Northern Bobwhite Abundance in Relation to Precipitation and Landscape Structure

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ABSTRACT Northern bobwhite (Colinus virginianus) populations have declined across their range. The decline is associated with broad-scale losses of their habitats. Additionally, the presence of essential, structural features provided by vegetation in the remaining habitats is contingent on variable spatial and temporal trends in precipitation. This complicates the management of the bobwhite’s habitats. We modeled counts of bobwhite coveys as a function of landscape structure and precipitation covariates from arid landscapes in southern Texas. Our results indicated that numbers of coveys in landscapes with greater amounts of woody cover were predicted to be highly independent of precipitation. This has important management implications because certain landscape structures associated with woody cover buffer bobwhite populations from drought. To facilitate management based on our results, we mapped our model predictions for covey counts. This allows managers to spatially prioritize where management interventions need to occur, and evaluate the potential efficacy for these interventions to create positive bobwhite population responses.

KEY WORDS bobwhite, brush, drought, ecology, FRAGSTATS, landscape, landscape structure, management, northern bobwhite, precipitation, shrubland.

Managers of northern bobwhite (Colinus virginianus) are beneficiaries of decades of prior research (Stoddard 1931, Rosene 1969, Roseberry and Klimstra 1984, Guthery 2002, Hernández and Guthery 2012) and applied this knowledge to stabilize numerous bobwhite populations at local, small scales. Despite localized success, range-wide populations of bobwhites have experienced a long-term decline since at least the mid-1960s (Sauer et al. 2011). Broad-scale loss and deterioration of habitats are primary causes for the population declines of bobwhites in different ecosystems (Brady et al. 1998, Veech 2006, Lohr et al. 2011, Blank 2012, Hernández et al. 2012). These studies indicate the factors limiting populations operate at large spatial scales. Therefore, if conservation is to be effective throughout the bobwhite’s range, then applications of some management actions need to be applied at larger spatial scales. This entails understanding how effects of weather and the landscape structure of cover types, together, operate at large scales.

The effect of weather on bobwhites in arid ecoregions is well understood. For example, a variety of different precipitation data have been used to draw correlative or linear relationships with different bobwhite population indices and estimates, collected at small and large scales (Rice et al. 1993, Bridges et al. 2001, Guthery et al. 2002, Lusk et al. 2002, Tri et al. 2013). These studies demonstrated significant, positive links between the quantity of precipitation and the direction of bobwhite population metrics. These relationships are strongly tied to the timing and amount of precipitation (Peterson 2001), which varies regionally across space, and can vary remarkably from year to year. Moreover, severe droughts followed immediately by tropical storms that deliver above-average precipitation to arid parts of Texas along the Gulf Coast strongly influence bobwhite survival and reproduction (proportion nesting, nesting rate, and nesting season length; Hernández et al. 2002, 2005), and are increasingly expected to be the norm as climate in this region changes (Norwine et al. 2007). Presumably, periods with minimal precipitation can reduce the amount of resources needed to carry out nesting, foraging, and brood-rearing activities, which can potentially create an ecological bottleneck.

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Parent et al. • Mapping Northern Bobwhite
(Wiens 1977), a condition under which severe weather limits resources, and by extension, species abundances (Williams and Middleton 2008).

Understanding composition and configuration (Li and Reynolds 1994) of land cover types on the landscape provides a means to formally quantify the surface of a landscape and permits comparisons in space and time. For example, landscapes with diverse composition of seral stages required by bobwhite have the capacity to influence estimates of abundance (Schairer et al. 1999, Veech 2006, Howell et al. 2009, Blank 2012). The configuration of cover types with these studies influences bobwhite populations less, but each study notes variation depends on the spatial scale at which these land cover configurations are quantified (i.e., scale-dependence; Howell et al. 2009, Duren et al. 2011).

Understanding how landscape structure influences bobwhites on landscapes in arid ecoregions would provide information about how bobwhite population abundances are spatially structured and how to prioritize and strategically place management interventions to habitats in areas with the greatest efficacy to benefit bobwhites. Additionally, if we know drought is a limiting factor to bobwhite populations through the creation of ecological bottlenecks, there are management implications associated with identifying landscape structures that can buffer bobwhite populations from drought. This requires a more thorough investigation into the composition and configuration of land covers that yield positive relationships with bobwhite population abundance, and how such relationships change with the quantity of precipitation. Our objectives were 3-fold: describe the timing of precipitation related to northern bobwhite abundance during a prolonged drought, determine how landscape structure influences northern bobwhite populations on arid landscapes, and understand how northern bobwhite populations respond to landscape structure with variable trends in precipitation. Finally, we wished to demonstrate the utility in mapping spatially explicit relationships. The ability to prioritize where to apply habitat management on the landscape given recent trends in precipitation would be an extremely valuable tool to bobwhite managers in arid ecoregions. Thus, an additional objective was to map predictions from our models for managers to prioritize and initiate management of northern bobwhite habitat.

STUDY AREA

The study area consisted of 333,866 ha and was comprised by the King Ranch (King Ranch, Kingsville, TX; Fig. 1). The ranch spanned 6 counties in Texas: Brooks, Jim Wells, Kenedy, Kleberg, Nueces, and Willacy. The ranch was approximately bound between the south and north latitudes from 26.6° to 27.7° and approximately between the east and west longitudes from −97.5° to −98.1°, respectively. Average elevation was 16 m (SD = 12 m) with gentle slopes that increased from <1 m along the Gulf Coast to occasional peaks of 52 m on western parts of the ranch. The ranch comprised 4 divisions (Encino, Laureles, Norias, Santa Gertrudis). All divisions were located in the Rio Grande Plains ecoregion (Gould 1975); however, the eastern edges of the Laureles and Norias divisions were located in the Gulf Prairies and Marshes ecoregion (Gould 1975). Divisions were further subdivided into 122 management units (i.e., fenced pastures), many of which were managed for white-tailed deer (Odocoileus virginianus) and bobwhites. Management units on the King Ranch were sufficiently large to contain multiple populations of bobwhite; the average size of each unit was 2,023 ha, which could support 135 coveys/unit assuming the average covey home range on our study area was 15 ha (Haines et al. 2004) and usable space was saturated in space-time (Guthery 1997). Thus, we defined each management unit as a landscape because they were ecologically capable of supporting multiple populations of bobwhites. Climate was semiarid and subtropical with prolonged periods of drought. Average annual precipitation (1971–2000) was 44.7 cm, and average annual temperature was 21.7°C (http://www.ncdc.noaa.gov/IPS/coop; Kingsville and Falfurrias weather stations). Average annual precipitation during the duration of our study was 54.96 cm (SD = 22.26), but much of this precipitation occurred during a wet period in 2010. Aside from 2010, our study area experienced prolonged, severe drought conditions based on the Palmer Drought Severity Index, particularly in 2009, 2011, and 2012 (see Fig. S1, available online at www.wildlifejournals.org). Major land uses on the ranch were cattle grazing, petroleum extraction, and fee-lease hunting (Fullbright and Bryant 2002). Major vegetation communities occurring on the study area included bluestem prairie (Schizachyrium scoparium), mesquite-granjenno thornbrush (Prosopis glandulosa–Celtis pallida), mesquite-bluestem savannah, oak-bluestem (Quercus virginiana, Quercus stellata) woodland, mesquite savanna, and cordgrass-bluestem (Spartina foliosa; McLendon 1991, Fullbright and Bryant 2002).

METHODS

Covey Counts

We performed bobwhite relative abundance surveys in conjunction with a general wildlife survey that also counted white-tailed deer, wild turkeys (Meleagris gallopavo), feral pigs (Sus scrofa), and other wildlife on the ranch. We performed these surveys by helicopter using a survey design based on a protocol to estimate bobwhite density at our study area via distance sampling used by Rusk et al. (2007) and Schnupp et al. (2012). Importantly though, compared to the general wildlife surveys, the altitude and speed of the helicopter during distance sampling was usually slower and lower to ensure detection of covey flushes, and so variation in covey flushes may exist between general wildlife surveys. We recorded the number of bobwhite coveys flushed (i.e., individual flocks) and survey effort (transect length; km).

Data from the general wildlife surveys were suitable for indexing bobwhite population abundance as long as the
relationship between the numbers of coveys flushed per survey effort changed proportionally with population abundance. A critical assumption then is that detection is constant over space and time. Violations of this assumption would suggest differential detection probabilities along a transect depending on vegetation. We do not believe variation in vegetation across space was a significant source of bias in our general wildlife surveys because our sampling took place during early morning hours after bobwhites leave their roosts to forage in open, herbaceous vegetation (Stoddard 1931); in essence there is no spatial heterogeneity in the cover they were using during the periods we performed our surveys. However, it is possible that variation in land uses through time influenced detection of bobwhite covey flushes. Because changes to herbaceous vegetation due to grazing, burning, or any other means that could change the composition and configuration of such covers accumulate over time, detection between these periods may not have been constant. We speculate that because the timing and amount of precipitation is an unpredictable process in arid regions such as ours (Norwine et al. 2007), management activities that could alter the structure of the vegetation (grazing, burning) would be tied to precipitation. Our study area received extensive drought during these survey periods and accordingly, very little grazing and burning activities occurred. The structure of the vegetation did not change appreciably through time to influence detection. Moreover, previous unpublished research has indicated that bobwhite population indices from general wildlife surveys change proportionally with distance-based helicopter surveys (M. J. Schnupp, King Ranch, unpublished data); thus, the general survey is robust to potential violations in the constant detection assumption.

Environmental Data
We acquired spatial dataset that interpolated monthly precipitation at a 4-km resolution from the PRISM Climate Group for each month and year of our study (http://prism.oregonstate.edu, Accessed 18 Jan 2014). We lagged covariates for precipitation between October and December by 1 year (precipitation during Oct 2009 was associated with covey counts in Sep 2010) because covey counts were collected in September of time $t$ and using covariates that have not occurred yet (i.e., time $t+1$) to predict covey

Figure 1. The study area is located in southern Texas, USA on 333,866 ha of the King Ranch in Kingsville, Texas. The ranch comprises 4 divisions and within each division are 122 landscapes.
counts in time $t$ would be misleading. We selected the precipitation covariates that would be used in our candidate models according to corrected Akaike’s Information Criterion (AIC) values from a set of univariate models for each month.

We used the Texas Ecological Systems Classification (TESC) dataset (Elliott et al. 2009), which is a land cover classification map based on ecological system classifications described by Comer et al. (2003). The TESC was derived using remotely sensed Landsat Thematic Mapper satellite data acquired in 2010 and abiotic variables (i.e., soil, hydrology, elevation, ecoregion) to classify cover types at a 10-m resolution. Although the TESC dataset describe land cover on our study area in 2010 only, it is unlikely that the overall structure of vegetation (i.e., grass, shrub, brush) varied considerably across a 5-year period (D. D. Diamond, Missouri Resource Assessment Partnership, University of Missouri, personal communication).

We reclassified the >50 land cover types in the TESC into 4 general types corresponding to the functional cover needs of bobwhite during various parts of their life history, and covers they do not use (Hernández and Guthery 2012). Specifically, these included 1) non-useable covers we do not expect quail to occupy, 2) grasslands that provide quail nesting cover via bunch grasses, 3) grasslands that provide brood-rearing cover that offers concealment from above via thick-canopied grasses, and 4) shrubland or brush covers that offer escape, resting, and thermal covers under different conditions (Table 1).

We further reclassified grassland cover based on soil type. Vegetation and soils are intricately related on arid rangelands because soil type can influence the distribution and physiognomy of vegetation (Box 1961). We obtained soil data from the Soil Survey Geographic Database (SSURGO) available from the United States Department of Agriculture (USDA) Natural Resource Conservation Service (NRCS; http://soildatamart.nrcs.usda.gov, Accessed 27 Jan 2013). We aggregated soil map units based on how they influence vegetation (Table 1). We classified soil based on attributes in the database that describe surface texture of soil: fine sand, fine sandy loam, loamy fine sand, and non-sandy. This created a polygon boundary of each soil class. We isolated grassland cover from the reclassified TESC dataset and overlaid it on the soil data to create 4 distinct classes of grassland based on soil type (Table 1). We merged these and the remaining cover types back into a single raster.

Table 1. We reclassified the Texas Ecological Systems Classification land cover dataset to a more general classification scheme based on the functional cover needs of bobwhite during various parts of their life history. Descriptions of cover are based on Elliott et al. (2009).

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>Life-history need</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-useable habitat (NU)</td>
<td>Covers such as marsh, open water, urban, or sand dunes that are not used by bobwhites</td>
<td>None</td>
</tr>
<tr>
<td>Grasslands</td>
<td>Covers dominated by herbaceous vegetation (both, pasture, and prairie) with &lt;25% woody cover</td>
<td></td>
</tr>
<tr>
<td>Loamy fine sand (LFSG)</td>
<td>Grasslands occurring on loamy fine sand soils</td>
<td>Nesting</td>
</tr>
<tr>
<td>Fine sandy loam (FSLG)</td>
<td>Grasslands occurring on fine sandy loam soils</td>
<td>Brood rearing, forage</td>
</tr>
<tr>
<td>Fine sand (FSG)</td>
<td>Grasslands occurring on fine sand soils</td>
<td>Nesting</td>
</tr>
<tr>
<td>Non-sandy (NSG)</td>
<td>Grasslands occurring on non-sandy soils such as loamy or clayey soils</td>
<td>Brood rearing, forage</td>
</tr>
<tr>
<td>Shrubland (SHRUB)</td>
<td>Cover consisting of shrubs (&lt;4 m tall) that account for &gt;25% of woody cover</td>
<td>Escape, resting, thermal</td>
</tr>
<tr>
<td>Brushland/woodland (BRUSH)</td>
<td>Cover consisting of trees (&gt;4 m tall) that account for &gt;75% of woody cover</td>
<td>Escape, resting, thermal</td>
</tr>
</tbody>
</table>

a Hansmire et al. (1988).
b Larson et al. (2010).
c Hernández and Guthery (2012).
Modeling

We used a 2-step approach to reduce the number of landscape structure covariates that would be considered in the development of our candidate models. First, we reviewed Li and Wu (2004) in efforts to identify metrics with intuitive interpretations. Additionally, we arbitrarily excluded covariates based on how well they could be translated to management applications. Based on these criteria, we identified 22 categories of metrics in FRAGSTATS, which expanded to 139 landscape structure covariates because when cover-level metrics are applied to each land cover type, the number of covariates multiplies according to how many cover types are used in data collection (see Table S1, available online at www.wildlifejournals.org). Second, we further reduced the 139 covariates by excluding collinear covariates ($r > 0.6$; retaining the covariate with the most intuitive application to management) and modeling each covariate in a univariate manner to identify important relationships. Specifically, we used AIC, to select the 2 best composition and configuration covariates associated with each of the land cover types required by bobwhite life-history needs (defined above; Table 1). Additionally, we selected the single best composition and configuration metric to define non-usable covers and overall landscape heterogeneity. We intentionally selected a single pair of composition–configuration covariates for non-usable covers and landscape heterogeneity. Non-usable cover comprised a small amount of the overall study area, and we wanted to avoid undue importance of non-usable covariates in the model because they are not variables that managers can augment (but are certainly of management interest). Few landscape heterogeneity covariates within <2 AIC, remained after our covariate reduction criteria. We developed a candidate set of models to evaluate how landscape structure of bobwhite land cover types and precipitation, individually and jointly (i.e., 2 main effects), affect covey counts (Appendix A). We explored precipitation–landscape structure interactions for covariates in our best-fitting models to evaluate if interactions improved model fit in a post hoc manner.

We modeled relationships between bobwhite counts and covariates using mixed effects negative binomial regression with landscapes being a random effect (Bolker et al. 2009, Irwin et al. 2013). Because sampling effort ($x = \text{km of transect sample}$) varied among landscapes, we used the natural logarithm of effort as an offset term in all models (Maunier and Punt 2004). There are multiple ways to parameterize the negative binomial distribution for regression analyses, and we used the common parameterization whereby the variance increases quadratically with the mean (i.e., NB2 parameterization of Hilbe 2011):

$$\text{Var}(Y) = \mu + \kappa \mu^2.$$  

where $Y$ is the observed value for total coveys counted, $\mu$ is the mean, and $\kappa$ is the scale parameter ($1/\kappa = \text{over-dispersion}$). Moreover, we used a log link to model the expected value of coveys counted as a function of hypothesized covariates:

$$\ln(\mu_y) = \ln(\text{Effort}_y) + \beta_0 + a_i + \sum_{q=1}^{Q} \beta_q X_{iq},$$

where $\text{Effort}_y$ is the km of transect sampled at landscape $i$ in year $j$, $\beta_0$ is the intercept, $a_i$ is the random intercept for landscape $i$, and $\beta_q$ is the effect of covariate $X_q$ on coveys for landscape $i$ in year $j$, where $Q$ is the total number of covariates. The random intercept for each site is assumed to be independent and identically distributed as $N(0, \sigma^2)$.

Covariate $X_{iq}$ were centered and standardized by subtracting the mean and dividing by their standard deviation.

We fit all models using the glmmADMB package in R (Version 3.0.2; R Foundation for Statistical Computing, Vienna, Austria). This package uses the computational power of the random effects module in AD Model Builder (hereafter ADMB, http://admb-project.org, accessed 18 Nov 2013; Fournier et al. 2012) to integrate out the random effects from the full likelihood and maximize the marginal likelihood function of the data (Bolker et al. 2013). We compared the set of candidate models using AIC, and AIC weights ($w_i$) that we calculated using the bblme package in R. We evaluated model fit of the top model by calculating root mean-squared error (hereafter RMSE), which effectively provides an estimate of average error between the fitted and observed values for each model on the scale of the observed data (i.e., measured in number of coveys). Because we did not expect the residuals to be normally distributed, we used Anscombe residuals to construct standard regression diagnostic plots for our models (e.g., residual-by-fitted value plots; Hilbe could predict our data by performing leave-one-out cross validation (LOOCV). Essentially, our top model was applied iteratively to each $n-1$ experimental units and the RMSE between predicted and observed covey counts was estimated. We compared error derived from our top model (RMSE$_{\text{model}}$) and derived from LOOCV (RMSE$_{\text{CV}}$) to determine if our model suitably predicted our data.

Mapping Model Predictions

We mapped predictions of covey counts from our top model to provide managers a means to prioritize and strategically place management interventions. Because precipitation varies, we mapped predictions under 3 precipitation scenarios: drought, average, and wet.

Historical minimums and maximums in precipitation occurred in 2009 ($\bar{x} = 31.22$ cm, SD = 2.80) and 2010 ($\bar{x} = 115.87$ cm, SD = 6.24); these years represented drought and wet precipitation scenarios, respectively, and should provide good contrast to visualize how covey predictions change across space with different amounts of precipitation. We derived the average precipitation scenario using the average values based on PRISM data collected between 2008 and 2012 (54.96 cm, SD = 22.26). This exceeds the 1971–2000 average for precipitation (44.7 cm) by 10 cm (http://www.ncdc.noaa.gov/ips/coop; Kingsville and Falfurrias weather stations). The PRISM dataset are collected at different spatial scales, during different periods of time, and in the presence of different trends in climate. Because the
difference is small, we suggest our 2008–2012 precipitation averages provide reasonable surrogates for average precipitation at our study area. We used the original rasters for landscape structure covariates created during moving window analyses in FRAGSTATS. We extracted the spatial random effects from our model and included the effort offset in predictions for each landscape (each value was held at its 5-year average). We extracted coefficient estimates for the fixed effects from our model and applied these to the covariate rasters to produce predictions of relative covey counts for each landscape using the raster calculator within ArcMAP (ArcGIS 10.1, ESRI, Redlands, CA).

RESULTS

We performed surveys of bobwhite coveys in September during 2008–2012 with 27,184 km of helicopter surveys. Average survey effort was 50 km/landscape \( (n = 122 \text{ units}; \text{ range } = 3–242 \text{ km}, \text{ SD } = 34 \text{ km/landscape}). \) Counts averaged across divisions and years were greatest on the Norias \( (n = 38 \text{ landscapes}; \bar{x} = 11.63 \text{ coveys/km}; \text{ SD } = 12.34), \) followed by Santa Gertrudis \( (n = 41; \bar{x} = 11.40; \text{ SD } = 10.53), \) Laureles \( (n = 23; \bar{x} = 9.00; \text{ SD } = 9.12),\) and Encino \( (n = 20; \bar{x} = 8.57; \text{ SD } = 7.50)\) divisions.

We identified 3 months that had consistently significant bobwhite–precipitation relationships: October (previous year), April (current year), and June (current year). Our 2-step covariate reduction approach yielded 16 landscape structure covariates (Table 2). Composition covariates included total area of all patches of a cover type or total area of all patches in ha, proportion of a cover type with respect to the overall landscape, and total length of edge in m. Configuration covariates were represented by indices of contagion and interspersion that included degree of patch clumping \( (\text{ range } = -1 \text{ to } 1);\) interspersion and juxtaposition \( (\text{ range } = 0 \text{ to } 100\%);\) a landscape shape index \( (\text{ range } = 1 \text{ to } \infty);\) estimates of area and edge, which included mean patch size and edge density measured in ha and m/ha, respectively; and indices of fragmentation, which included number of patches and patch density, denoted by \( n \) patches, and \( n \) patches/ha, respectively.

Modeling

Our best-fitting model consisted of the 3 precipitation covariates; 4 landscape structure covariates including area of shrubland, area of brush, patch density of shrubland, and interspersion and juxtaposition of brush; and 2 landscape heterogeneity covariates: total area and number of patches. Only 1 other model in our candidate set was of similar parsimony but accounted for a negligible proportion of Akaike weight (Appendix A). We explored precipitation–landscape structure interactions, but these did not improve model fit according to AICc. Cross-validated prediction error

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### Table 2. Covariates reflecting land cover composition and configuration of management units (landscapes) that we identified as covariates affecting bobwhite abundance in southern Texas, 2008–2012, using univariate-negative binomial regressions from a larger suite of candidate covariates. We selected the top pair of covariates for each vegetation cover according to corrected Akaike’s Information Criterion (AICc). We defined essential bobwhite covers by combining composition and configuration covariates.

<table>
<thead>
<tr>
<th>Heterogeneity</th>
<th>Cover</th>
<th>Composition</th>
<th>Configuration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>Non-usable cover (NUC)</td>
<td>TE</td>
<td>LSI</td>
</tr>
<tr>
<td></td>
<td>Nesting cover (NC)</td>
<td>PLAND_LFSG</td>
<td>ED_LFSG</td>
</tr>
<tr>
<td></td>
<td>Brood/forage cover (BFC)</td>
<td>TE_FSG</td>
<td>MPS_FSG</td>
</tr>
<tr>
<td></td>
<td>Escape/resting/thermal cover (ERTC)</td>
<td>PLAND_FSLG</td>
<td>CLUMPY_FSLG</td>
</tr>
<tr>
<td>Landscape</td>
<td>Landscape heterogeneity (LH)</td>
<td>LSI_NSG</td>
<td>ED_LFSG</td>
</tr>
</tbody>
</table>

\( ^a \) TE, total edge (m); PLAND_LFSG, percent loamy fine sand grasslands (%); TE_FSG, total edge of fine sand grassland (m); PLAND_FSLG, percent fine sandy loam grasslands (%); PLAND_NSG, percent non-sandy grasslands (%); CA_SHRUB, area of shrubland (ha); CA_BRUSH, area of brush (ha); TA, total area (ha).

\( ^b \) LSI, landscape shape index; ED_LFSG, edge density of loamy fine sand grasslands (m/ha); MPS_FSG, mean patch size of fine sand grassland (ha); CLUMPY_FSLG, clumpiness of fine sandy loam grasslands as a measure of fragmentation; LSI_NSG, landscape shape index for non-sandy grasslands; PD_SHRUB, patch density of shrubland (no. patches/100 ha); IJI_BRUSH, interspersion and juxtaposition of brush (%); NP, number of patches.

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### Table 3. Parameter estimates for a negative binomial regression between northern bobwhite covey counts \( (n = 573) \) and covariates for precipitation, landscape structure, and spatial heterogeneity. The model is based on data collected from 2008 to 2012 on the King Ranch southern Texas. Covariates were centered and standardized by subtracting their mean and dividing by their standard deviation so they can be interpreted on the same scale. Because the log of expected counts are modeled in negative binomial models, we exponentiated our coefficient estimates and converted them to percent changes.

<table>
<thead>
<tr>
<th>Covariate (^a)</th>
<th>Coefficient (%)</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-81.75</td>
<td>-9.63</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Apr</td>
<td>0.88</td>
<td>6.700</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Jun</td>
<td>-0.34</td>
<td>-2.710</td>
<td>0.007</td>
</tr>
<tr>
<td>Oct</td>
<td>-1.26</td>
<td>-6.280</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>CA_SHRUB</td>
<td>0.01</td>
<td>1.260</td>
<td>0.207</td>
</tr>
<tr>
<td>CA_BRUSH</td>
<td>0.02</td>
<td>2.810</td>
<td>0.005</td>
</tr>
<tr>
<td>PD_SHRUB</td>
<td>5.31</td>
<td>2.820</td>
<td>0.005</td>
</tr>
<tr>
<td>IJI_BRUSH</td>
<td>0.20</td>
<td>0.770</td>
<td>0.441</td>
</tr>
<tr>
<td>TA</td>
<td>-0.01</td>
<td>-1.840</td>
<td>0.065</td>
</tr>
<tr>
<td>NP</td>
<td>-0.01</td>
<td>-0.090</td>
<td>0.925</td>
</tr>
</tbody>
</table>

\( ^a \) Apr, April precipitation (mm); Jun, June precipitation (mm); Oct, October precipitation in previous year (mm); CA_SHRUB, area of shrubland (ha); CA_BRUSH, area of brush (ha); PD_SHRUB, patch density of shrubland (no. patches/ha); IJI_BRUSH, interspersion and juxtaposition of brush (%); TA, total area (ha); NP, number of patches.
was similar between the top model and LOOCV analyses ($\text{RMSE}_{\text{model}} = 7.765$, $\text{RMSE}_{\text{CV}} = 7.921$). The model fit well but over-predicted small, outlying counts. Finally, covey counts indeed were overdispersed ($1/\kappa = 4.63$, $SE = 0.48$) providing support for use of the negative binomial framework.

Our best-fitting model indicated April precipitation, area of brush, and patch density of shrubland positively influenced covey counts, whereas landscape heterogeneity (total area) and notably, precipitation in June and October negatively influenced counts (Table 3). Several covariates in our supported model did not have significant relationships with covey counts (area of shrubland, interspersion and juxtaposition of brush, and number of patches). To facilitate interpretation of this model, we created effects plots for all possible combinations of precipitation–landscape structure covariates in which significant relationships existed with covey counts. These plots strictly reflect contribution of 2 main effects when all other values are held at their mean, and not an interaction. We present the 3 plots that yielded the largest effect sizes in covey counts for 1-unit changes in covariates when standardized for the range of values that each covariate can take on. This included April precipitation, area of brush, and patch density of shrubland (Fig. 2). More specifically, precipitation and landscape structure covariates for brush and shrubland had the greatest positive effect on covey counts at their maximum recorded values.

Under the best possible simulation conditions for bobwhites (i.e., wet, high-precipitation scenarios), predicted relative covey counts averaged 13.50 coveys (Fig. 3). During drought scenarios, 17 landscapes (management units) on the ranch were predicted to maintain moderate to high covey counts $>13.50$ coveys (Fig. 3). The elevated covey counts in these 17 units resulted from greater areas of brush and higher densities of shrubland patches, despite receiving less precipitation in 2008–2012 (Table 4). Our model also predicted low-to-moderate covey counts at 71 of 122 landscapes in wet years apparently because they contained markedly fewer shrubland patches and smaller quantities of brush (Table 4).

**DISCUSSION**

Precipitation regulates the height, structure, and by extension, the function of vegetation with respect to bobwhites (Rice et al. 1993, Bridges et al. 2001, Hernández et al. 2002). If the timing of precipitation is not synchronized with important bobwhite life-history events (nesting, brood rearing), then vegetation may not be functionally usable (Lusk et al. 2001). Accordingly, understanding the quantity and timing of precipitation during
periods of drought has important management implications. Our study took place during a particularly dry period (4 of 5 years were classified as drought; see Fig. S1, available online at www.wildlifejournals.org) on arid landscapes in southern Texas and allowed us to evaluate this effect.

Past research has demonstrated positive relationships between precipitation and various aspects of bobwhite population demographics (Bridges et al. 2001, Hernández et al. 2005, Lusk et al. 2009). Our results are inconsistent with previous studies, however, because we detected both positive and negative relationships with precipitation. For example, covey counts were most sensitive to precipitation in April at our study. This is not surprising because even during wet years in Texas, spring precipitation initiates bobwhite nesting (Lehmann 1946) and has been associated with improved nesting success through herbaceous vegetation.

Table 4. We modeled relative bobwhite covey counts on the King Ranch in southern Texas from 2008 to 2012 under simulated wet, average, and dry (drought) conditions. Under the best possible simulation conditions for bobwhites (i.e., wet, high-precipitation scenarios), relative covey counts averaged 13.50 coveys/management unit. Yet, even during simulated drought conditions, predicted covey counts were >13.50 (moderate–high) at 17 management units, and moderate–high at 51 management units under average precipitation scenarios. Average (SD) April precipitation (mm), patch density of shrubland (PD_SHRUB; no. patches/100 ha), and area of brush (AREA_BRUSH; ha) at these sites under each precipitation scenarios were numerically greater than sites where predicted covey counts were low–moderate (<13.50 coveys/management unit).

<table>
<thead>
<tr>
<th>Precipitation scenario</th>
<th>n</th>
<th>Predicted coveys</th>
<th>Obs. coveys</th>
<th>Apr. precip</th>
<th>PD_SHRUB</th>
<th>AREA_BRUSH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Below average precipitation</td>
<td>17</td>
<td>Moderate–high</td>
<td>25.09 (14.12)</td>
<td>34.74 (37.02)</td>
<td>5.89 (3.54)</td>
<td>594.56 (1,185.56)</td>
</tr>
<tr>
<td></td>
<td>105</td>
<td>Low–moderate</td>
<td>7.78 (6.72)</td>
<td>37.22 (37.70)</td>
<td>4.30 (3.56)</td>
<td>302.06 (719.2)</td>
</tr>
<tr>
<td>Above average precipitation</td>
<td>51</td>
<td>Moderate–high</td>
<td>16.43 (12.04)</td>
<td>35.15 (37.79)</td>
<td>5.37 (3.64)</td>
<td>491.15 (962.58)</td>
</tr>
<tr>
<td></td>
<td>71</td>
<td>Low–moderate</td>
<td>5.39 (4.64)</td>
<td>38.28 (37.39)</td>
<td>3.84 (3.41)</td>
<td>224.84 (641.19)</td>
</tr>
</tbody>
</table>
growth (Parmalee 1955, Lehmann 1984). Additionally, spring precipitation likely synchronizes bobwhite brood rearing to coincide with peak invertebrate availability. Invertebrates are essential to the survival of bobwhite chicks (Campbell-Kissock et al. 1985, Giuliano et al. 1996), and their availability in brood-rearing cover used by bobwhites is contingent on the timing of precipitation (Wisdom 1991). Accordingly, even small quantities of spring precipitation during drought can elicit strong, positive population responses in bobwhites.

We also demonstrated that bobwhite covey counts on our landscapes were negatively related to summer and fall precipitation, which runs counter to existing long-term, broad-scale studies at other arid landscapes (Guthery et al. 2002, Tri et al. 2012). One hypothesis that may explain negative bobwhite-precipitation relationships in our study can be explained by the effect late-season precipitation has on bobwhite nesting phenology. Amidst persistent drought bobwhites attempted to nest in the presence of considerable June and October precipitation (see Fig. S2, available online at www.wildlifemagazines.org). Nesting attempts in October are rare, but do occur in southern Texas (Lehmann 1984) likely because precipitation appears to be a key determinant in the timing of breeding (Trewella 2014). Under these circumstances, the bobwhite hatch occurs out of sync and many habitat features critical to brood rearing are not available or are insufficient. This effect on bobwhites manifested as a negative bobwhite-precipitation relationship in our models. This phenomenon is well documented in a variety of avian taxa and systems and is a major influence on avian population abundances (Williams and Middleton 2008).

Seventeen landscapes in our study area supported high relative abundances of bobwhites despite persistent droughts. This suggests another factor buffers bobwhites from the effects of drought. The existence of positive relationships between bobwhite population responses and landscape structure covariates may provide this buffer. We show covey counts of bobwhites were positively related to landscapes at our study area containing higher densities of shrubland patches and greater interspersion of brush cover. This is consistent with previous work that has shown bobwhites respond positively to greater composition of early seral habitats that fulfill certain life-history requirements (Schaifer et al. 1999, White et al. 2005, Howell et al. 2009, Duren et al. 2011, Blank 2012). However, the features of early seral habitat important to bobwhite usually do not contain brush cover types. Brush covers are more important for loafing (Johnson and Guthery 1988), escape, or concealment from predators (Roseberry and Klimstra 1984), and thermal escape to reduce exposure to excessive heat (Guthery et al. 2005). Moreover, because long-term bobwhite population persistence can be accomplished on as little as 11% brush cover (DeMaso et al. 2014), managers usually devote substantial resources to reduce brush (Hernández and Guthery 2012). Thus, the presence of landscape structure covariates describing brush cover in our models is curious. We hypothesize that early seral habitat features provided by grassland cover types may be unavailable or unusable to bobwhites during drought. Under these conditions, shrubland and brush cover may be the only vegetation available for bobwhites to meet the cover needs dictated by their life history. For example, it is reasonable to assume that shade created by shrubland and brush cover increases soil moisture (an important determinant in invertebrate abundance in arid regions; Wallwork 1972), which could provide forage covers during drought. A similar population response to soil moisture gradients in logged and non-logged forest was reported for capercaillie (Tetrao urogallus) in a forest ecosystem (Stuen and Spids 1988) and migratory birds on playa wetlands under various flooding scenarios (Anderson and Smith 2000).

That predicted counts of coveys are greatest in the presence of abundant spring precipitation is not surprising; this is well established in the quail literature. However, that covey counts in some landscapes are consistently high or low irrespective of drought, presumably because of landscape structure, has important management implications. This indicates landscape structure and precipitation operate jointly to affect bobwhite population responses. This suggests some landscapes contain habitat features capable of buffering bobwhite populations from drought. If managers understand relationships between bobwhite population response and the landscape structure associated with these habitat features, then these drought-tolerant landscape conditions can be reproduced on other arid landscapes (or at the very least, landscapes can be managed to be more drought-tolerant). We offer a simplistic example from our study to demonstrate the application of these ideas to other landscapes. At our study, the 17 landscapes with consistently high counts of bobwhites regardless of drought contained an average of 422 ha of shrubland and 594 ha of brush. To simplify, a bobwhite likely views shrubland and brush patches as woody cover, in which 1,016 ha (11% of each landscape) exist on average at each of the 17 landscapes, distributed at an average density of 6 patches/100 ha (Table 4), under intermediate interspersion (approx. 60%). Put differently, if managing a 100-ha landscape we would strive for ≥6 patches of woody cover with intermediate interspersion and an average patch size of 1.83 ha (i.e., a rectangular patch with 135-m sides, or circular patch with a 76-m radius) that comprised 11% cover of the landscape. This is roughly analogous to previous recommendations of strip-motte patterns in the configuration of woody cover (Hernández and Guthery 2012). More generally, bobwhite counts during persistent drought were highly sensitive to even small amounts of brush; thus, regardless of configuration, simply having some minimum area of suitable brush cover for bobwhites is of principal importance.

The conversion of shrubland and brush covers to usable space often is the primary aim of habitat management for bobwhites (Hernández et al. 2007). Unfortunately, this management task also is costly in terms of economics and logistics (Hernández and Guthery 2012). Because management resources are finite, an obvious advantage of translating
model results into maps is the capability to visualize spatial patterns of predictions, and spatially prioritize where management should occur on the landscape. We suggest performing the above exercise in conjunction with a map of the model predictions to weigh the costs associated with management interventions with the potential population response it may elicit.

We acknowledge the inferences we used to draw these conclusions are specific to our landscapes. Although the extent to which these relationships are representative of random samples at other landscapes is not clear, we speculate the landscape structure of brush on managed or unmanaged landscapes is relatively uniform across the arid portions of the bobwhite range. This idea needs to be challenged and represents an avenue for future research. Another assumption about our model that needs to be evaluated is the threshold effect of bobwhite–landscape structure relationships. Our top model indicated positive relationships with the landscape structure of shrubland and brush covers, suggesting the composition and configuration of these covers can conceivably be increased indefinitely to the benefit of quail. Clearly, though some intermediate or threshold level exists. Finally, it should also be noted that landscape structure covariates depicting bobwhite nesting and brood-rearing covers were curiously absent from our top models. Factors augmenting vital rates of quail (DeMaso et al. 2011, Parent et al. 2012) and their nesting habitat availability (Rader et al. 2011) can potentially limit bobwhite populations, but this was not detected by our models. Several explanations exist for this observation. It is possible habitat features of nesting and brood-rearing cover types do not translate well to land cover dataset. Land cover dataset coarsely describe vegetation and may not effectively model bobwhite cover that is mediated by fine-scale processes (Gallant 2009). Thus, our classification scheme, which was developed according to field studies describing micro-site characteristics of nesting and brood-rearing cover, may not have adequately represented the broad-scale features of nesting and brood-rearing habitat. Alternatively, in the presence of frequent drought, these habitat features may not have been available uniformly across time and space as indicated by our land cover dataset.

**MANAGEMENT IMPLICATIONS**

This study provided support for the concept that bobwhite distribution in arid landscapes responds to precipitation and landscape structure. If precipitation is absent during key periods for bobwhite, then essential structural cover types such as nesting or brood-rearing cover may be unavailable or unusable. When configuration and composition at our study area are taken collectively, and in the presence of drought, relative counts of bobwhites are expected to be greatest on landscapes containing large areas of well-interspersed shrubland and large areas of brush distributed as many patches. Although shrubland and brush cover types may buffer bobwhite populations from drought, not all landscapes in the arid portion of the bobwhite’s range contain these favorable habitats. This suggests management applications that facilitate the conversion of these woody covers to suitable compositions and configurations can mitigate future drought-induced ecological bottlenecks that reduce bobwhite populations. These buffer sites could easily be worked in to existing habitat management approaches because most strategies involve the creation of strips or strip–mottes. Performing these tasks in conjunction with a map of model predictions has tangible benefits to managers because it can prioritize where management needs to occur.

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**LITERATURE CITED**


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APPENDIX A. CANDIDATE MODELS

A candidate set of models to test hypotheses depicting how landscape structure affects northern bobwhite abundance during extreme variability in precipitation. Each candidate model consists of combinations of precipitation and pairs of configuration and composition covariates defining essential bobwhite cover types. The models were built to reflect hypotheses about how precipitation and land cover influence bobwhite abundance. We fit models using negative binomial regression with bobwhite counts representing the response variable. We collected data at 122 landscapes on the King Ranch in southern Texas from 2008 to 2012. We determined model fit by corrected Akaike’s Information Criterion (AICc) and ranked models according to ΔAICc, and weight (wi) with K representing total number of model parameters. Months indicate a covariate for precipitation during the month shown, NUC is none-useable cover, NC is nesting cover, BFC is brood or forage cover, ERTC is escape, resting, or thermal cover, LH is landscape heterogeneity. We used various combinations of configuration and composition covariates for specific vegetation types to define covers.

<table>
<thead>
<tr>
<th>Candidate models</th>
<th>ΔAICc</th>
<th>K</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct + Apr + Jun + ERTC + LH</td>
<td>0</td>
<td>12</td>
<td>0.8</td>
</tr>
<tr>
<td>Oct + Apr + Jun + NC + LH</td>
<td>3</td>
<td>14</td>
<td>0.18</td>
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<tr>
<td>Oct + Apr + Jun + ERTC</td>
<td>7.1</td>
<td>10</td>
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</tr>
<tr>
<td>Oct + Apr + Jun + LH</td>
<td>10.6</td>
<td>8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Oct + Apr + Jun + NUC + LH</td>
<td>11.3</td>
<td>10</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Oct + Apr + Jun + BFC + LH</td>
<td>12.4</td>
<td>10</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Oct + Apr + Jun + NC</td>
<td>17.8</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Oct + Apr + Jun + NUC</td>
<td>21.7</td>
<td>8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>All rain</td>
<td>28</td>
<td>6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Oct + Apr + Jun + BFC</td>
<td>29.2</td>
<td>8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NC + LH</td>
<td>42.7</td>
<td>11</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>ERTC + LH</td>
<td>46.8</td>
<td>9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>LH</td>
<td>52.4</td>
<td>5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NUC + LH</td>
<td>53.3</td>
<td>7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>BFC + LH</td>
<td>55.1</td>
<td>7</td>
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</tr>
<tr>
<td>ERTC</td>
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<td>7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NUC</td>
<td>65.4</td>
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<td>&lt;0.001</td>
</tr>
<tr>
<td>NC</td>
<td>66</td>
<td>9</td>
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</tr>
<tr>
<td>Oct</td>
<td>66.7</td>
<td>4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Jun</td>
<td>73.5</td>
<td>4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>BFC</td>
<td>77.5</td>
<td>5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Apr</td>
<td>77.8</td>
<td>4</td>
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</tr>
</tbody>
</table>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s website.