089.94	0.90	1.00	0.96
	CDS	Stratified f(0)	HN+hp	5	1.34	5090.79			
	MCDS	Date	HN	4	1.34	5090.79	0.70	0.80	0.70
	CDS	-	UN+cos	2	1.39	5090.85	0.90	0.80	0.80
	CDS	Stratified f(0)	HN+cos	4	1.54	5090.99			
	CDS	Stratified f(0)	UN+cos	5	3.10	5092.56			
	MCDS	Stratified f(0)	HR	5	9.69	5099.15	0.70	0.60	0.64
2020–2021	CDS	-	HN	1	0.00	5336.61	0.80	0.90	0.77
	CDS	-	HR+sp	2	1.20	5337.81	1.00	1.00	0.891
	CDS	-	UN+cos	2	1.52	5338.14	1.00	1.00	0.842
	CDS	Stratified f(0)	UN+cos	5	2.68	5339.29	-	-	-
	CDS	Stratified f(0)	HR+sp	8	2.68	5339.29	-	-	-
	MCDS	Date	HN	4	3.24	5339.85	0.70	0.80	0.78
	CDS	Stratified f(0)	HN+hp	5	3.34	5339.95	-	-	-
	CDS	Stratified f(0)	HN+cos	6	3.81	5340.42	-	-	-
	MCDS	Date	HR	5	5.24	5341.86	1.00	1.00	0.88

[a] Analysis: CDS = Conventional Distance Sampling; MCDS =Multiple Covariate Distance Sampling
[b] Covariate Date = month of survey (early November, mid-December, late January, early March).
[c] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX B. Model selection and results from season analysis (November, December, January, March) using conventional distance sampling with a pooled detection function, conventional distance sampling with a stratified detection function, and multiple covariate distance sampling with month as covariate for line-transect distance sampling surveys via helicopter platform on the nonhunted site during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and three goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S = Kolmogorov-Smirnov.

Year	Analysis[a]	Covariate[b]	Key function[c]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2018–2019	CDS	Stratified f(0)	HN	4	0.00	2188.04	-	-	-
	CDS	Stratified f(0)	UN+cos	3	0.22	2188.26	-	-	-
	MCDS	Date	HR	5	4.20	2192.24	0.90	0.80	0.81
	CDS	Stratified f(0)	HR+sp	8	7.69	2195.73	-	-	-
	CDS	-	HN	1	30.48	2218.52	0.70	0.70	0.44
	CDS	-	UN	1	31.21	2219.25	0.70	0.80	0.56
	CDS	-	HR+sim	3	33.64	2221.69	1.00	1.00	0.81
2019–2020	CDS	Stratified f(0)	HR+sim	8	0.00	2472.66	-	-	-
	CDS	Stratified f(0)	UN+cos	6	2.42	2475.08	-	-	-
	CDS	-	HR+sim	2	2.43	2475.09	0.80	0.80	0.52
	CDS	-	UN+cos	1	2.53	2475.19	0.50	0.50	0.12
	CDS	-	HN	1	2.88	2475.54	0.70	0.60	0.24
	CDS	Stratified f(0)	HN+cos	7	3.67	2476.33	-	-	-
	CDS	Stratified f(0)	HN+hp	5	4.84	2477.50	-	-	-
	MCDS	Date	HN	4	5.97	2478.63	0.70	0.70	0.48
	MCDS	Date	HR	5	8.19	2480.85	0.80	0.80	0.67
2020–2021	MCDS	Date	HN	4	0.00	4695.94	1.00	1.00	0.95
	CDS	Stratified f(0)	UN+cos	5	0.06	4696.00	-	-	-
	CDS	Stratified f(0)	HN	4	0.13	4696.07	-	-	-
	MCDS	Date	HR	5	2.19	4698.13	1.00	1.00	0.95
	CDS	Stratified f(0)	HR+sp	9	4.73	4700.68	-	-	-
	CDS	-	UN+cos	1	5.12	4701.06	1.00	1.00	0.97
	CDS	-	HN	1	6.52	4702.46	1.00	1.00	0.97
	CDS	-	HR	2	8.25	4704.19	1.00	1.00	0.93

[a] Analysis: CDS = Conventional Distance Sampling; MCDS =Multiple Covariate Distance Sampling
[b] Covariate Date = month of survey (early November, mid-December, late January, early March).
[c] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX C. Model selection and results of conventional distance sampling (CDS) estimates of bobwhite density per periodic survey (individual CDS per month) from November to March on the hunted site during the 2017–2018, 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and 3 goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S = Kolmogorov-Smirnov.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2017–2018	December	UN+cos	1	0.00	1027.40	0.90	0.90	0.87
		HN	1	0.59	1027.99	1.00	1.00	0.89
		HR	2	0.86	1028.26	1.00	1.00	0.97
		UN	0	51.26	1078.66	0.00	0.00	0.00
2018–2019	November	UN+cos	1	0.00	1101.11	0.90	0.90	0.93
		HN	1	0.24	1101.35	0.90	1.00	0.95
		HR+sim	2	1.01	1102.12	1.00	1.00	0.98
		UN	0	44.19	1145.29	0.00	0.00	0.00
	December	HR	2	0.00	818.67	1.00	1.00	1.00
		HN+cos	2	0.98	819.95	1.00	1.00	1.00
		UN+cos	3	2.63	821.30	1.00	1.00	0.99
		HN	1	7.66	826.33	0.10	0.10	0.10
		UN	0	96.37	915.04	0.00	0.00	0.00
	February	HN	1	0.00	644.29	0.80	0.80	0.94
		UN+cos	1	0.36	644.65	0.50	0.50	0.69
		HR	2	0.58	644.87	1.00	1.00	0.93
		UN	0	37.11	681.41	0.00	0.00	0.00
	March	UN+cos	1	0.00	509.42	0.60	0.70	0.73
		HN	1	0.77	510.19	0.70	0.70	0.76
		HR	2	0.77	510.19	1.00	1.00	1.00
		UN	0	17.87	527.29	0.00	0.00	0.00
2019–2020	November	UN+cos	1	0.00	1956.38	0.30	0.30	0.16
		HN+cos	2	1.17	1957.55	0.60	0.70	0.55
		HN+hp	2	1.44	1957.82	0.70	0.80	0.64
		HN	1	1.77	1958.15	0.30	0.30	0.14
		HR	2	3.45	1959.83	0.70	0.70	0.69
		UN	0	91.74	2048.12	0.00	0.00	0.00
	December	HN	1	0.00	1251.09	0.90	0.90	0.89
		UN+cos	1	0.74	1251.83	0.90	0.90	0.83
		HR+sp	3	3.41	1254.50	1.00	0.90	0.89
		HR	2	3.73	1254.82	0.60	0.70	0.78
		UN	0	49.97	1301.06	0.00	0.00	0.00
	January	HN	1	0.00	1013.39	0.90	0.90	0.61
		UN+cos	1	0.57	1013.96	0.70	0.80	0.42
		HR	2	2.34	1015.73	0.50	0.60	0.46
		UN	0	18.68	1032.07	0.00	0.00	0.00
	March	UN+cos	1	0.00	869.53	0.90	1.00	0.91
		HN	1	0.26	869.80	0.90	0.90	0.82
		HR	2	2.02	871.56	1.00	1.00	1.00
		UN	0	12.00	881.53	0.00	0.00	0.00
2020–2021	November	UN+cos	1	0.00	1980.92	0.80	0.90	0.86
		HR	2	1.28	1982.20	1.00	1.0	0.93
		HN+cos	2	2.11	1983.03	1.00	1.0	0.93
		HN	1	2.18	1983.10	0.50	0.6	0.60

APPENDIX C. Continued.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
		UN	0	31.33	2012.25	0.00	0.00	0.00
	December	HN	1	0.00	1663.73	0.50	0.60	0.52
		HR	2	0.02	1663.74	1.00	1.00	0.98
		UN+cos	2	0.94	1664.67	0.70	0.80	0.78
		UN	0	20.03	1683.75	0.00	0.00	0.00
	January	UN+cos	1	0.00	1058.49	0.70	0.70	0.68
		HN	1	0.45	1058.94	0.80	0.90	0.87
		HR	2	0.63	1059.11	1.00	1.00	0.99
		UN	0	25.35	1083.84	0.00	0.00	0.00
	March	HN	1	0.00	631.41	0.90	1.00	0.83
		HR	2	0.37	631.78	0.90	0.90	0.96
		UN+cos	1	1.12	632.52	0.90	0.90	0.77
		UN	0	4.90	636.31	0.05	0.05	0.07

[a] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX D. Model selection and results of conventional distance sampling (CDS) estimates of bobwhite density per periodic survey (individual CDS per month) from November to March on the nonhunted site during the 2017–2018, 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and 3 goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S =Kolmogorov-Smirnov.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2017–2018	December	UN+cos	1	0.00	880.01	0.80	0.90	0.91
		HN	1	0.98	881.00	0.70	0.80	0.85
		HR	2	1.36	881.37	1.00	1.00	1.00
		UN	0	25.04	905.05	0.00	0.00	0.00
2018–2019	November	HN+cos	2	0.00	739.13	0.70	0.80	0.58
		HN	1	0.38	739.51	0.30	0.40	0.36
		HR	2	1.26	740.39	0.50	0.60	0.40
		UN+cos	3	1.29	740.42	0.70	0.80	0.60
		UN	0	58.99	798.12	0.00	0.00	0.00
	December	UN+cos	1	0.00	564.08	0.70	0.70	0.60
		HR	2	1.02	565.10	1.00	1.00	1.00
		HN	1	1.15	565.23	0.70	0.70	0.61
		UN	0	19.51	583.59	0.00	0.00	0.00
	February	HN	1	0.00	532.91	0.90	1.00	0.86
		UN+cos	1	0.06	532.97	0.80	0.80	0.70
		HR	2	1.80	534.71	1.00	1.00	0.93
		UN	0	9.71	542.62	0.00	0.01	0.01
	March	HR	2	0.00	601.12	0.150	0.20	0.14
		UN	0	1.97	603.10	0.300	0.15	0.08
		HN	1	2.06	603.19	0.150	0.20	0.21
2019–2020	November	UN+cos	2	0.00	809.40	0.90	0.90	0.84
		HR	2	0.37	809.77	1.00	1.00	0.97
		HN+cos	2	2.72	812.12	0.90	0.80	0.87
		HN	1	3.88	813.28	0.20	0.30	0.26
		UN	0	19.25	828.65	0.00	0.00	0.00

APPENDIX D. Continued.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
	December	UN+cos	1	0.00	605.18	0.50	0.60	0.49
		HN	1	0.38	605.56	0.70	0.70	0.74
		HR	2	1.04	606.22	0.90	1.00	0.75
		UN	0	8.17	613.34	0.01	0.01	0.00
	January	HR	2	0.00	545.80	0.40	0.40	0.18
		UN+cos	2	2.71	548.52	0.30	0.30	0.15
		HN+cos	3	3.64	549.44	0.40	0.50	0.25
		HN+hp	2	3.88	549.68	0.30	0.30	0.12
		HN	1	4.54	550.34	0.15	0.15	0.09
		UN	0	19.12	564.92	0.00	0.00	0.00
	March	HN	1	0.00	498.75	1.00	1.00	1.00
		UN+cos	1	0.01	498.76	1.00	1.00	1.00
		HR	2	2.24	500.99	1.00	1.00	1.00
		UN	0	3.00	501.75	0.05	0.05	0.06
2020–2021	November	UN+cos	1	0.00	1731.07	0.50	0.60	0.45
		HN	1	0.29	1731.35	0.70	0.80	0.56
		HR	2	0.88	1731.94	0.70	0.90	0.72
		UN	0	36.31	1767.37	0.00	0.00	0.00
	December	HN	1	0.00	1302.70	0.80	0.90	0.76
		UN+cos	1	0.47	1303.17	0.60	0.70	0.56
		HR+sp	3	2.72	1305.42	1.00	1.00	0.99
		HR	2	2.77	1305.47	1.00	1.00	0.99
		UN	0	65.63	1368.33	0.00	0.00	0.00
	January	HN	1	0.00	891.65	0.80	0.80	0.75
		UN+cos	1	0.21	891.86	0.70	0.80	0.56
		HR	2	1.46	893.11	0.80	0.90	0.92
		UN	0	8.44	900.09	0.01	0.01	0.00
	March	UN+cos	1	0.00	593.93	1.00	1.00	0.80
		HN	1	0.29	594.22	1.00	1.00	0.90
		HR	2	2.40	596.33	0.70	0.80	0.79
		UN	0	15.79	609.71	0.00	0.00	0.00

[a] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX E. The ratio of bobwhites lost to bobwhites harvested (α–additivity), the proportional reduction in posthunt population (p_α), and proportional reduction in one fall population to the next (β–additivity) on the hunted site during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Population changes calculated using the difference in density estimates between the various seasonal surveys (early November, mid-December, late January, and early March) according to line-transect distance sampling via helicopter platform.

Year	Period	α–additivity[a]	p_α[b]	β–additivity[c]
2018–2019	Season	1.96	-0.30	-1.22
2019–2020	Season	0.61	-0.11	1.43
2020–2021	Season	-1.22	0.21	
2018–2019	Early[d]	-	-	-
	Middle	1.03	-7.0	-
	Late	0.20	-3.9	-
2019–2020	Early	4.40	15.2	-
	Middle	1.84	9.9	-
	Late	3.49	16.8	-
2020–2021	Early	-6.62	0.5	-
	Middle	-1.14	15.5	-
	Late	-5.31	-16.4	-

[a] α–additivity = $[N_{nonhunt} – N_{hunt}]$ / Harvest, see Guthery (2002)

[b] $p_\alpha = [N_{nonhunt} – N_{hunt}] / N_{nonhunt}$, see Guthery (2002)

[c] β–additivity = $[N_{nonhunt\ fall\ yr2} – N_{hunt\ fall\ yr2}] / N_{nonhunt\ fall\ yr1}$, see Guthery (2002)

[d] Rates not estimated during the early period due to an increase in overall density from early November to mid-December (Woodard et al. 2019).