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# NORTHERN BOBWHITE RESPONSE TO POSTGRAZING VEGETATION MANAGEMENT AND RECOVERY IN SOUTH TEXAS

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## ABSTRACT

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) requires habitat structure and composition with grass cover for nesting, predator avoidance, and thermal refuge and forb cover for feeding on phytophagous arthropods and seeds. During the past 2 decades, many land managers with interest in promoting quail hunting opportunities have reduced or completely eliminated livestock across South Texas, USA, rangelands. Resting the land from grazing allows vegetation—especially grasses and forbs—to recover and thus provide nesting and foraging habitat for bobwhite and other birds. How bobwhite respond to postgrazing vegetation recovery is of keen interest to rangeland quail managers, but this topic is poorly known because case histories with quantitative data are lacking. Our objective was to investigate how bobwhite respond to the vegetation changes following removal of cattle grazing. Our study was conducted on a private ranch in Jim Hogg County, Texas and involved 3 different categories of postgrazing recovery and management: 1 area at 15 years post-cattle grazing where the landscape has been brush-sculpted and is actively managed since removal of cattle, 1 area at 3 years post-grazing with a previous stocking density of 7 ha/animal unit (high stocking density), and 1 area at 3 years post-grazing with a previous stocking density of 14 ha/animal unit (moderate stocking density). We trapped, radio-marked, and located bobwhites from March to September during 2015–2016 on the 3 comparative units. We estimated nest survival, adult breeding-season survival, home range size, and early winter density. We hypothesized that the 15-year postgrazing site would have higher early winter density, higher adult breeding season survival, and higher nest survival along with smaller mean home range size compared to the 2 more recently grazed sites. On average, the probability of a nest surviving the 23-day incubation period was highest on the 15-year postgrazing site at  $0.61 \pm 0.12$  (mean nest survival  $\pm$  standard error), with estimates of  $0.32 \pm 0.12$  on the 3-year moderate postgrazing site and  $0.33 \pm 0.12$  on the 3-year high postgrazing site. Adult breeding season survival did not differ among the 3 sites, and was instead influenced mostly by month within the season, probably a result of summer heat. An adult bobwhite had a  $0.48 \pm 0.04$  probability of surviving the breeding season. Early winter density, after summer and fall production was complete, increased on all sites from 2015 to 2016 and was consistently highest on the 15-year postgrazing site. Home range sizes on the 15-year and 3-year moderate postgrazing sites were significantly larger than on the 3-year high postgrazing site. Additionally, landscape features around nest sites suggest lingering differences among the sites, supporting higher nest survival on the 15-year postgrazing site. These findings suggest that in South Texas, bobwhite populations can attain densities of approximately 2.0–2.9 birds/ha within 5 years after removal or reduction of cattle, given adequate rainfall.

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**Key words:** *Colinus virginianus*, distance sampling, habitat, management, nest success, northern bobwhite, South Texas, survival, vegetation

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Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite(s)) and livestock have been coexisting in southern Texas, USA, rangelands for well over a century and a half, beginning with European settlement of this region. Over time, however, cattle grazing has altered much of the landscape in ways that can be detrimental to quail. Historically, brush in the region was limited to riparian corridors and areas protected from fire (Schmidly 2002). As the ranching industry grew, livestock populations and fire suppression efforts, in concurrence with rises in atmospheric carbon dioxide levels, led to vast increases in brush across the landscape (Van Auken 2000). By the mid-20th century, much of the open grassland areas had been lost (Johnston 1963, Archer and Smeins 1991). Grazing was historically viewed by biologists as detrimental to bobwhite abundance because bobwhites prefer habitat structure with grass cover for nesting and evading predators (Stoddard 1931, Lehmann 1937). Guthery (1997) proposed that the ideal goal of quail management was to maximize usable space, making all of an available area (such as an entire pasture, which on large South Texas ranches may be up to 4,000 ha) usable by bobwhite at all times. Although the encroachment of brush on a landscape may seem detrimental, brush is an important habitat component for bobwhite as it provides thermal refuge, which is especially important during dry years. It has been found that bobwhite can persist under a range of brush canopy cover conditions. Recommendations from 5% to 85% woody canopy can be found in the literature (Guthery 1986, Guthery et al. 2000). However, a landscape with too little (<5%) brush over the long term can lead to lower bobwhite densities (DeMaso et al. 2014).

Many studies have examined the response of bobwhite under different highly variable grazing regimes (Hammerquist-Wilson and Crawford 1981, Schulz and Guthery 1988, Wilkins and Swank 1992). However, the results of these studies were inconclusive as to which grazing regimes best benefit bobwhite. There has been increasing interest in managing landscapes to increase bobwhite populations for hunting purposes because the bobwhite has declined over much of its historical range (Brennan 1991, Hernández et al. 2013). Bobwhite hunting is of great economic importance to Texas, and many landowners have been reducing stocking densities or eliminating cattle completely to promote vegetation regrowth in hopes of improving quail habitat (Fulbright and Bryant 2002, Hernández and Guthery 2012). How bobwhite respond to these postgrazing landscapes is not well understood. Confounding factors such as stocking densities, different grazing systems, and precipitation patterns can make specific predictions about timing of recovery difficult.

The primary objective of our study was to quantify and compare variations in bobwhite responses on 3 different sites where cattle have been removed: 1 area of 15-years postgrazing where the landscape has been brush-sculpted and had been actively managed for bobwhite during this period; 1 area of 3 years postgrazing at a high stocking density (7 ha/animal unit [AU]), and 1 area of 3 years postgrazing at a moderate stocking density (14 ha/AU; Figure 1). We hypothesized that

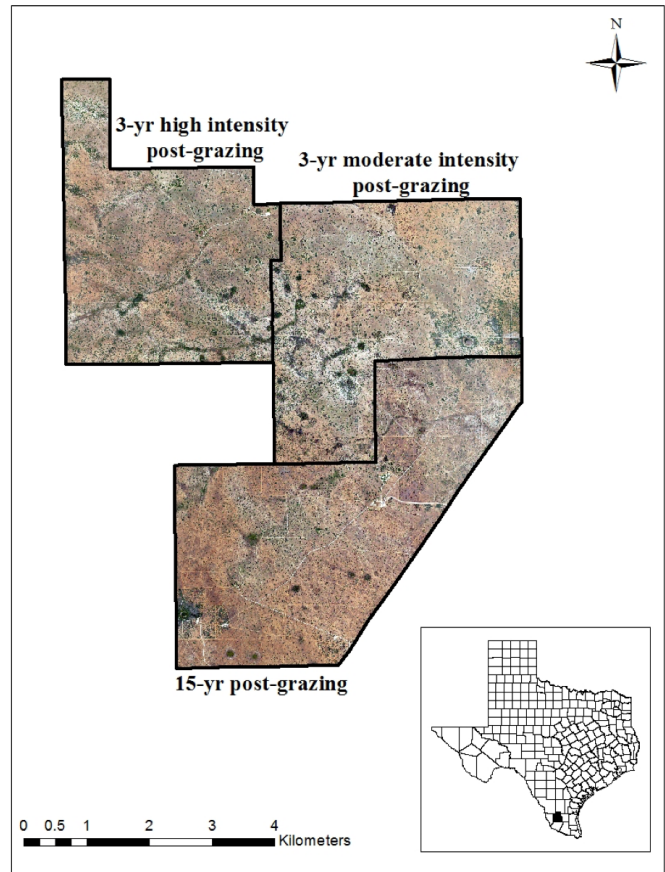


Fig. 1. Study area with 3 postgrazing sites in Jim Hogg County, Texas, USA.

the 3 years postgrazing site which had been grazed at high intensity would have the lowest amount of usable space (Guthery 1997). Furthermore, we hypothesized that bobwhite nest survival, adult breeding season survival, and early winter population density estimates would be lowest on the site with 3 years postgrazing at high intensity and highest on the 15-year postgrazing site with restoration. Because of potentially lower proportions of usable space, we also hypothesized that home range size on the area of 3 years postgrazing at high intensity would be larger compared to the 3-year postgrazing at moderate intensity and 15-year postgrazing sites.

## STUDY AREA

Our research was conducted on a private ranch in Jim Hogg County, Texas (27°6'55.10"N, 98°47'41.01"W). This ranch is in the Rio Grande Plains ecoregion (Gould 1975). The production of wild bobwhite for hunting is the primary management priority of this ranch. Mean annual rainfall for the study area was 60.4 cm (1981–2010) with precipitation peaking in May and September (Western Regional Climate Center 2015). Temperatures range from an average low of 16.1° C to an average high of 28.8° C (Western Regional Climate Center 2015). The most common soil types are Delmita

loamy fine sand, Delmita fine sandy loam, and Nueces-Sarita association. Common woody species include honey mesquite (*Prosopis glandulosa*), brasil (*Condalia hookeri*), granjeno (*Celtis pallida*), Texas persimmon (*Diospyros texana*), Mexican olive (*Cordia boissieri*), catclaw acacia (*Acacia greggii*), and hogplum (*Colubrina texansis*). Common forbs include croton (*Croton* spp.), palafoxia (*Palafoxia* spp.), cowpen daisy (*Verbesina encelioides*), and partridge pea (*Chamaecrista fasciculata*). Common grasses in the area are Lehmann lovegrass (*Eragrostis lehmanniana*), red lovegrass (*Eragrostis secundiflora*), buffleggrass (*Pennisetum ciliare*), Texas grama (*Bouteloua rigidisetia*), hairy grama (*Bouteloua hirsuta*), seacoast bluestem (*Schizachyrium scoparium*), and purple threeawn (*Aristida purpurea*).

Additional study area details can be found in Smith (2017).

## METHODS

### Study Design

The study consisted of 3 sites of postgrazing vegetation recovery as follows: 1 area at 15 years postgrazing where the landscape has been brush-sculpted and is actively managed since removal of cattle, 1 area of 3 years post-cattle grazing with a previous stocking density of 7 ha/AU (high stocking density), and 1 area of 3 years post-cattle grazing at a previous stocking density of 14 ha/AU (moderate stocking density; Figure 1). Because our study sites lacked true replication, inferences should be restricted to these study areas (Wester 1992).

*Fifteen years postgrazing site.*—This site was approximately 1,552 ha and was subject to long-term continuous grazing until around 2000 when the previous owner removed cattle from the property. Long-term cattle stocking densities for this property are unknown prior to about 2000, after which for several years the landscape was dominated by leatherstem (*Jatropha dioica*) with some buffleggrass (*Pennisetum ciliare*) and sparse native bunch grasses (Brennan, observations from ranch visits prior to this study). After cattle were removed, the site was treated with herbicides to combat the leatherstem and promote the growth of native grasses. A large-scale brush-sculpting operation was done in 2013. On this site many roads are disked, and mesquite is treated using individual plant treatment (IPT) to control it. Of our 3 sites, this site was the most intensively managed for bobwhite throughout the year as it contains the primary hunting routes. Due to the repeated brush control and the length of time since grazing, this site also had the most herbaceous cover of the 3 sites.

*Three years postgrazing site at moderate grazing density.*—This site is approximately 1,248 ha and was grazed at a level of 14 ha/AU before cattle were removed in 2013. This area has largely been left to recover since cattle removal. It does have a larger amount of brush than the actively managed site, but less than the previously highly grazed site. Disking of hunting routes is done to promote forb production.

*Three years postgrazing site at high grazing density.*—This site is approximately 1,133 ha and was subjected to high grazing density at approximately 7 ha/AU before cattle were removed in 2013. This site has areas that were subjected to brush management techniques by the previous owner that were not suitable for creating quail habitat. These past management practices have resulted in areas of monotypic stands of young mesquite growth. This site has the largest amount of brush cover of the 3 areas. Routes on this site are also disked, but due to many inaccessible areas it is not heavily hunted.

### Trapping and Radio-telemetry

We trapped bobwhites from March to July in 2015–2016 using funnel traps baited with grain sorghum (*Sorghum bicolor*; Stoddard 1931). During 2015, we trapped bobwhites along roads and monitored them only on the 15-year postgrazing site and the 3-year high density postgrazing site due to time constraints. During 2016, bobwhites were monitored on the 3-year moderate density postgrazing site, as well as on the other two sites monitored in 2015. During 2016, we created a 500-m buffer inside the boundaries of the 3 study sites to minimize the potential of bobwhites moving among study sites. We stratified trap sites using a 20-ha grid across the buffered area of each study site. One trap was placed near the center of each grid cell to achieve uniform trapping effort. We hid all traps under shrubs to provide canopy cover and help prevent predation and mitigate heat stress. If additional woody cover was needed, we placed freshly cut limbs over the trap. Traps were set before sunrise and checked every 2–3 hours until they were closed at sunset (Abbott et al. 2005). If the daily temperature rose above 35° C, we closed traps before noon and then reopened them in the evening when the temperature fell. After bobwhites were captured, we weighed them and determined age and sex (Rosene 1969). We fitted each bird with a size 7 aluminum band (Fair et al. 2010). We radio-marked 20–25 females that weighed  $\geq 150$  g with a 5–6.5 g necklace-style radio transmitter (American Wildlife Enterprises, Monticello, FL, USA) at each of the 3 study sites to maintain a sample size of 60–75 birds (Hernández et al. 2004). Males were radio-marked if we were not successful at trapping females. No more than 3 birds from each trap site were radio-marked so we could maximize the number of coveys with radio-marked birds. We located radio-marked birds 2–3 times/week using a hand-held, 3-element Yagi antenna. We took bobwhite locations (individual birds, activity unknown) and nest locations at the point of sighting a bobwhite using a hand-held Global Positioning System (GPS). If a bird was found to be in the same location twice during different days, we assumed it was incubating and placed flagging tape about 20 m from the nest in the 4 cardinal directions. Incubating birds were not approached closer than 20 m to limit disturbance to the nest site. Once a nest site was located, it was monitored every 2–3 days from a distance  $\geq 20$  m to determine nest fate. Usually because the incubating bobwhite moved away from the nest site without returning, we defined the outcome as either success or failure, based on the nest condition, shell



contents, and shell condition, all of which indicated whether the chicks hatched successfully or were lost to predation. Once nesting was completed, clutch size was determined from successful nests where possible. Bobwhite trapping, handling, and tracking were done in accordance with the Texas A&M University-Kingsville Institutional Animal Care and Use protocols 2013-04-16-A5 and 2016-02-26.

### Vegetation Measurements

**Macrohabitat.**—We used 2014 National Agriculture Imagery Program natural color/color infrared aerial photography of our study sites at 1-m resolution to quantify the landscape structure of our study sites (Figure 2a). We performed an unsupervised classification (convergence threshold of  $\geq 95\%$ ) in ERDAS IMAGINE 2015 (Hexagon Geospatial, Norcross, GA, USA) to classify the landscape into 3 categories (woody, herbaceous, and bare ground) (Figure 2b). Roads on the study site were digitized using ArcGIS 10.4 based on aerial photography definition at scale 1:500 (Esri Inc., Redlands, CA, USA). We conducted an accuracy assessment by generating 200 random points in each of the 4 images that made up our study area and classified the points into 1 of the 3 categories by visual assessment plus field verification (Perotto-Baldivieso et al. 2009, Mata et al. 2018). Additionally, we took 300 points in the field, classified them into 1 of the 3 categories, and compared them to the classified image. We assessed accuracy using a confusion matrix and had an overall accuracy for the classification of 90% (Congalton 1991).

**Microhabitat.**—We measured nest vegetation characteristics of a nest-centered point and a random point. These vegetation measurements were taken only during 2016 due to logistical constraints in 2015. Random points were chosen by generating a random compass bearing and distance between 50 m and 100 m away from the nest; this method was similar to those used in Lusk et al. (2006). Vegetation measurements took place no more than 14 days after nest completion to avoid changes in structure between nesting and sampling times. We estimated percent canopy cover of woody, grass, forb, and bare ground at each nest site and at its corresponding random location using a 1-m<sup>2</sup> frame centered over the nest or random point (Daubenmire 1959). Additionally, we measured distance from the nest clump to the nearest woody cover.

### Aerial Surveys for Density Estimates

During December 2015 and 2016, respectively, we conducted line transect distance sampling surveys by helicopter on our 3 study sites; we followed the sampling methods and protocols described by Schnupp et al. (2013) and Rusk et al. (2007). This method of bobwhite density estimation has been shown to work well in rangelands (Rusk et al. 2007, DeMaso et al. 2010). Our survey was conducted from a 4-seat R-44 with room for a pilot and 3 observers (Rio Grande Helicopters, Laredo, TX, USA). The same 3 observers were used throughout each survey to avoid observer bias. The 2 rear observers were responsible for locating coveys on their

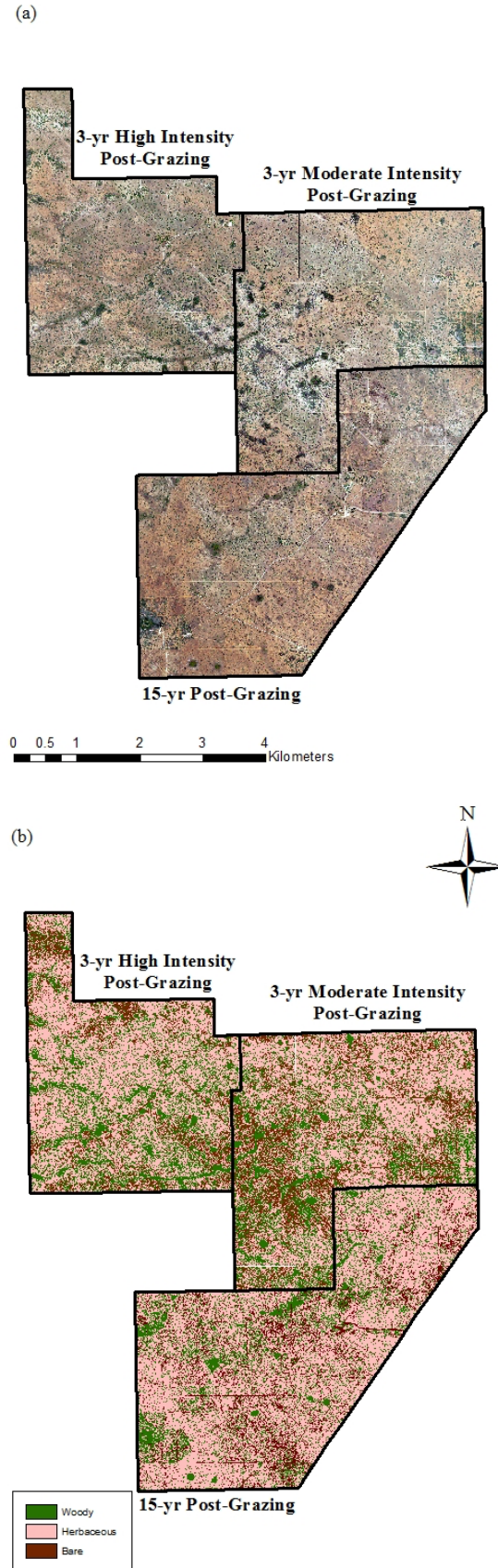


Fig. 2. Map of a) original unclassified 2014 National Agriculture Imagery Program natural color/color infrared aerial photography and b) final classified images of the study area, Jim Hogg County, Texas, USA.

sides of the helicopter while the front-seat observer located coveys in front of the helicopter. When a covey was detected, the helicopter hovered while the rear-seat observers marked the covey location with a laser rangefinder that measured distance, compass bearing, and angle of inclination from the helicopter (Trimble LaserAce 1000, Trimble Navigation Ltd., Sunnyvale, CA, USA). The laser rangefinders were linked to a Juno handheld GPS unit controlled by the front-seat observer which documented detections with covey size and GPS locations (Trimble Juno 5 series handheld, Trimble Navigation Ltd., Sunnyvale, CA, USA) (Schnupp et al. 2013).

During 2015, our survey design consisted of 23 east-west transects across the entire ranch (all 3 sites). Transects were placed 400 m apart for 50% coverage of the area with a total survey effort of 95 km and a survey time of 3.5 hours (Figure 3a). In 2016, survey coverage was increased to 100% with 42 east-west transects placed 200 m apart for a total survey effort of 194 km and survey time of 7 hours (Figure 3b). Surveys were flown at an altitude of 7–10 m and a speed of 37 km/hr (Schnupp et al. 2013). The entire ranch was flown in 1 day each year.

### Statistical Analyses

**Adult Breeding Season Survival.**—We calculated breeding season (Apr–Aug) survival using the “known fate” platform in Program MARK (White and Burnham 1999). This method is often used with telemetry data because it assumes that resighting probability is equal to 1. We created encounter histories for each radio-marked bobwhite according to the LDLDLDD format described in White and Burnham (1999). We coded the encounter history for each bobwhite in 1 of 3 ways: 10 means the bobwhite survived the interval, given it was alive at the start of the interval, 11 = the bobwhite died during the interval, given it was alive at the start of the interval, and 00 = the bobwhite was censored for the interval. For example, an individual with the encounter history 1010101100 was alive at the beginning of month 1, survived in months 2 and 3, and died in month 4. We built 12 candidate models in Program MARK and chose a best model based on Akaike’s Information Criterion values with a correction for small sample size ( $AIC_c$ ).

**Nest Survival.**—We used the nest survival platform in Program MARK to estimate bobwhite daily nest survival on our study areas (Mayfield 1961, 1975; Dinsmore and Dinsmore 2007). Nests found late in the incubation period due to later trapping were excluded so as to not bias these estimates ( $n = 2$ ). The nesting season was defined as the day we found the first nest to the day the last successful nest hatched over the 2 nesting seasons monitored. We ran 10 candidate models using the nest survival platform in Program MARK examining whether nest survival differed by 1) site, 2) year, and 3) time. Models were ranked using  $AIC_c$ . Program MARK estimates daily nest survival; these estimates were then extrapolated to the 23-day incubation period to estimate overall probability of a nest surviving. The site model was used to generate estimates for the 3 different postgrazing sites. However, due to high model

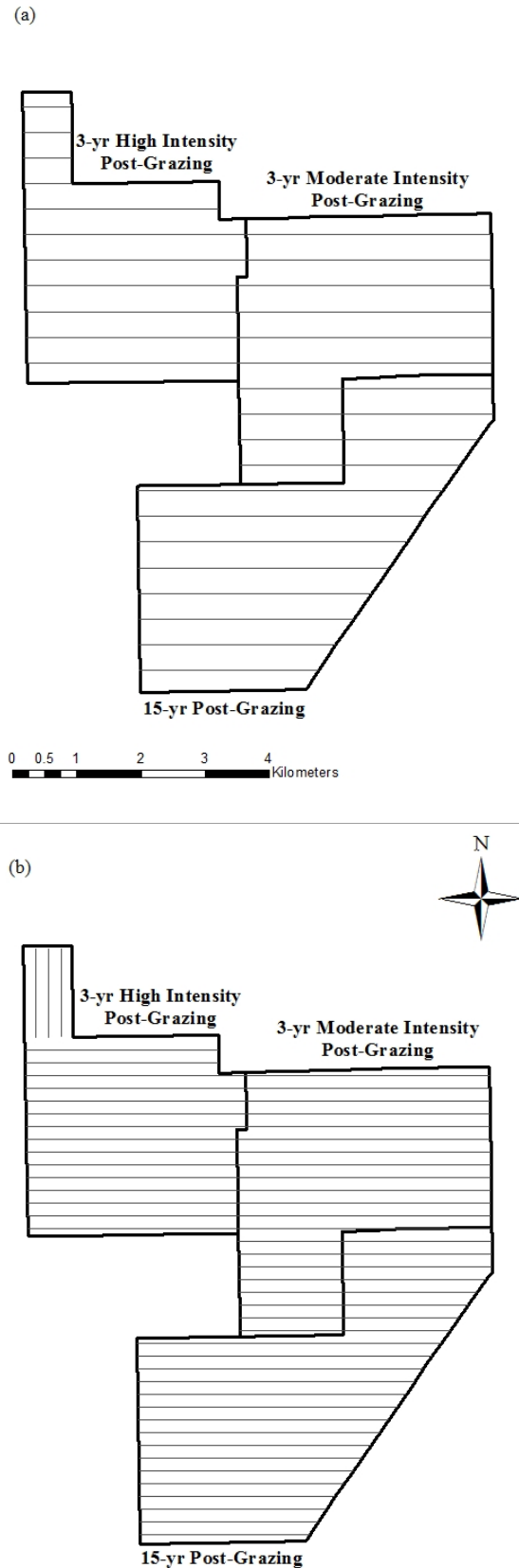


Fig. 3. Aerial survey design for northern bobwhite (*Colinus virginianus*) density estimation based on distance sampling a) during 2015 with transects placed 400 m apart and b) during 2016 with transects placed 200 m apart across the 3 postgrazing sites, Jim Hogg County, Texas, USA.

uncertainty, averaging was also used to predict nest survival on the 3 sites during the 2 years of the study. The delta method was then used to generate standard errors and confidence intervals for the model averaged estimates (Powell 2007).

*Home Range.*—We estimated home range size for radio-marked bobwhites with  $\geq 20$  locations based on a 95% and 50% core area using a fixed kernel home range with cross-validation in BIOTAS 2.0 (Ecological Software LLC, Hegymagas, Hungary, 2005) (Tri et al. 2014). We used the fixed kernel estimator, using least squares cross-validation to choose the smoothing parameter; this approach is assumed to provide accurate results with smaller variances compared to other animal home range estimation methods (Seaman and Powell 1996, Seaman et al. 1999). While most recommend at least 30–50 locations for the most accurate results, Haines et al. (2009) showed evidence that mean home range size and coefficients of variation leveled off at about 20 locations. Locations of bobwhite were assumed to be independent of one another since they could travel across their entire home range between each sampling event (White and Garrott 1990). We compared mean home range and core area size among the sites using an analysis of variance (alpha level of 0.05) using SPSS (version 24.0; IBM Corp., Armonk, NY, USA).

*Macrohabitat.*—During 2015–2016 we monitored 102 nests. In order to determine how often quail nests on the study area were in woody, herbaceous, and bare ground, bobwhite nesting locations were pooled between years, and we compared usage of the 3 classes by nesting bobwhites in proportion to their availability using a chi-square contingency analysis with a significance level of 5% (Brennan et al. 1987).

Around each nest site, we created buffers of 5 different sizes (10, 20, 30, 40, 50 m) using ArcGIS. The 5 different buffers were selected because we wanted to see how the influence of different landscape metrics might differ as distance from the nest site increased. We calculated 8 metrics of landscape structure that describe elements of woody cover for each study site and also around individual nest sites among the 3 postgrazing sites using FRAGSTATS (version 4.2; University of Massachusetts, Amherst, MA, USA). We selected 8 landscape metrics that, in our view, represent spatial elements of vegetation structure that contribute to meeting the annual cycle habitat needs of northern bobwhite in South Texas. There are undoubtedly scores of different landscape metrics that meet this criterion, but many of these metrics are difficult to understand. Thus, we selected only basic and easy-to-interpret landscape metrics known to be components of northern bobwhite habitat in rangeland environments. The selected metrics were: aggregation index (AI, %), mean patch area (AREA\_MN, ha), Euclidean nearest neighbor distance distribution (ENN\_MN, m), edge density (ED, m/ha), interspersed and juxtaposition index (IJI, %), patch density (PD, #/100 ha), percent of landscape (PLAND), and mean shape index distribution (SHAPE\_MN) (He et al. 2000, Perotto-Baldivieso et al. 2011, Pellissier et al. 2012, Zemanova et al. 2017). We compared these metrics between the 3 postgrazing sites (at each of the 5 buffer sizes)

by a PROC MIXED procedure in SAS 9.4 (SAS Institute Inc., Cary, NC, USA, 2017). For each of these analyses a variance-covariance matrix was selected using  $AIC_c$  and the distribution of residuals was then examined for normality. In order to satisfy the normality assumption, we analyzed percent of landscape, mean patch area, Euclidean nearest neighbor distance distribution, and mean shape index distribution on the log-scale and then back-transformed for final data reporting.

*Microhabitat.*—We compared vegetation characteristics (percent bare ground, percent forbs, percent grasses, and distance to woody vegetation) between two locations (nest sites and paired random points) in the 3 study sites. We used a linear mixed model with a fixed location effect (nest site or paired random point) and a random effect to account for variation among pairs of locations. The same analysis and model were applied to all pairs across all 3 study sites for an overall examination of characteristics between nest sites and paired random points.

*Density Estimation.*—We estimated density of bobwhite population on the 3 sites of interest using Program Distance version 7.0, release 1 (March 2015, <https://distancesampling.org/Distance/old-versions/distance70.html>). This program allows for the selection of 4 key functions (uniform, half normal, hazard, and negative exponential) and 3 different adjustment terms (cosine, simple polynomial, and hermite polynomial). The best detection function has 100% detection on the line ( $g(0) = 1$ ) and decreases monotonically with good model fit and small variance (Buckland et al. 2001). Density estimates are calculated by Program Distance as,

$$\bar{D} = \frac{n}{2\hat{\mu}L} \times E(s)$$

$$\text{var}(\bar{D}) = \bar{D}^2 \times \{[\text{CV}(n)]^2 + [\text{CV}\{f(0)\}]^2\}$$

where  $D$  is density,  $n$  is the number of coveys detected and  $u$  is the estimate of effective half-width,  $L$  is the length of transects,  $E(s)$  is the average covey size,  $CV$  is the coefficient of variation, and  $f(0)$  is the probability density function of detected distance from the line, evaluated at 0 distance.

Preliminary analysis of the data involved fitting 4 initial models: half normal with no adjustment, hazard rate with no adjustment, uniform with cosine, and half normal with cosine. Using these models, we selected cut points and a truncation distance if necessary. Once cut points and a truncation distance for the data were chosen, we reevaluated the data with the previous 4 models in addition to hazard rate with simple polynomial and half normal with hermite polynomial models. We determined model fit by examining the Kolmogorov-Smirnov and Cramer-von Mises tests. We selected a best model for our data using  $AIC_c$  and goodness-of-fit tests.

*Density Surface Modeling.*—Development of recent spatial analysis techniques has allowed researchers to account for spatial distribution when using distance sampling to estimate abundance (Hedley and Buckland 2004, Hedley et al. 2004). The development of density surface models (DSMs) allows for improved precision of density estimates



compared to conventional distance sampling (Hedley et al. 2004). We created DSMs using both geographic information system (GIS) and the statistical package R (version 3.3.2; R Foundation for Statistical Computing, Vienna, Austria). The dataset for building the DSMs was created in GIS and R was used for model fitting, selection, and density prediction using the ‘dsm’ package for R (Miller et al. 2013).

Density surface models of bobwhite abundance across the surveyed areas were based on the transect lengths, width of truncation distance was specified by the detection function model, and number of detections on each study site. Because both density and environmental factors of interest can vary over this distance, transects were split into relatively small segments where density was assumed to be constant. We used recommendations from Miller et al. (2013) and divided each transect into 100-m segments, which was about twice the truncation distance from each of our conventional distance sampling analyses.

We used color infrared aerial photography of our study sites from 2014 at 1-m resolution to create an NDVI used for covariate classification. We classified this map using unsupervised classification (convergence threshold of  $\geq 95\%$ ) in ERDAS IMAGINE 2015 to divide the landscape into 2 categories (woody and non-woody). An accuracy assessment of this classification was conducted by generating 200 random points in each image that made up our study area and classifying them into the 2 categories by visual assessment plus field verification (Perotto-Baldivieso et al. 2009, Mata et al. 2018). We used 5 metrics of woody cover, Normalized Difference Vegetation Index (NDVI) and geographic location (x,y) as the independent variables for the DSM. The 5 metrics of woody cover were: edge density (ED, m/ha), landscape shape index (LSI), mean patch area (AREA\_MN, ha), patch density (PD, #/100 ha), and percent of landscape (PLAND). Accuracy was assessed using a confusion matrix and met the minimum standard of  $\geq 85\%$  (Congalton 1991). We used

FRAGSTATS version 4.2 to analyze the 5 classification metrics using a moving-window approach using a 100-m radius based on quail movement biology as well as for fitting with segment sizes and truncation distances. We thus created a raster map for each covariate metric across the entire study area that was used to build the corresponding prediction grid of the DSM in R.

These habitat covariate data were associated with each transect segment by interpolating each raster dataset at the segment midpoint. The prediction grid template was created using a 100-m grid constant raster in GIS, clipped to the extent of the study area. We then used backwards selection to determine a best model. Covariates that were not significant, had extreme outliers, or were highly correlated ( $>0.8$ ) were removed. A top model was chosen based on maximum deviance explained and best model fit.

## RESULTS

### Adult Breeding Season Survival

We trapped and banded 119 bobwhites and deployed 50 radio transmitters during 2015. During 2016, we trapped and banded 202 bobwhites and placed radio transmitters on 77 birds. Adult survival was most influenced by a quadratic time trend (Table 1). Bobwhites had a  $0.48 \pm 0.04$  probability of surviving the breeding season (Apr–Aug). Monthly survival was highest in April and then decreased to a low point in June and July, with a slight improvement in August (Figure 4).

### Nest Survival

During 2015, we located 52 nests: 33 on the 15-year postgrazing site and 19 on the 3-year postgrazing site. In 2016, we found 50 nests: 20 on the 15-year postgrazing site, 14 on the 3-year moderate postgrazing site, and 16 on the 3-year high

Table 1. List of all models run using the known fate platform in Program MARK to estimate northern bobwhite (*Colinus virginianus*) adult breeding season survival on the study area during 2015 and 2016 in Jim Hogg County, Texas, USA.

Model name	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> weight	Model likelihood	Number of parameters	Deviance
S(quadratic time trend)	361.3974	0.0000	0.71251	1.0000	3	355.6450
S(time)	363.5267	2.1293	0.24571	0.3449	5	353.3951
S(site+quadratic time trend)	367.6595	6.2621	0.03112	0.0437	9	349.2612
S(linear time trend)	372.7154	11.3180	0.00248	0.0035	2	368.6893
S(site*time+year)	373.1247	11.7273	0.00202	0.0028	15	342.1485
S(site)	373.6430	12.2456	0.00156	0.0022	3	367.5906
S(.)	373.7178	12.3204	0.00150	0.0021	1	371.7091
S(site*time)	374.6130	13.2156	0.00096	0.0013	15	343.5368
S(year)	375.0155	13.6787	0.00079	0.0011	2	370.9894
S(site+year)	375.3968	13.9994	0.00065	0.0009	4	367.3093
S(site+linear time trend)	376.0827	14.6853	0.00046	0.0006	6	363.8981
S(site*year)	377.1469	16.0195	0.00024	0.0003	5	367.2853



postgrazing site. Nest survival was most influenced by site but also by time of initiation within the season (Table 2). Overall, the 15-year postgrazing site had a higher probability of a nest surviving the 23-day incubation period at  $0.61 \pm 0.12$  (mean nest survival + standard error) compared to a probability of  $0.32 \pm 0.12$  and  $0.33 \pm 0.12$  on the 3-year moderate density and 3-year high postgrazing sites respectively (Figure 5). Early (April) nests and late season nests (August) had a lower survival across all sites and years (Figures 6, 7). In 2015 the 15-year postgrazing site had a consistently higher nest survival probability than the 3-year high postgrazing site. In 2016, the 15-year postgrazing site was slightly higher than either of the 3-year postgrazing sites, which both had similar nest survival estimates.

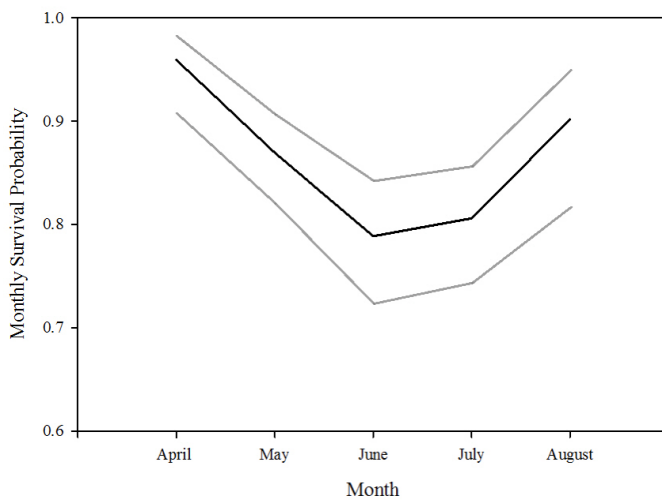


Fig. 4. Mean (dark line  $\pm$  95% confidence interval, upper and lower gray lines) estimates of adult breeding season survival (Apr–Aug) for northern bobwhite (*Colinus virginianus*) over the entire study area during 2015 and 2016, Jim Hogg County, Texas, USA.

## Home Range Estimates

We estimated 50% and 95% kernel home ranges for 62 birds across each study site both years. The mean 50% core area estimate on the 15-year postgrazing site was  $2.7 \pm 0.3$  ha ( $n = 29$ ) with a range of 0.2–8 ha. The mean estimate on the 3-year moderate postgrazing site was  $2.8 \pm 0.5$  ha ( $n = 10$ ) with a range of 1–7 ha. The mean estimate on the 3-year high postgrazing site was  $4 \pm 0.5$  ha ( $n = 23$ ) with a range of 0.3–11 ha. There were no differences in 50% core area sizes between the 15-year postgrazing site and the 3-year moderate postgrazing site ( $P \geq 0.93$ ) and the 3-year moderate postgrazing site and the 3-year high postgrazing site ( $P \geq 0.13$ ). However, there was a significant difference in 50% core area size between the 15-year postgrazing site and the 3-year high postgrazing site ( $P \geq 0.02$ ) (Figure 8a).

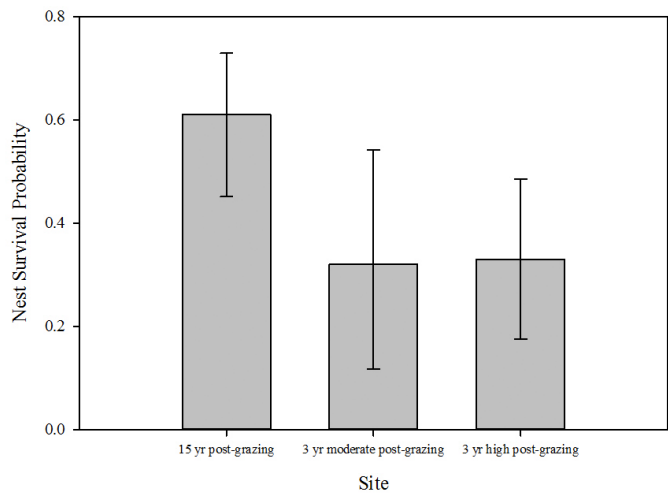


Fig. 5. Mean ( $\pm$ 95% confidence interval) estimates of northern bobwhite (*Colinus virginianus*) nest survival across the 23-day incubation period from the S(site) model in Program MARK for the 3 postgrazing sites during 2015 and 2016 in Jim Hogg County, Texas, USA.

Table 2. List of all models run using the nest survival platform in Program MARK to estimate northern bobwhite (*Colinus virginianus*) nest survival on the study area during 2015 and 2016 in Jim Hogg County, Texas, USA.

Model name	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> weight	Model likelihood	Number of parameters	Deviance
S(site)	263.0957	0.0000	0.27132	1.0000	3	257.0778
S(site+quadratic time trend)	263.1746	0.0789	0.26083	0.9613	5	253.1298
S(site+linear time trend)	264.6977	1.6020	0.12179	0.4489	4	256.6679
S(site*linear time trend)	265.0895	1.9938	0.10012	0.3690	6	253.0268
S(site*year)	265.3185	2.2228	0.08929	0.3291	5	255.2738
S(year)	266.5145	3.4188	0.04910	0.1810	2	262.5055
S(.)	266.8148	3.7191	0.04226	0.1558	1	264.8118
S(site*quadratic time trend)	267.2994	4.2037	0.03316	0.1222	9	249.1648
S(linear time trend)	268.5499	5.4542	0.01775	0.0654	2	264.5410
S(quadratic time trend)	268.9724	5.8767	0.01437	0.0530	3	262.9546

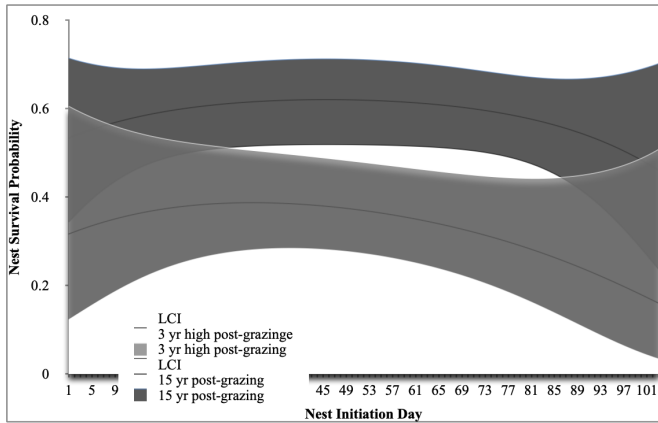


Fig. 6. Mean ( $\pm 95\%$  confidence interval) model averaged estimates of northern bobwhite (*Colinus virginianus*) nest survival during 2015 on 2 postgrazing sites, Jim Hogg County, Texas, USA.

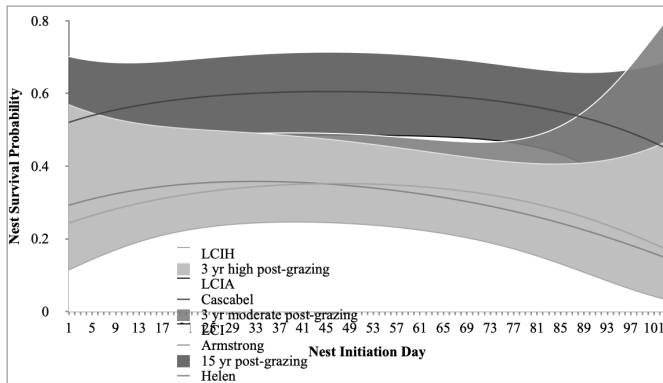


Fig. 7. Mean ( $\pm 95\%$  confidence interval) model averaged estimates of northern bobwhite (*Colinus virginianus*) nest success during 2016 on the 3 postgrazing sites, Jim Hogg County, Texas, USA.

The mean 95% kernel home range estimate on the 15-year postgrazing site was  $13.0 \pm 1.2$  ha ( $n = 29$ ) with a range of 0.5–29 ha. The mean estimate on the 3-year moderate postgrazing site was  $12.9 \pm 1.4$  ha ( $n = 10$ ) with a range of 7–21 ha. The mean estimate on the 3-year high postgrazing site was  $19.4 \pm 1.7$  ha ( $n = 23$ ) with a range of 5–41 ha. There was no difference between 95% kernel home range size on the 15-year postgrazing site and the 3-year moderate postgrazing site ( $P \geq 0.98$ ). However, there were differences between the 3-year high postgrazing site and the 15-year postgrazing site ( $P \geq 0.002$ ) and between the 3-year high postgrazing site and the 3-year moderate postgrazing site ( $P \geq 0.03$ ) (Figure 8b).

## Vegetation

**Macrohabitat.**—In 2015 and 2016, we found 102 nests across the 3 study sites. Across the entire study area, birds used herbaceous cover for nesting in a higher proportion (%) relative to its availability (%) (Table 3). On the 15-year and 3-year moderate postgrazing sites, bobwhites used nest sites in all the vegetation cover types in proportion to their availability

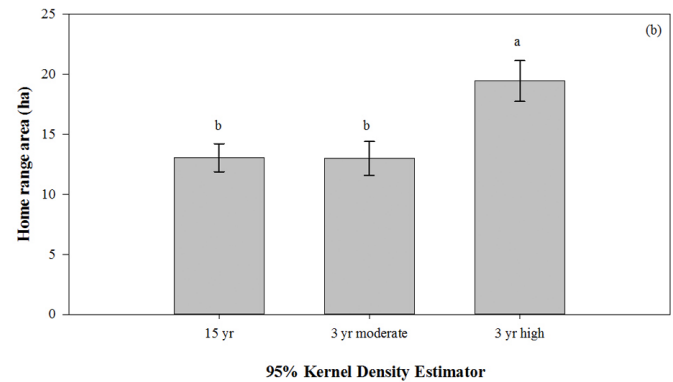
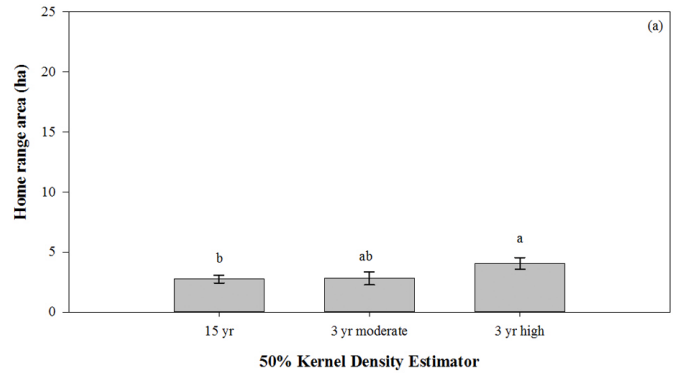


Fig. 8. Mean ( $\pm$ standard error) estimates of a) 50% kernel density estimator home ranges and b) 95% kernel density estimator home ranges of northern bobwhite (*Colinus virginianus*) during 2015 and 2016 on the 3 postgrazing sites, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ( $P > 0.05$ ) different.

(Table 3). However, on the 3-year high postgrazing site we observed bobwhites using more herbaceous cover and less woody cover for nesting than expected (Table 3).

At the individual site scale, percent woody cover, edge density, and mean patch area, were lowest on the 15-year postgrazing site (Table 4). Patch density and interspersed and juxtaposition were highest on this site (Table 4). Euclidean nearest neighbor distance was similar among the 3 sites. Aggregation index and mean shape index were just slightly smaller on the 15-year postgrazing site (Table 4). Notably, the 3-year moderate postgrazing site estimates for these metrics fell between the 15-year and 3-year high postgrazing sites in all but 2 of the metrics measured.

At a smaller scale, landscape structure around nest sites differed among the 3 sites. At 10-, 20-, and 30-m buffers around the nest site, percentage of woody cover was significantly higher on the 15-year postgrazing site; however, at the 40- and 50-m buffer sizes the 3-year moderate postgrazing site was not different from the 15-year postgrazing site. The 3-year moderate postgrazing site consistently had a lower

Table 3. Chi-square contingency analysis of macrohabitat use by northern bobwhite (*Colinus virginianus*) nests across 3 postgrazing sites during 2015 and 2016 in Jim Hogg County, Texas, USA.

Study area cover type	Number of bobwhite nests			P
	Proportion	Observed	Expected <sup>a</sup>	
Entire study area				
Bare ground	25.6	22	26	<0.025
Herbaceous	58.4	73	60	
Woody	16.0	7	16	
15-year postgrazing				
Bare ground	22.0	9	12	>0.10
Herbaceous	63.9	38	34	
Woody	14.1	6	7	
3-year moderate postgrazing				
Bare ground	27.2	3	4	>0.10
Herbaceous	52.1	10	7	
Woody	20.7	1	3	
3-year high postgrazing				
Bare ground	28.8	10	10	<0.05
Herbaceous	57.8	25	20	
Woody	13.5	0	5	

<sup>a</sup> Expected values based on proportions of available cover type

Table 4. Mean estimates of percent of landscape, patch density, edge density, mean patch area, mean shape index, Euclidean nearest neighbor distance, aggregation index, and interspersed and juxtaposition index for woody cover on the 3 postgrazing sites in Jim Hogg County, Texas, USA.

Site	Metric							
	% of woody cover	Patch density (#/100 ha)	Edge density (m/ha)	Mean patch area (ha)	Mean shape index	Euclidean nearest neighbor distance (m)	Interspersed and juxtaposition index (%)	Aggregation index (%)
15-yr postgrazing	22.0162	9849.7458	1935.3337	0.0022	1.2106	3.1991	37.2149	78.0142
3-yr moderate postgrazing	27.1804	8505.7808	2184.0097	0.0032	1.2406	3.1887	35.2341	79.9137
3-yr high postgrazing	28.7581	8958.1309	2318.0203	0.0032	1.248	3.0703	27.2789	79.8759

percentage of woody cover across all buffer sizes (Figure 9a). Woody patch density was statistically greater on the 15-year postgrazing site compared to the 2 recently grazed sites at the 10 and 20-m buffer sizes. At the 30-, 40-, and 50-m buffers the 3-year moderate postgrazing site had patch density estimates that were between the patch density estimates on the 15-year and 3-year high postgrazing sites (Figure 9b). Edge density estimates were statistically greater on the 15-year postgrazing sites across all buffer sizes. The 2 recent postgrazing sites had statistically similar estimates across all buffer sizes (Figure 9c). Mean woody patch area was very small and similar among the 3 sites at the 10-m buffer size, but began to diverge and increase with increasing buffer sizes (Figure 9d). Mean shape index was highest on the 15-year postgrazing

site at the 10- and 20-m buffer sizes, but the 3-year moderate postgrazing site increased to similar estimates at the 30-, 40-, and 50-m buffer sizes (Figure 9e). Euclidean nearest neighbor distance was greatest on the 3-year high postgrazing site at the 10-m buffer size and gradually decreased as the buffer size increased (Figure 9f). Aggregation index was similar on all 3 sites at the 10-m buffer size; the 15-year and 3-year moderate postgrazing sites at the 50-m buffer size ended with a similar estimate that was significantly greater than the estimate for the 3-year high postgrazing site (Figure 9g). Finally, the 15-year postgrazing site had a significantly greater interspersed and juxtaposition index than the other sites at all 5 buffer sizes, while the 2 recent postgrazing sites had similar estimates of this metric across all buffer sizes (Figure 9h).

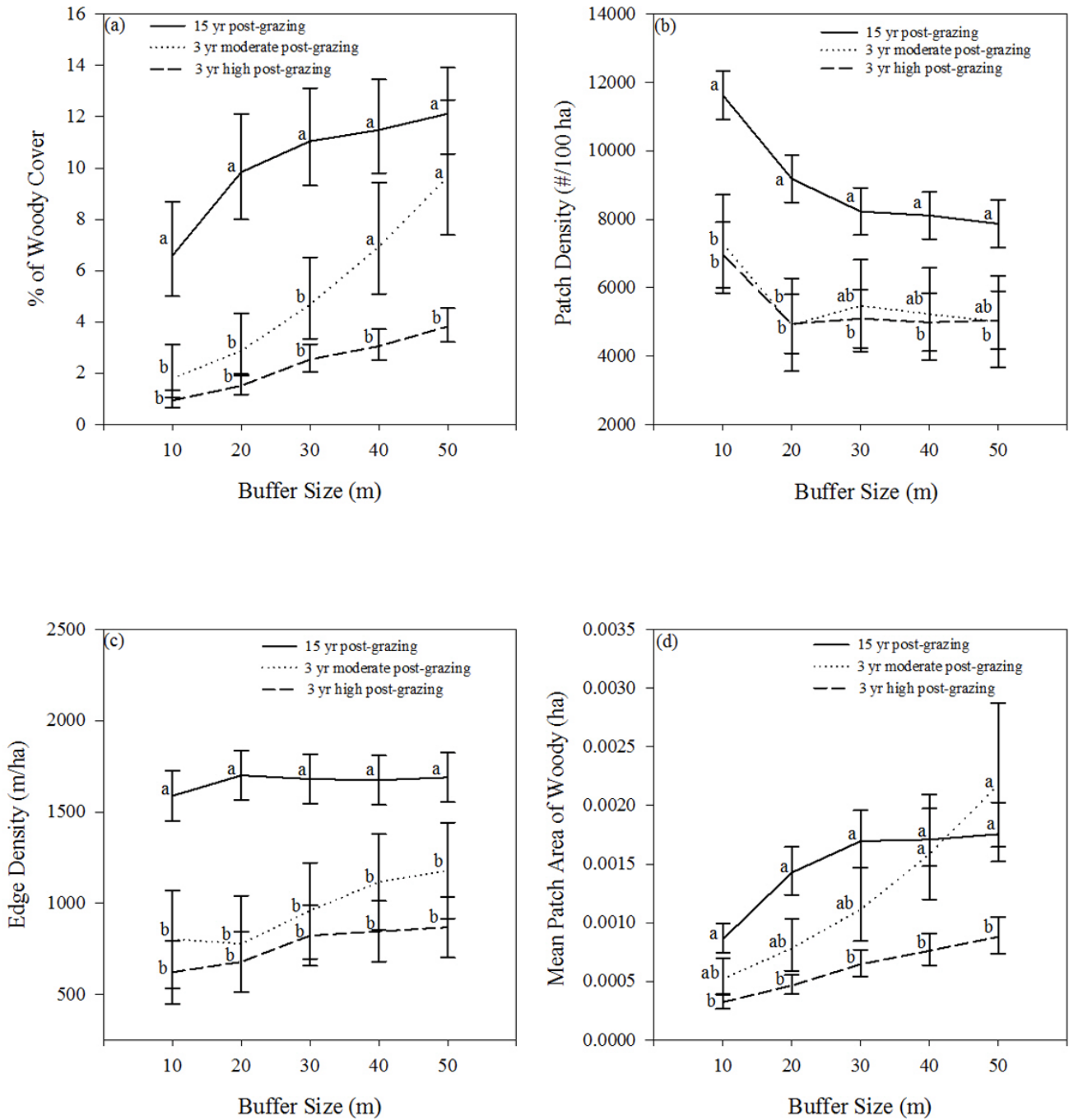


Fig. 9. Mean estimates of a) percent of landscape, b) patch density, c) edge density, d) mean patch area, e) mean shape index, f) Euclidean nearest neighbor distance, g) aggregation index, and h) interspersion and juxtaposition index for woody cover on northern bobwhite (*Colinus virginianus*) nest sites (n = 102) on the 3 postgrazing sites during 2015 and 2016 in Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ( $P > 0.05$ ) different.



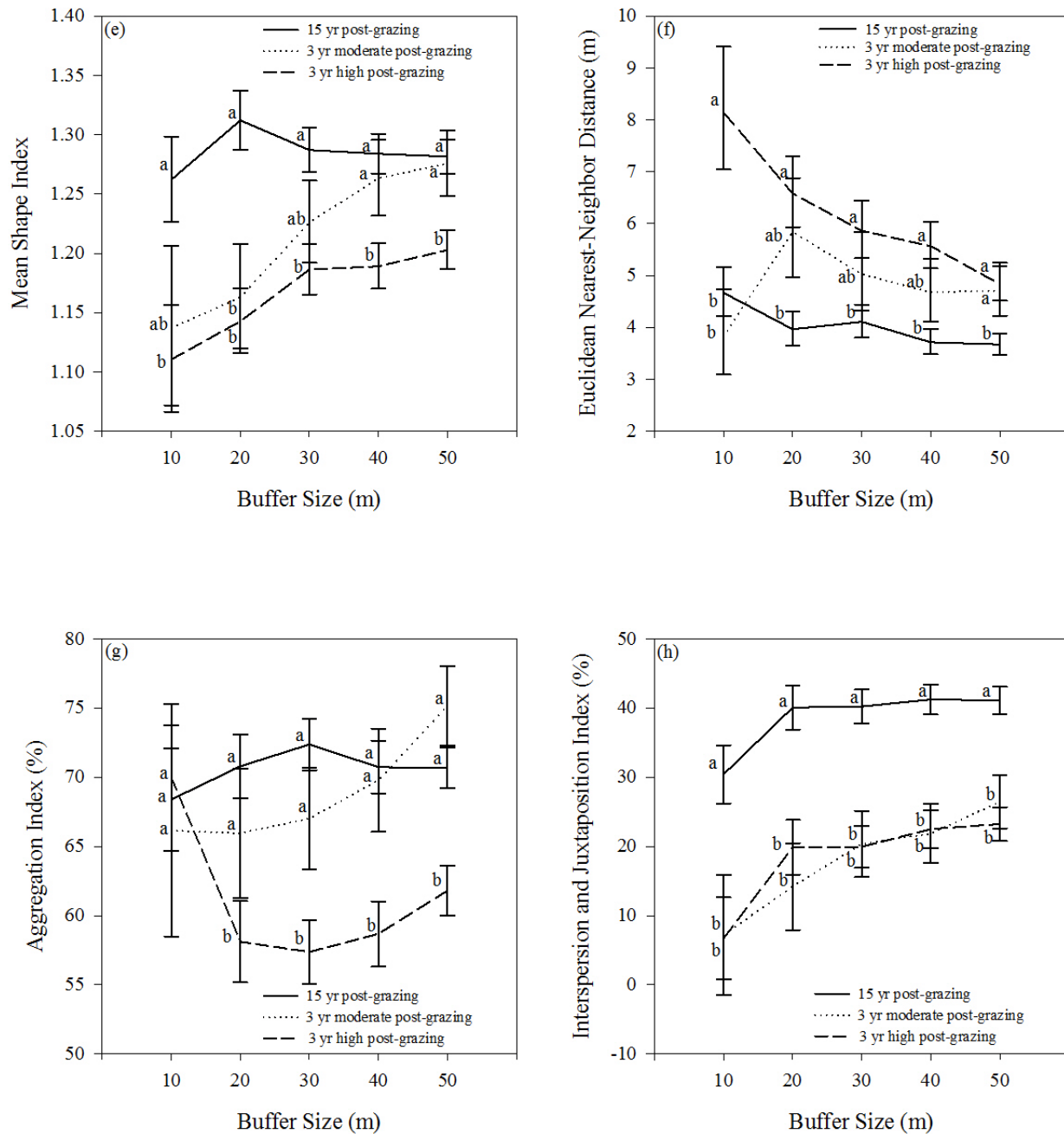


Figure 9 continued.

*Microhabitat.*—Across the entire study area, nest sites ( $n = 50$ ) had 3 vegetation characteristics that were significantly different from random points (Figure 10). Nest sites had a greater percentage of woody cover and less bare ground than did random locations. At the individual site level, nest locations on the 15-year postgrazing ( $n = 20$ ) and 3-year high postgrazing ( $n = 16$ ) sites generally showed no significant difference in vegetation characteristics compared to random locations (Figures 11, 12, 13). However, nest sites ( $n = 14$ ) on the 3-year moderate postgrazing site had significantly less bare ground than the paired random points (Figure 12).

## Density Estimation

For the 2015 distance sampling data, we used a half-normal detection function with metrics of patch density, landscape shape index, and edge density in the density surface model to predict density (Table 5). During 2016, bobwhite density estimates increased on all sites and the best model was a half normal function with cosine adjustment plus the metrics of percent of landscape, patch density, edge density, and landscape shape index (Table 5). Bobwhite density across all 3 study sites was greater in 2016 than 2015. Density in 2015 was similar between the 15-year postgrazing site and the 3-year

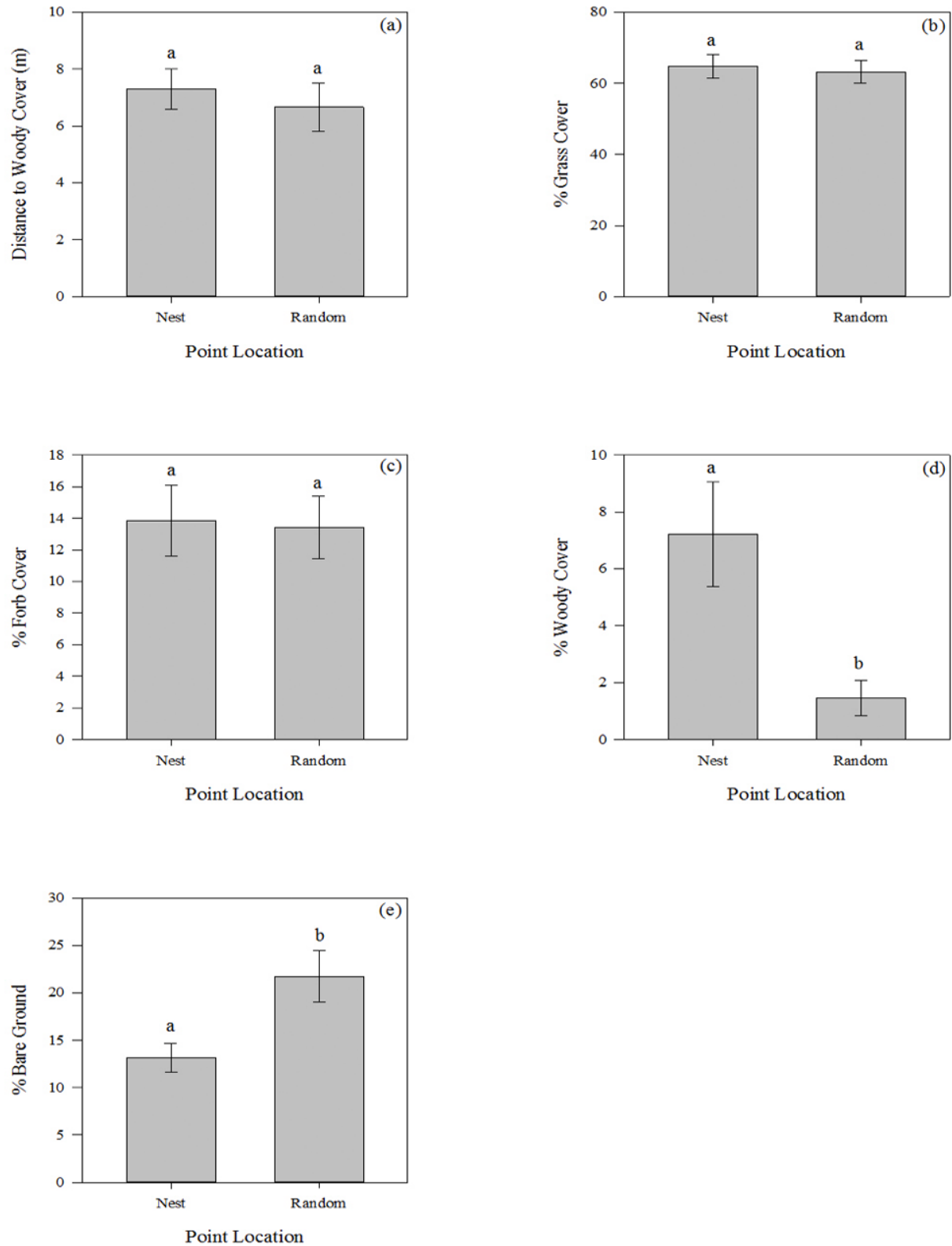


Fig. 10. Mean ( $\pm$ standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite (*Colinus virginianus*) nest sites (n = 50) and random locations (n = 50) pooled across the 3 postgrazing sites during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ( $P > 0.05$ ) different.

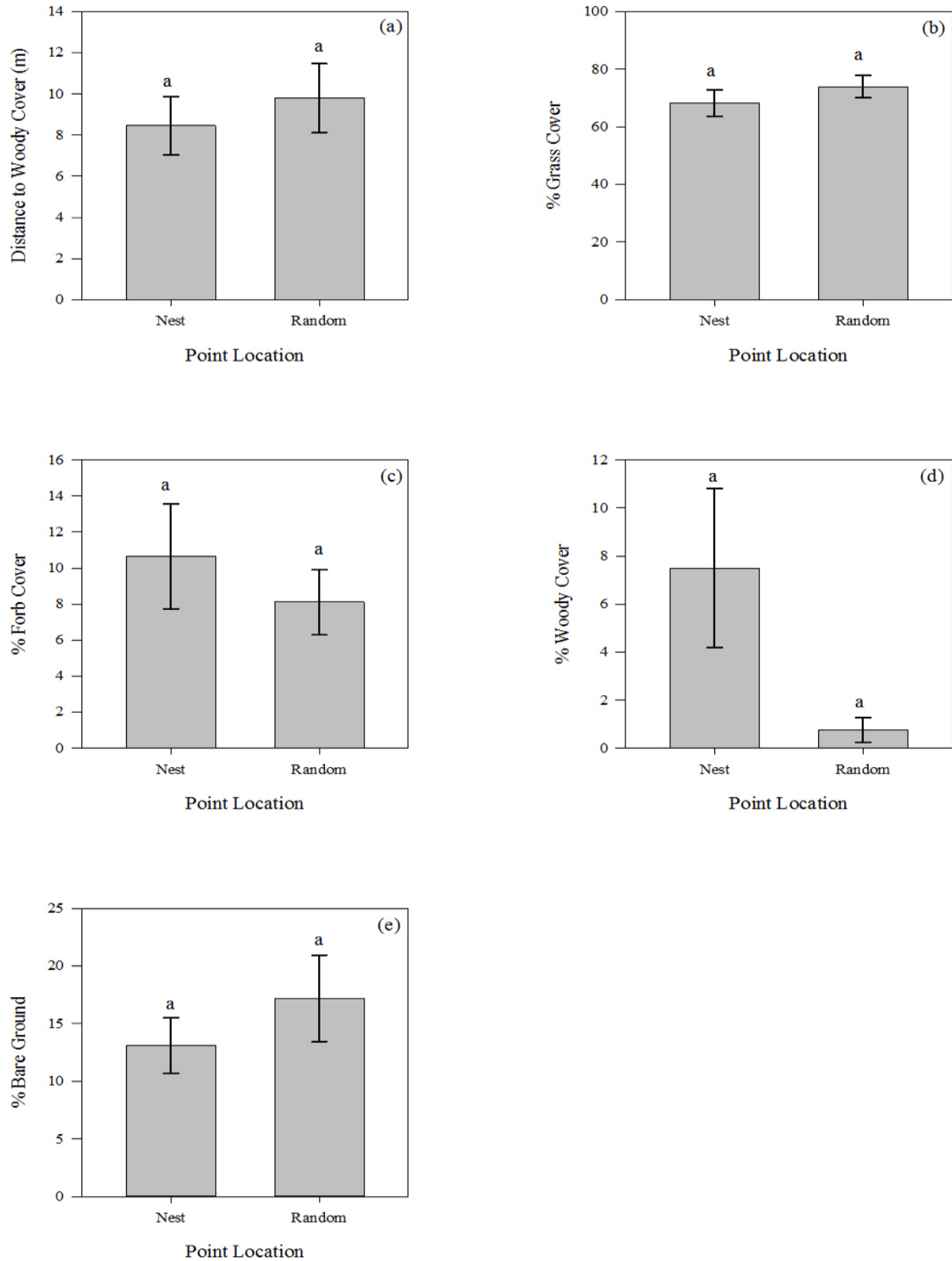


Fig. 11. Mean ( $\pm$ standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite (*Colinus virginianus*) nest sites (n = 20) and random locations (n = 20) on the 15-year postgrazing site during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ( $P > 0.05$ ) different.

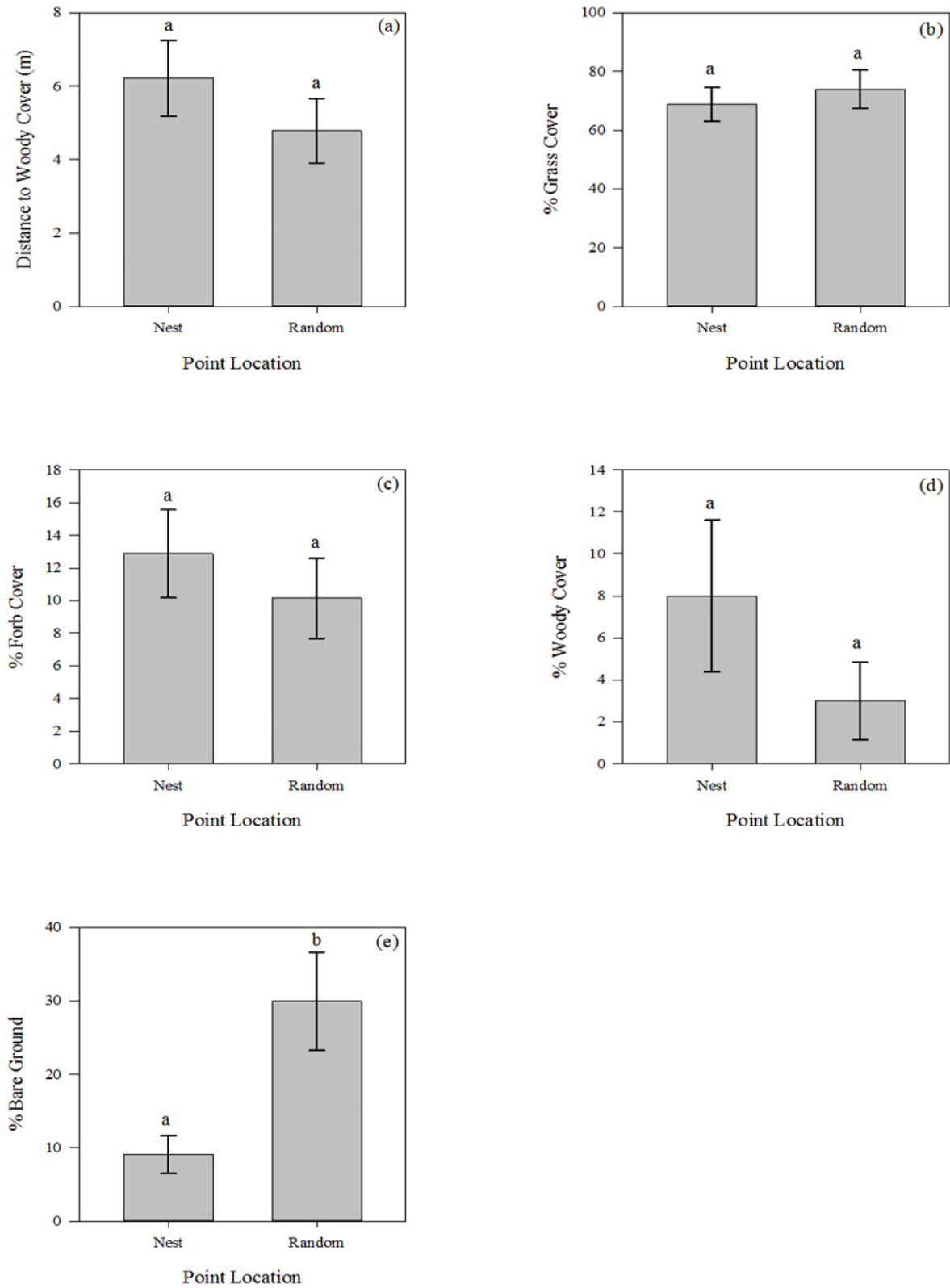


Fig. 12. Mean ( $\pm$ standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite nest sites ( $n = 14$ ) and random locations ( $n = 14$ ) on the 3-year moderate postgrazing site during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ( $P > 0.05$ ) different.



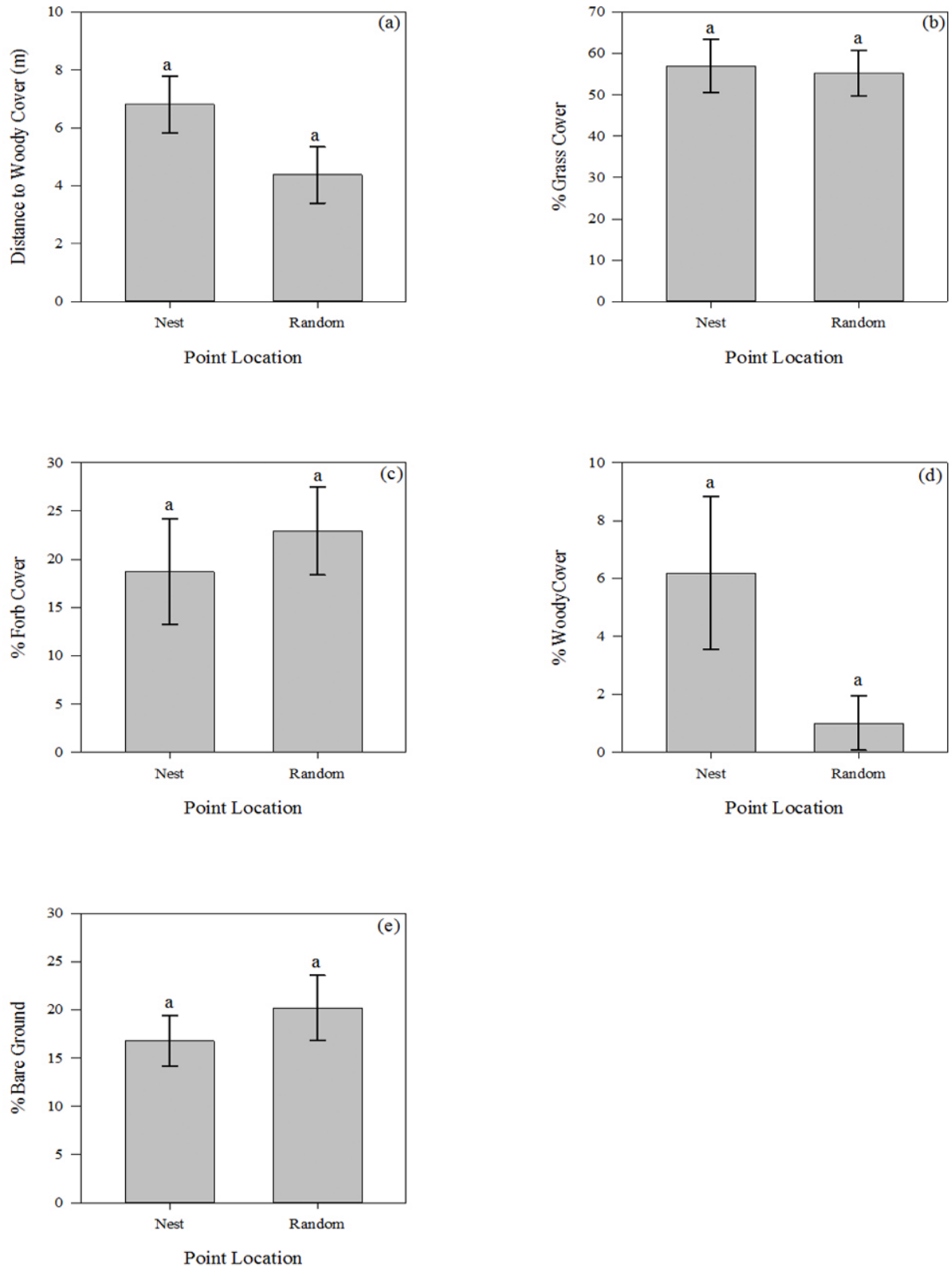


Fig. 13. Mean ( $\pm$ standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite (*Colinus virginianus*) nest sites ( $n = 16$ ) and random locations ( $n = 16$ ) on the 3-year high postgrazing site during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ( $P > 0.05$ ) different.

moderate postgrazing site at  $1.87 \pm 0.14$  birds/ha and  $1.82 \pm 0.14$  birds/ha, but these densities were higher than the 3-year high stocking density postgrazing site, which had a density of only  $0.92 \pm 0.06$  birds/ha (Table 6; Figure 14). During 2016,

density was highest on the 15-year postgrazing site at  $3.68 \pm 0.25$  birds/ha with the 3-year moderate postgrazing site at  $2.86 \pm 0.20$  birds/ha and the 3-year postgrazing site once again with the lowest density at  $2.01 \pm 0.14$  birds/ha (Table 7; Figure 15).

Table 5. Detection functions and covariates used to build density surface models for northern bobwhite (*Colinus virginianus*) in 2015 and 2016 from aerial surveys across the 3 postgrazing sites, Jim Hogg County, Texas, USA.

Survey	Detection function model	Covariates	Deviance explained
2015	Half-normal	s(x) + s(y) + s(ED) + s(LSI) + (PD)	15.1
2016	Half-normal + cosine	s(x) + s(y) + s(ED) + s(LSI) +s (PD) +s(PLAND)	9.3

Table 6. Number of transects (k), total transect length (L, km), number of covey detections (n), detection probability (p), effective strip width (ESW, m), density (D, birds/ha), coefficient of variation (CV), and 95% confidence intervals (CI[D]), from the 2015 survey on the 3 postgrazing sites, Jim Hogg County, Texas, USA.

Site	k	L	n	p	ESW	D		
						D	CV	95% CI(D)
15-yr postgrazing	12	39	74			1.87	7.45	1.62–2.16
3-yr postgrazing (moderate)	10	30	39			1.82	7.45	1.57–2.10
3-yr postgrazing (high)	11	26	22			0.92	7.45	0.79–1.06
Total	33	95	135	0.59	38.16	1.57	7.45	1.35–1.81

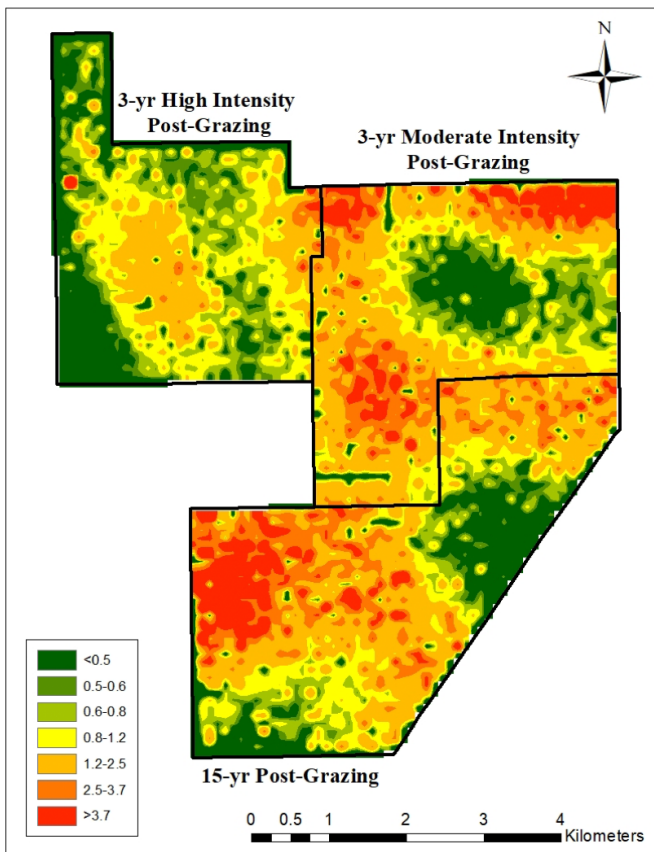


Fig. 14. Density surface model of northern bobwhite (*Colinus virginianus*) density (birds/ha) across the 3 postgrazing sites, Jim Hogg County, Texas, USA, 2015.

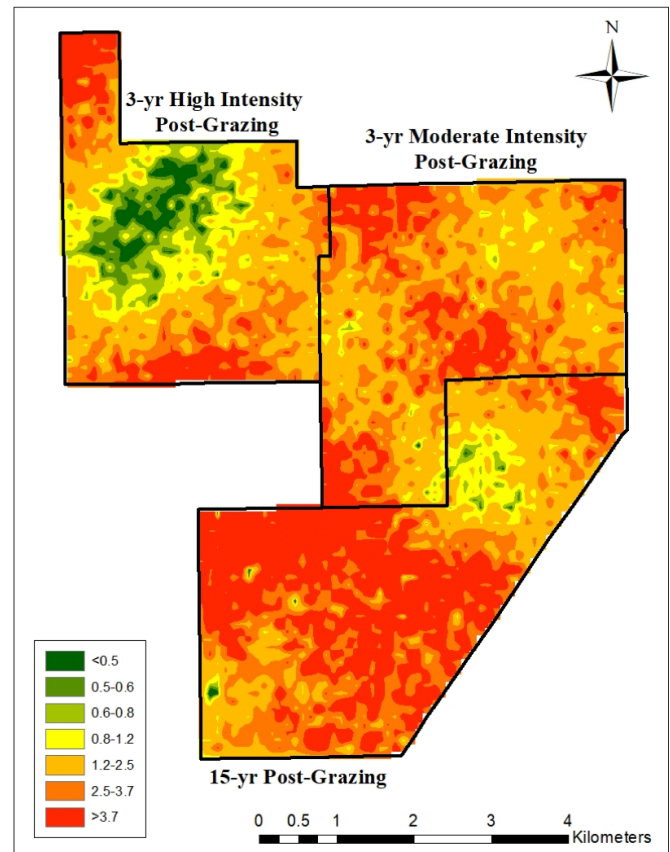


Fig. 15. Density surface model of northern bobwhite (*Colinus virginianus*) density (birds/ha) across the 3 postgrazing sites, Jim Hogg County, Texas, USA, 2016.

Table 7. Number of transects (k), total transect length (L, km), number of covey detections (n), detection probability (p), effective strip width (ESW, m), density (D, birds/ha), coefficient of variation (CV), and 95% confidence intervals (CI[D]), from the 2016 survey on the 3 postgrazing sites, Jim Hogg County, Texas, USA.

Site	k	L	n	p	ESW	D		
						D	CV	95% CI(D)
15-yr postgrazing	25	77	155			3.68	6.84	3.22–4.21
3-yr postgrazing (moderate)	21	63	90			2.86	6.84	2.50–3.27
3-yr postgrazing (high)	18	54	61			2.01	6.84	1.81–2.37
Total	64	194	306	0.42	20.829	2.91	6.84	2.54–3.32

## DISCUSSION

### Adult Breeding Season Survival

We predicted that there would be differences in bobwhite breeding season survival among our 3 sites. However, while breeding season survival was not different among sites or between years, it was strongly influenced by month within the breeding season. Survival was highest during the beginning of the season in April, and was lowest in June and July, with a slight increase in August. This pattern has been seen before in Kansas, where bobwhite of both sexes on cropland and rangeland areas experienced steadily decreasing survival from April through August (Taylor et al. 1999). A linear time trend in breeding season survival has also been documented in translocated bobwhite on the Rolling Plains of Texas (Downey et al. 2017). Our estimate of  $0.48 \pm 0.04$  for surviving the breeding season was higher than other estimates in Texas and the southeastern United States (Sisson et al. 2006, Grahmann 2013, Downey et al. 2017). Month-to-month variation in thermal dynamics based on variation in operative temperatures also likely contributed to this pattern.

### Nest Survival

Our nest survival estimates were influenced by both site and date of initiation within the season, with the probability of a nest surviving the 23-day incubation period peaking during the middle of the nesting season. While all our sites showed a temporal trend in nest survival, the 15-year postgrazing site survival was greater than the other 2 sites, with nearly double the probability of nest survival at the peak of the season, partially supporting our hypothesis. Bobwhite nest survival estimates in the literature vary widely (Klimstra and Roseberry 1975, Burger et al. 1995, Taylor et al. 1999, Lusk et al. 2006); our estimates were similar to estimates recently documented across South Texas (Lutz 2016). Avian nest success has been documented to improve on areas rested from grazing (Ammon and Stacey 1997). Lehmann (1984) suggested that bobwhite nest survival would increase later in the summer as there tends to be more mast and increasing alternate prey for predators. During a 4-year study in South Texas, Rader et al. (2007) also found that daily nest survival of bobwhite increased with

increasing temperature. Puckett et al. (1995) documented improved bobwhite nest survival from spring to summer.

### Home Range Size

Home range size was smallest on the 15-year postgrazing and 3-year moderate postgrazing sites. These results somewhat supported our hypothesis that home range size would be smallest on the 15-year postgrazing site as it had been released from grazing the longest and is exclusively managed for bobwhite. The similar home range size on the 3-year moderate postgrazing site may indicate a more recovered landscape than the 3-year high postgrazing site, which had a significantly larger home range size. Larger home range size for a particular species can be an indication of 1) less usable space per unit area, 2) or low densities of food resource, as birds may need to actively search for resources in a larger area to meet their requirements (Guthery 1997). Overall, our estimates of bobwhite home range size were similar to other studies in South Texas, which had estimates ranging from  $9.97 \pm 0.54$  ha to  $26.7 \pm 1.34$  ha (Haines et al. 2009, Buelow et al. 2011, Tri et al. 2014). Estimates of home range size for bobwhite varied from 3.5 ha to 282 ha across their range (Brennan et al. 2014). However, in South Texas bobwhite home range size estimates tend to be smaller than in other parts of their range. This pattern may be due to the large area of continuous bobwhite habitat in South Texas and habitat management exclusively for bobwhite in outer parts of their range, such as the southeastern coastal plain (Hernández et al. 2002, Terhune et al. 2007).

### Vegetation Composition and Structure

While there were few differences in vegetation composition and structure between nests and random locations at the microhabitat scale, landscape structure around nest sites showed differences that suggest the 15-year postgrazing site may contain vegetation features that are more suitable to higher nest survival, such as higher woody edge density, patch density, and interspersed. Landscape structure, in addition to weather factors, may be an important factor in determining annual bobwhite production success. While overall percentages of woody and herbaceous vegetation types among our study sites were similar, the structure and arrangement of these cover types on the landscape is crucial. The 15-year postgrazing site

had higher woody patch density and higher interspersed and juxtaposition at the management unit scale and around nest sites compared to the more recently grazed sites.

Parent et al. (2016) noted that even in drought years, bobwhite counts were positively linked to higher shrub patch density and higher brush cover interspersed using 30-m resolution data. This lends support to our findings of greater bobwhite density on the 15-year postgrazing site as well as greater nest survival and nest sites in areas which had greater woody patch density, edge density, and interspersed of woody cover. Though bobwhites persist in a variety of brush densities, there may be an upper boundary of brush cover that limits bobwhite usable space (Guthery 1997). By examining landscape structure around nesting sites, we found that bobwhites placed their nests in areas with a lower percentage of woody cover and with smaller woody patch areas than found at the management-unit scale. The 3-year high postgrazing site in particular has a larger amount of contiguous brush growth, which could impact the amount of suitable area for nesting.

## Density

Density estimates on the 3 study sites supported our hypothesis; we observed the highest bobwhite density on the 15-year postgrazing site. Bobwhite population density increased on each site between 2015 and 2016. While some of this increase was likely influenced by rainfall, the improvement may also suggest that these landscapes, especially the more recently grazed sites, are continuing to recover and thereby support more bobwhites. The greater bobwhite density on the more recovered sites in our study is consistent with other studies that examined avian response to eliminating cattle grazing. In Texas, Lusk et al. (2002) found bobwhite abundance dropped as cattle density increased. Other studies in riparian habitats saw similar trends in bird species richness and abundance when comparing recently or currently grazed sites to those rested from grazing (Taylor 1986, Dobkin et al. 1998, Krueper et al. 2003, Nelson et al. 2011, Earnst et al. 2012).

Bobwhite density has been consistently linked to rainfall (Peterson 2001), and weather patterns and their effects on the vegetation are highly correlated to quail abundance in the South Texas Plains (Bridges et al. 2001). South Texas had above-average rainfall in 2015 and 2016, which resulted in high bobwhite density on all 3 sites, especially in 2016. Differences in density among the sites may have been more significant in drier years as drought has been shown to amplify differences in bird abundance between postgrazing and currently grazed areas (Bock and Bock 1999).

## Overall Population Response

Throughout our study we found evidence from bobwhite habitat and population data that supported our research hypotheses. Determining differences between or among grazing treatments on landscapes can be extremely difficult, even with long-term monitoring, due to many confounding factors such as precipitation, pasture size, and lack of replication (Mashiri et al. 2008). Response of a landscape to

removal of livestock ideally needs to be monitored from the time of cattle removal and over the long term in order to account for weather patterns, especially in semiarid environments (Frank et al. 2014). When this study began, the landscape had already been rested for 3 years on the recent postgrazing sites. This, combined with the above-average rainfall during our monitoring, may have limited our ability to detect significant differences in certain metrics as the 3-year postgrazing sites may have already partially recovered. Without pretreatment and initial posttreatment data after cattle removal, we can only surmise that there may have been more stark differences in bobwhite population metrics among the 3 sites during the first few years of recovery. However, these results suggest that the 15-year postgrazing site still supports higher bobwhite density and nest survival compared to the 3-year postgrazing sites. We saw evidence that the 3-year moderate density postgrazing site may be more recovered than the 3-year high density postgrazing site; bobwhite density was still high and home range size was similar to the 15-year postgrazing site.

Historical overgrazing had led to brush encroachment on much of the South Texas landscape (Archer and Smeins 1991). However, many studies have shown that simply excluding cattle from the landscape does not necessarily halt the brush invasion that may have been set in motion by overgrazing (Chew 1982, Bock et al. 1984). While grazing removal generally improves native landscapes, it is necessary to have reasonable timeline expectations and also consider complementary management strategies to improve results (West et al. 1984).

The 15-year postgrazing site is managed for bobwhite hunting, and continuous brush management using herbicide is implemented throughout the year. This site is an example of how purposeful management in removing cattle after overgrazing along with specific brush management for bobwhite and bobwhite hunting has been successful in improving bobwhite populations. Brush management targeting the young mesquite encroachment, especially on the 3-year high postgrazing site, may be necessary for improving the landscape structure to support more abundant bobwhite populations. We hypothesized that over time bobwhite population metrics on the 3-year moderate and 3-year high postgrazing sites will continue to improve and then stabilize, at which point additional management may be necessary to increase numbers to the levels on the 15-year postgrazing site. Long-term monitoring of all 3 sites would be able to account for annual precipitation variation, and allow for intelligent management decisions. The additional use of satellite imagery and classification combined with density surface models to examine relationships between bobwhites and specific landscape metrics on the 3 sites could be used to target specific areas of the study area that may be improved by various land management techniques. While multiple interacting factors limit inferences to our study area, these results can inform managers about bobwhite preferences in postgrazing landscapes and potentially provide ideas for future restoration strategies and suggestions for purposeful



management, as well as general estimates of time to pasture recovery after cattle removal.

## MANAGEMENT IMPLICATIONS

Our results support the management philosophy that reduction or removal of cattle, especially after many years of continuous grazing, may be a useful step in improving habitat for bobwhite in rangeland environments. In South Texas, managers may be able to expect bobwhite population recovery on previously moderately stocked landscapes to about 2 or more bobwhite/ha within about 3–5 years as long as adequate rainfall occurs during that time frame. In any case, it is necessary that quail managers have realistic expectations for the time to recovery after cattle grazing has been removed to improve quail habitat. It is also critical that managers understand numerous different factors that may influence the rate of quail habitat and population improvement, including rainfall patterns, previous stocking densities, range condition, and landscape structure when making decisions about cattle removal and subsequent land management actions.

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