THE CLIMATE OF *COLINUS* AND *CALLIPEPLA*:

CURRENT PATTERNS WITH FUTURE IMPLICATIONS

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Abstract: Climate change is a ubiquitous phenomenon that affects species at multiple spatial scales. Species' trends that are currently being observed may have future implications for conservation within the context of a dynamic climate. We monitored northern bobwhite (*Colinus virginianus*; here-after "bobwhite") and scaled quail (*Callipepla squamata*) space use and survival trends at a local scale, while also modeling the potential biogeographic responses of all temperate North American quail to predicted patterns of climate change. For instance, provision of artificial surface water during periods of extreme drought may not be warranted in future decades if water availability is decreased and if such provisions provide no benefit to species. Both bobwhite and scaled quail exhibited behavioral responses to the provision of anthropogenic surface water during periods of extreme drought by selecting for areas within 700 m of surface water. The probability of space use was greater in areas closer to water for bobwhite during the non-breeding season ($\overline{\beta}$ = -0.06, SE = < 0.01) and for scaled quail during the breeding season ($\overline{\beta}$ = -0.31, SE = 0.07). However, the presence of surface water sources did not influence survival or nesting success of bobwhite or scaled quail, thus this management practice is not supported. In general, all temperate North American quail are predicted to lose areas of environmental suitability except the Gambel's quail (*Callipepla gambelii*). Most species indicate a loss in southern latitudinal distributions. Bobwhite and scaled quail are predicted to lose areas of high relative abundance, where-as mountain quail (*Oreortyx pictus*) and California quail (*Callipepla californica*) are predicted to retain areas of high relative abundance. Local patterns of heterogeneity in thermal conditions may determine the magnitude of the responses of many of these species to climate change. We predicted that during periods of thermal extremes (<-15° C and >35° C), space use is least available for bobwhite. Furthermore, areas useable during the coldest thermal conditions are not similar to useable areas during periods of extreme heat events. These results further emphasize the need to understand local patterns and how they might affect regional responses in the context of climate change.

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CHAPTER I

BEHAVIORAL RESPONSES AT DISTRIBUTION EXTREMES: HOW ARTIFICIAL SURFACE WATER CAN AFFECT QUAIL MOVEMENT PATTERNS

ABSTRACT Supplementing wildlife populations with resources during times of limitation has been suggested for many species. The focus of our study was to determine responses of northern bobwhite (*Colinus virginianus*; Linnaeus) and scaled quail (*Callipepla squamata*; Vigors) to artificial surface-water sources in semi-arid rangelands. From 2012-2014, we monitored quail populations via radio telemetry at Beaver River Wildlife Management Area, Beaver County, Oklahoma. We used cumulative distribution functions (CDF) and resource utilization functions (RUF) to determine behavioral responses of quail to water sources. We also used Program MARK to determine if water sources had any effect on quail vital rates. Our results indicated that both northern bobwhite and scaled quail exhibited behavioral responses to the presence of surface-water sources. Northern bobwhite selected for areas < 700 m and < 650 m from water sources during the breeding and non-breeding season, respectively. However the non-breeding season response was weak ($\overline{\beta}$ = -0.06, SE = < 0.01) and the breeding season ($\overline{\beta}$ = 0.01, SE = 0.02) response was non-significant based on RUFs. Scaled quail selected for areas < 650 m and < 250 m from water sources during the breeding and non-breeding season, respectively. The breeding

season RUF ($\overline{\beta}$ = -0.31, SE = 0.07) indicated a stronger response for scaled quail than bobwhite. Conversely, there was no direct effect of surface water on quail vital rates or nest success during the course of our study. Although water may affect behavioral patterns of quail, we found no evidence that it affects quail survival or nest success for these two species.

INTRODUCTION

Understanding the ecology of species at their distribution limits has important implications to conservation (Grinnell 1917, MacArthur 1972). Limits in a species' distribution can provide insight into examining potential constraints on populations, or how populations may adapt to unique conditions that infrequently occur within the core of a species' distribution (Sexton et al. 2009). The availability of resources for wildlife, such as food, water, and cover (Leopold 1933) on distribution extremes may influence a species in ways that may not occur away from the periphery of its distribution. Furthermore, population responses and/or persistence can vary along gradients of resource and environmental variables, leading to the formation of distribution limits (Birch 1953).

Sympatric populations of northern bobwhite (*Colinus virginianus*; hereafter "bobwhite") and scaled quail (*Callipepla squamata*) offer a unique opportunity to study the influence of limiting resources on space use and vital rates, as these populations typically occur on the western and eastern extremes of the species' distributions, respectively (Schemnitz 1964). Within this region and other semi-arid and arid rangelands, the importance of water as a potentially limiting resource has been emphasized and the supplementation of water to enhance wildlife habitat continues to be a subject of debate among biologists (Rosenstock et al. 1999). Recommendations for provision of artificial surface water may be a result of actual observable depletions of available surface water in ecosystems or from analogies of human situations in which water supplementation is necessary (Campbell 1960).

Particular attention has been paid to providing surface-water sources to various species of quail in semi-arid and arid rangelands (Glading 1943), as the potential for population responses and economic payoffs is more likely in dry environments (Campbell 1960). However, ambiguity in tangible benefits of surface water to quail have existed since early results from studies by Grinnell (1927) and Vorhies (1928), though many of these studies relied purely on observational data to support or refute any benefits of surface-water sources. Due to limited data and ambiguous results, researchers and managers continue to try to assess if and when quail respond and/or benefit from the presence of artificial surface-water sources.

Generally speaking, scaled quail tend to be more drought tolerant than bobwhite (Schemnitz 1964) as they have better osmoregulation during times of extreme water deprivation (Giuliano et al. 1998). Because of this difference in physiology, a greater response of bobwhite to the provision of artificial surface-water sources in semi-arid regions would be predicted. Although direct individual use of surface water has been documented in bobwhite populations (Prasad and Guthery 1986, Lehmann 1984), results on population responses to artificial surface-water sources have been mixed. For instance, Guthery and Koerth (1992) determined that water supplementation did not benefit bobwhite, particularly when water was not a limiting factor. Conversely, Hiller et al. (2009) determined that both non-nesting bobwhite and bobwhite nest locations were located significantly closer to surface-water sources compared to random locations, while Dunkin et al. (2009) provided evidence of bobwhite breeding and non-breeding selection to areas ≥ 250m and ≤ 600m from surface-water sources. Such studies suggest that bobwhite may be responding behaviorally to the presence of surface-water sources, though do not indicate if such behavioral responses result in increased vital rates.

Similarly, there have been contrasting results when studying the response of scaled quail to surface-water sources. Direct use of surface-water sources have been documented for scaled quail, though at relatively low rates that may not be biologically meaningful (Campbell 1960). Additionally, scaled quail in Oklahoma were observed at locations closer to water than would be expected at random, though it was not determined whether this behavior was from direct use of water or from responding to other elements of habitat such as vegetation (Schemnitz 1961). Ultimately, it has been suggested that scaled quail may satisfy their water requirements from food sources and that providing surface-water sources is not necessary (Campbell et al. 1973).

In North America, an understanding of rangeland faunal responses to the provisioning of surface water will become increasingly important in future decades, as many of these rangelands are predicted to experience unprecedented droughts as a result of climate change (Cook et al. 2015). Furthermore, ground water withdrawal by humans often exceeds water recharge in aquifers within these rangeland systems (Dennehy et al. 2002, Moore et al. 2012), and recharge of these aquifers is predicted to be further reduced under future climate scenarios (Rosenberg et al. 1999). As such, the efficacy of providing artificial water sources for rangeland wildlife may be confounded by increased water demand and decreased water availability.

In this paper, we present results of the most comprehensive study to date examining bobwhite and scaled quail population responses to surface-water sources. By addressing multiple facets of potential population responses, we hope to provide greater insight as to whether surface water confers any benefit to these two quail species. We assessed the direct benefit of water provision through increased quail vital rates, changes in resource selection of quail from provision of surface water, and the confounding effects related to artificial surface water and vegetation cover. Our objectives were to determine if sympatric populations of bobwhite and scaled quail respond behaviorally to artificial surface-water sources in a semi-arid region at the species' distribution extremes. More specifically, we wanted to determine at what spatial scale birds may be behaviorally responding to water, whether or not the probability of space use by quail increased as distance from water decreased, and quantify any differences in vegetation cover between used and unused water sources. We also sought to estimate any relation between quail vital rates (nest success and adult survival) and presence of surface-water sources that may ultimately influence overall population levels.

METHODS

Study Area

Beaver River Wildlife Management Area (WMA), located in Beaver County, Oklahoma (lat 36°50'21.62"N, long 100°42'15.93"W), consists of approximately 11 315 ha managed by the Oklahoma Department of Wildlife Conservation (ODWC).

Most of the WMA consists of upland rangelands and the floodplain of the Beaver River. Much of the upland areas are dominated by tivilo fine sand soils, while the floodplain is dominated by lesho silty clay loam. Dominant grasses on upland sites consist of buffalograss (*Buchloe dactyloides*), little bluestem (*Schizachyrium scopariu)*, and bromes (*Bromus* spp.; non-native). Dominant forbs on upland sites include western ragweed (*Ambrosia psilostachya*), queen’s delight (*Stillingia sylvatica*), and Texas croton (*Croton texensis*). Dominant shrubs on upland sites include yucca (*Yucca glauca*), sand sagebrush (*Artemisia filifolia*), sand plum (*Prunus angustifolia*), and fragrant sumac (*Rhus aromatica*). Dominant grasses in the floodplain areas include weeping lovegrass (*Eragrostis curvala*; non-native), little bluestem, and switchgrass (*Panicum virgatum*). Dominant woody plants in the floodplain include fragrant sumac, sand plum, salt cedar (*Tamarix spp*; non-native), eastern cottonwood (*Populus deltoides*), and sugarberry (*Celtis laevigata*). Western ragweed is the dominant forb in the floodplain areas.

Over the course of our study (2012-2014), average temperatures in summer ranged from 19.56-22.28, 25.72-27.22, and 26.78-30.06˚C during May, June, and July, respectively. The long term (1895-2014) average regional temperature during this period is 25.28˚C. Average temperatures in the winter ranged from -0.83-2.17, 1.28-1.33, and -0.33-2.39˚C during December, January, and February, respectively. The long term average regional temperature during this period is -3.78˚C. Annual precipitation was 34.44, 50.29, and 39.42 cm in 2012, 2013, and 2014 respectively. The long term annual precipitation for this region is 49.63 cm. Climate data were obtained from the Beaver Mesonet station (Brock et al. 1995, McPherson et al. 2007).

During our data collection period (1 April 2012–31 March 2014), the WMA was classified under drought conditions ranging from severe to exceptional, and at no time was our study area out of drought conditions (The National Drought Mitigation Center, Lincoln, Nebraska, USA). Management practices consist of cattle grazing (1 stocker/16 acres, grazed for 150 days; only during 2012), strip discing, and food plot establishment.

Aerial imagery consisting of 2 x 2 m resolution was obtained during July 2012 and used in our classification of six major vegetation types across the WMA: sand sagebrush, shortgrass/yucca, mixed grass, mixed shrub, riparian grassland, and salt cedar. Anthropogenic surface-water sources (hereafter: water sources) consisted of windmills with water tanks, solar water wells, and gallinaceous guzzlers with overhead cover (Glading 1943). There was only one permanent water source on our study site that was natural (pond < 0.01 ha), thus we limited the scope of our analysis to artificial surface-water sources. Furthermore, we did not categorize water sources (i.e., guzzlers vs windmills) in our analysis as the central focus of our study was to determine use of all anthropogenic water sources in general. Water sources were examined each season (breeding and non-breeding) and year to confirm whether they provided water. From 2012 to 2013, the number of water sources functioning across the WMA decreased from 48 (2012) to 36 (2013). These 12 water sources were non-functioning because grazing on the WMA was discontinued due to continued drought conditions. As such, these water sources were not repaired after they ceased working. The density of water sources was 236 ha · water source in 2012 and 314 ha · water source in 2013 (Figure S1).

Radio-telemetry

We captured bobwhite and scaled quail between February-October 2012-2013 using walk-in funnel traps (Stoddard 1931). Captured quail were banded with leg bands (size 7) and fitted with a necklace-style radio transmitter weighing 6 g (crystal-controlled, two-stage design, pulsed by a CMOS multivibrator, Advanced Telemetry Systems, Isanti, Minnesota, USA) based on meeting a minimum body mass requirement (130 g). As our study area was located along the Beaver River corridor, areas used by scaled quail within the boundaries of the WMA were restricted primarily to the upland boundaries that were shared with private landowners. This limited the trapping efforts, and ultimately our sample size, for scaled quail during our study in comparison to bobwhite, which were located throughout the majority of the WMA.

Radio-marked individuals were located a minimum of three times per week using a scanning receiver and a handheld Yagi antenna (Advanced Telemetry Systems, Inc, Isanti, MN). We located quail by homing (White and Garrot 1990) within 15 m and recorded the distance and azimuth to the actual quail location while also marking the Universal Transverse Mercator (UTM) coordinates of the observer with a GPS unit (Garmin International, Inc, Olathe, Kansas, USA). We recorded locations of quail at different times on subsequent days to capture the variability of diurnal patterns. To accomplish this, we grouped birds by different sections of the WMA, and alternated the order in which each section was monitored across days. Our trapping and handling methods comply with the protocol determined by Oklahoma

State University's Institutional Animal Care and Use Committee Permit (no. AG-11-22).

Cumulative Distribution Functions

Cumulative distribution functions (CDF) were used to determine selection-avoidance-neutral behavior of quail in relation to distance from water sources during the breeding and non-breeding seasons. We defined the breeding season as 1 April-30 September and the non-breeding season as 1 October–31 March (Burger et al. 1995a). A form of this method of analysis was presented by Kopp et al. (1998) and subsequently used by Dunkin et al. (2009) in a similar analysis of anthropogenic structure effects on bobwhite. This analysis provides a continuous method of determining selection-avoidance-neutral behavior for data with large sample sizes and allowed us to determine the spatial scale at which quail were responding to water sources. Such large sample sizes can often lead to statistical significance in a model without any biological meaning (Abelson 1995, Guthery 2008). CDFs are also beneficial in that we are able to use the entirety of our location data in the analysis. Dunkin et al. (2009) describes deriving an estimate of selection-avoidance-neutral behavior by subtracting the relative cumulative frequency ($G(x)$) of used locations by the cumulative frequency ($F(x)$) of random locations$[G(x) - F(x)]$. CDFs are the integral of probability density functions (PDFs; Wackerly et al. 2002) and thus can be useful in determining selection-avoidance behavior in relation to continuous resource variables (Dunkin et al. 2009). This equation creates a function, in which a positive slope in the function indicates selection, and negative slope indicates avoidance, and a slope nearing 0 indicates a neutral relationship. The $G(x) - F(x)$ function was calculated for every 50 m interval (i.e, 0-49.99 m, 50-99.99 m, etc.), and we pooled these estimates between years for both breeding and non-breeding seasons for both bobwhite and scaled quail. We determined a non-significant relationship if confidence limits overlapped 0, which would result from increased variability between years.

Thirty random points (Martin et al. 2012) were created for every water source within our study area. We then estimated the Euclidean distance (m) from bird locations to artificial surface-water sources and random (or "pseudo" water source) locations. A total of 30 iterations were carried out in which pseudo water sources were randomly selected from our pool to estimate a bird's location to a pseudo-water source. The number of pseudo water sources randomly selected for each iteration was equivalent to the number of actual water sources present across the WMA at the specific time period.

To account for the potential confounding effects of vegetation on selection of areas close to artificial surface-water sources, we determined any differences in vegetation cover within selection buffers around used versus non-used water sources using PROC NPAR1WAY in SAS 9.4 (Statistical Analysis System Institute Inc, Cary, North Carolina, USA). The selection buffer was based on a radius equal to the maximum distance (m) from a water source in which selection behavior was determined. We assumed a water source was used if a bird location was within selection buffers around individual water sources. A utilization-availability analysis, as outlined by Neu et al. (1974), was used to determine vegetation types that were selected more than expected by bobwhite and scaled quail. We used the results from our utilization-availability analysis to compare % cover of selected vegetation types within and outside selection zones, while also relating this to the proportion of total bird points within and outside selection zones. Thus, if the majority of a representative vegetation type was outside the zone of selection, but the majority of points were within the zone of selection, we concluded that vegetation was not the sole driver of quail space use.

Space Use and Resource Utilization Functions

To validate relationships estimated from the CDFs, we also estimated the relationship of distance to surface-water sources on estimated probability of space use by a bird by estimating resource utilization functions (RUF; Marzluff et al. 2004, Millspaugh et al. 2006). RUFs allowed us to directly compare space use to distance from surface-water sources for individual birds during the breeding season and for coveys during the non-breeding season. Space use by individual quail within coveys is non-independent (Janke and Gates 2013, Brooke et al. 2015) therefore we estimated RUFs for coveys during the non-breeding season to meet the assumption of independence of space use between individuals (Marzluff et al. 2004). The RUF method is advantageous over other resource selection methods because it treats each individual as the experimental unit rather than each location, while also restricting space use of a bird to an estimated home range, rather than by an arbitrary boundary (Marzluff et al. 2004). As CDFs use the entire population of bird locations to assess the influence of a resource variable on space use, RUFs allowed us to confirm the estimated relationship based on a sub-sample (individual birds or coveys with $\geq$ 20 locations) of our location data. For instance, if a CDF indicated an attraction to surface water, the RUF would allow us to determine if the concentration of locations became denser as the distance from water lessened.

Seasonal home ranges for individuals or coveys having $\geq$20 radio-telemetry locations (DeVos and Mueller 1993, Taylor et al. 1999) were created using the 95% fixed-kernel method (Worton 1989, Seaman et al. 1999) through the Geospatial Modelling Environment (GME; Spatial Ecology LLC, USA). A 95% limit was used to better compare our results with previously published literature that estimates quail space use (Lohr et al. 2011, Janke and Gates 2013, Peters et al. 2015). The likelihood cross-validation bandwidth estimator was used to obtain kernel density (KDEs) estimates (Horne and Garton 2006), which provided us with a unique smoothing parameter (*h*; Worton 1989) for each individual that we subsequently used in our RUF calculations.

Utilization distribution rasters were created for each bird by assigning a use value ranging from 1 to 95% based on the relative volume of the utilization distribution (Marzluff et al. 2004, Kerston and Marzluff 2010). The utilization distributions were constrained to each bird or covey's 95% volume contour determined from the previous step. Each cell was 10 X 10 m, which was also representative of the resolution of our distance to surface water environmental layer. Once utilization distributions were created, we extracted use and distance to water (m) values to points centered within every cell located in the utilization distribution. The distance to surface water layer was estimated using the Spatial Analyst Euclidian Distance tool in ArcGIS 10.2 (ESRI 2011).

After extracting use and distance to water values within each home range, the relationship of space use to distance from water was estimated on a cell-by-cell basis which produced a coefficient of resource use for each individual. We used the Ruf.fit package in Program R (ver. 3.1.1, R Foundation for Statistical Computing, Vienna, Austria) to estimate coefficients of resource use for our sample. To stay consistent with methods from our CDF analysis, we only computed RUFs for individuals that had the entirety of the estimated home range within the boundary of Beaver River WMA. Estimates of space use were $\log_e$-transformed to meet the linearity assumption for multiple regression models. To estimate the influence of surface water on our overall population, mean standardized β coefficients ($\overline{\beta}$) were calculated by season and species with conservative estimates of variance that incorporates inter-individual variation (Marzluff et al. 2004). We considered standardized coefficients to be statistically significant if 95% confidence intervals did not overlap 0. Furthermore, a *t* test was used to test the significance of our standardized coefficients against a null model where of $\overline{\beta} = 0$ ($\alpha = 0.95$; Marzluff et al. 2004). Because our resource variable was a distance (m) measure, negative coefficients indicated that surface water had a greater than expected effect on space use, while positive coefficients indicated that surface water had a less than expected effect on space use (Marzluff et al. 2004). Finally, the number of individual birds or coveys that had significant positive, negative, or non-significant relationships to surface water were determined to display differences among individuals (Winder et al. 2013).

Survival analysis

To determine if the presence of surface-water sources had any influence on bobwhite and scaled quail survival, we estimated seasonal survival rates coded on weekly time intervals (26 total intervals) using the known fate model with a logit link function in Program MARK for each species and season combination (White and Burnham 1999). We censored the first seven days after a bird was released in our analysis to control for a potential short-term effects of capturing and radio-marking (Guthery and Lusk 2004), and used a staggered-entry method to analyze survival with the known fate model (Pollock et al. 1989). This method left-censors individual's encounter histories until they are captured and enter the monitored population. We right-censored individuals because of emigration from the study area, radio failure or loss, or when unknown fates occurred. We only analyzed survival of birds that had $\geq$ 20 locations and had estimated home ranges that were completely within the boundary of our study site so that we could stay consistent with our other analyses.

We included group metrics (age, sex, season, and home range size (ha)) and variables related to surface-water sources determined by our previous analyses (presence of water in a home range, number of an individual's locations within our zone of selection, and RUF β coefficients) in our survival analysis to address our research objective. We also included a temporal and null model in our analysis. For the non-breeding season, RUF β coefficients were estimated for individuals based on covey associations. We used a ΔAIC_c value of < 2 (Burnham and Anderson 2002), to determine the most parsimonious model for explaining variance in survival. However, we assumed that any exploratory variables contained in models performing worse than our null model did not contribute any relative importance to quail survival.

Nesting

Beyond adult survival, we also tested whether or not artificial surface-water sources had any influence on nest success. Quail were considered to be nesting if they were located at identical subsequent locations in the breeding season (Burger et al. 1995*b*). Once a bird was nesting, we marked (GPS) the location near the nest while the radio-marked quail was present. We located the actual nest when the radio-marked quail was away from the nest or after hatch or abandonment. Once a quail was nesting, the incubation status (whether the quail is still nesting) was monitored daily by locating the radio-collared adult. We continued to monitor nests until they hatched or failed. A nest was defined as successful if $\geq$ 1 egg hatched. We compared the Euclidean distance (m) of successful and unsuccessful nests to surface-water sources and to pseudo water sources (random points). Randomization of pseudo water source locations was identical to the methods described for our CDF analysis. Statistical significance of successful and unsuccessful nest distances to water and pseudo water sources was estimated based on the nature of the 95% confidence intervals (Hiller et al. 2009).

Estimates of nest location distances to surface-water sources were pooled between species because of a low sample size for scaled quail nests (n = 12). Variance between successful and failed nests were unequal (F-value = 2.94; $p <$ 0.01), therefore the Satterthwaite confidence limits were used to test for significance using PROC TTEST in SAS 9.4.

RESULTS

During the study, radio transmitters were placed on 487 bobwhite and 131 scaled quail. From this sample, we obtained a total of 5 569 and 6 180 bobwhite breeding season and non-breeding season locations respectively, and 1 108 and 1 922 scaled quail breeding season and non-breeding season locations, respectively. We were able to estimate home ranges for 80 bobwhite and 10 scaled quail in the breeding season and 25 bobwhite and 2 scaled quail covey ranges during the non-breeding season. During the 2012 and 2013 breeding season, we located a total of 61 nests, of which 49 were bobwhite and 12 were scaled quail.

Cumulative Distribution Functions

Based on the slopes of our CDFs, both bobwhite and scaled quail locations were closer to artificial surface-water sources than expected (Figure 1). Scaled quail exhibited significant selection for distances 100-650 m in the breeding season (Figure 1A). Scaled quail exhibited a much weaker response to surface-water sources during the non-breeding season compared to the breeding season. Specifically, a positive relationship was indicated from 50-250 m, however this was not significant based on confidence intervals and the overall sample resulted in a weak sigmoidal relationship (Figure 1B). Bobwhite exhibited significant selection behavior at distances 350-700 m from water sources during the breeding season, while selecting for distances 50-650 m during the non-breeding season (Figures 1C and 1D).

For bobwhite, there were a total of 34 and 24 surface-water sources that were considered used during the breeding and non-breeding seasons, respectively (Table 1). During the breeding season, water sources considered used by bobwhite had more mixed shrub cover within the zone of selection compared to water sources considered unused. During the non-breeding season, water sources considered used by bobwhite had more cover of sand sagebrush within the zone of selection compared to water sources considered unused. Not surprisingly because of sample size and habitat requirements, scaled quail used fewer water sources than bobwhite, with only 13 and 7 used during the breeding season and non-breeding season, respectively (Table 2). During the breeding season, water sources considered used by scaled quail had less cover of salt cedar and riparian grassland and more cover of sand sagebrush within the zone of selection when compared to water sources considered unused. Water sources considered used by scaled quail during the non-breeding season had no significant differences in vegetation cover within the zone of selection when compared to water sources considered unused.

Our utilization distribution analysis resulted in four vegetation types being used more than expected (Tables 3 and 4). From these results, we determined the proportion of these selected vegetation types within their respective zones of selection around all water sources for each species and each season, as well as the proportion outside of the zones of selection (Tables 5 and 6). For both species, there were more locations within zones of selection than would be expected based on the proportion of selected vegetation types also within zones of selection, excluding the non-breeding season scaled quail sample. Specifically, during the breeding season, scaled quail exhibited the most pronounced relationship, in which 65% of their locations were within the zone of selection with water (< 650 m) while 53% of the total available preferred vegetation types were located outside the zone of selection (Table 6). Likewise, bobwhite during the non-breeding season exhibited a strong relationship, in which 56% of their locations were within the zone of selection with water (< 650 m) and 67% of the total available preferred vegetation types were located outside this zone (Table 5).

Resource Utilization Functions

After filtering our sample of individuals to the boundary of the WMA, we were able to estimate RUFs for 117 individuals. A total of ten RUFs were estimated for scaled quail individuals in the breeding seasons and two coveys in the non-breeding seasons. We estimated 80 RUFs for bobwhite individuals in the breeding seasons and 25 coveys during the non-breeding seasons. As our sample of estimable RUFs for scaled quail coveys was low ($n = 2$), we did not attempt to obtain $\overline{\beta}$ for this sample.

Results from our RUF analysis concurred with the CDF relationships we estimated for our scaled quail breeding season and bobwhite non-breeding season samples (Table 7). Though our sample for breeding season scaled quail individuals was relatively low compared to our bobwhite sample the $\overline{\beta}$ coefficient indicated a strong positive influence of space use related to distance from artificial surface-water sources ($\overline{\beta} = -0.31$, SE = 0.07, 95% CI = -0.44 to -0.17). Likewise, space use by non-breeding bobwhite was positively related to distance from artificial surface-water sources ($\overline{\beta} = -0.06$, SE = 0.0002, 95% CI = -0.064 to -0.063), although this effect was much weaker than the scaled quail relationship. Space use related to distance from artificial surface-water sources for bobwhites during the breeding season was not significant ($\overline{\beta} = 0.01$, SE = 0.02, 95% CI = -0.03 to 0.06).

Adult and Nest Survival in Relation to Water

A total of 146 bobwhite and 28 scaled quail individuals were used in our survival analysis. For our bobwhite sample, no models performed better than the null model, suggesting we did not include variables that strongly influenced bobwhite survival (Table 8). Home range size (ha) was considered the best performing covariate in explaining scaled quail survival (β = -0.014, SE = -0.026 to -0.002) and no water variables performed above the null model (Table 9). We were unable to include the RUF β coefficient as a variable in our scaled quail survival analysis because of our low sample size. However, the β model for our bobwhite sample was not considered to be a competing model as it performed worse than our null model.

The mean difference of distance from surface water between successful and failed nests was -66.8 m (SE = 128.9, 95% CI = -327.7 to 196.0), indicating there was no statistical difference between these samples as confidence intervals overlapped 0 (Table 10). However, successful nests (and the pooled sample of all nests) were closer to artificial water sources compared to pseudo water sources ($P = 0.01$) whereas failed nests were not significantly closer to actual water sources when compared to their distance to random locations ($P = 0.18$).

DISCUSSION

We found that northern bobwhite and scaled quail exhibited a behavioral response to the presence of artificial surface-water sources in a semi-arid rangeland. These results were the most pronounced for scaled quail during the breeding season. Bobwhite behavioral responses were weaker, particularly within 350 m of water. These results indicated that placement of artificial surface-water sources in a semi-arid rangeland can influence quail behavioral patterns, at least in some years. Further, we found that quail were selecting areas closer to water even when appropriate vegetation cover was available away from surface-water sources. This relationship indicates that there was a direct influence of surface water to the behavioral responses observed during our study beyond that which was driven by coarse scale vegetation cover and composition alone.

Our nesting results indicate that nest-site selection may be influenced by the presence of artificial surface-water sources. However nest success was unaffected by the presence of these water sources. Previously, bobwhite have been shown to locate nests closer than expected to surface-water sources, though no difference in the distances between hatched and failed nests to water was observed (Hiller et al. 2009). Inhibition to reproduce and reproductive failure can occur when quail are exposed to water deprivation (Cain and Lien 1985, Guthery and Koerth 1992, Giuliano et al. 1995), so there may be benefits in locating nests closer to surface-water sources during times of potential stress from water loss. However, drought occurred during the entirety of our study and yet there was no relationship between nest success and distance from water sources. Therefore, nesting quail were likely obtaining water from other sources such as food or dew (Guthery 1999). To our knowledge, there is no study relating nest site selection to the presence of surface-water sources for scaled quail. Unfortunately, the low sample size (*n* = 12) during our study did not allow us to compare interspecific differences in behavioral responses of bobwhite and scaled quail when choosing a nest site.

The weak bobwhite behavioral response occurring closer to water sources was similar to results from other semi-arid regions of the bobwhite’s distribution in which non-significant use occurred at distances < 250m (Dunkin et al. 2009). Although the $\overline{\beta}$ for breeding bobwhite did not indicate a significant effect towards surface-water sources, more than 50% of the birds in the sample had β estimates indicating a significant positive relationship with space use and distance to surface water. As discussed earlier, needs for water supplementation of bobwhite are typically not supported (Guthery 1999), though this may be influenced by preformed water sources already available in the environment (Hernández et al. 2007). Furthermore, bobwhite behavioral responses to surface-water sources may be related to bobwhite seeking thermal refugia at water sites (via guzzlers) or to increased food availability from better soil moisture conditions (Hiller et al. 2009). Although we do not rule out these possibilities, our results also indicate non-breeding season behavioral responses, in times when these alternative benefits (particularly thermal refugia) may not be occurring.

Similar to bobwhite, scaled quail also exhibited behavioral responses to surface-water sources during the course of our study, though a non-significant relationship was observed at close distances (< 100 m) during the breeding season. Very little research exists exploring such responses of scaled quail to surface water, and those that do exist provide mixed conclusions (Campbell 1960, Schemnitz 1961). The physiological differences between scaled quail and bobwhite in relation to water requirements (Giuliano et al. 1998) could allow for the prediction that scaled quail responses to surface water should be weaker compared to bobwhite. Furthermore, because our study site is on the distribution limits of both species, adaptive behavioral responses to novel climate conditions could be expected (Sexton et al. 2009) in which bobwhite may have stronger responses to surface water, though this was not supported by our breeding season data. Typical precipitation levels present within these species' respective distributions vary drastically (Robinson 1956, Schemnitz 1964, Giuliano et al. 1999), and scaled quail are considered to be more adapted to arid environments than bobwhite (Schemnitz 1964). However, response to and use of surface-water sources by desert Galliformes has been widely documented (Kam et al. 1987, Delehanty et al. 2004, O'Brien et al. 2006, Larsen et al. 2007, Lynn et al. 2008).

We observed ambiguous relationships between site selection and areas within distances adjacent to water sources (i.e., 0-350 m), which resulted in neutral selection. A few factors could have contributed to these ambiguous results. Dunkin et al. (2009) indicates that mutually contradicting effects between a structure and the area it is located in may result in a neutral relationship closer to the structure. For instance, if a water source was indeed acting as an attractant, but was situated in a cover type that is avoided by quail, the net result may be a neutral relationship. Furthermore, this neutral relationship may be a result of a potential trade-off between resource use (and time allocated for using that resource) and predation risk (Brown 1999). However we were not able to directly test this hypothesis with our data.

Water sources (such as guzzlers) could potentially increase quail survival by providing needed cover during critical weather events. Conversely, indirect negative effects, such as predation, could be more pronounced at artificial surface-water sources if water were limiting during times of drought by potentially creating predator sinks (Rosenstock et al. 1999, Hall et al. 2013). However, data generally suggest that predation of varying wildlife species is not more pronounced at watering sites in semi-arid and arid regions (Krausman et al. 2006, Hall et al. 2013). Our results suggest there are no direct effects of surface water to quail survival.

The density of available water sources on our study site was 236 ha · water source in 2012 and 314 ha · water source in 2013. Previous recommendations have suggested a density of 121 ha · water source (Hernández and Guthery 2012). Based on our CDFs, the presence of artificial surface-water sources affected quail movement up to ~700 m for bobwhite and ~650 m for scaled quail. Taking the maximum value of the two, an ideal distribution (from a quail behavioral standpoint) of artificial surface-water sources across our study site would result in ~1400 m between each surface water source. This would result in a density of 1 water source per 154 ha, which may already exist on many rangelands in which grazing of livestock occurs within the distribution of bobwhite and scaled quail.

IMPLICATIONS

We found that artificial surface-water sources affected quail behavior but not vital rates. We suggest that management efforts focused on increasing or sustaining quail populations through water supplementation on semi-arid rangelands are unfounded. Because bobwhite and scaled quail can often obtain sufficient water through arthropods and succulent vegetation (Campbell et al. 1973, Guthery 1999), managing conditions that increase vegetation cover and arthropod abundance may be more effective in conserving quail populations than providing artificial surface-water sources.

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Table 1. Comparison of vegetation cover within northern bobwhite selection zones around used (breeding season *n* = 34; non-breeding season *n* = 24) and unused (breeding season *n* = 14; non-breeding season *n* = 12) artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA. Bold denotes significant differences (α = 0.05).

Cover Class	Breeding season						Non-breeding season					
	Used		Unused				Used		Unused			
	Mean	SE	Mean	SE	*Z*	*P*	Mean	SE	Mean	SE	*Z*	*P*
Riparian grassland	0.02	0.01	0.06	0.02	1.91	0.06	0.03	0.05	0.06	0.08	0.69	0.49
Bare Ground	0.01	< 0.01	0.01	< 0.01	0.28	0.78	0.01	0.01	0.01	0.01	-0.82	0.41
Exposed soil/sparse vegetation	0.01	< 0.01	0.02	0.01	-0.42	0.67	0.01	0.02	0.01	0.01	-1.02	0.31
Mixed shrub	0.11	0.02	0.06	0.02	**-2.01**	**0.04**	0.11	0.09	0.08	0.12	-1.8	0.07
Salt cedar	0.02	0.01	0.03	0.01	0.86	0.39	0.03	0.04	0.02	0.04	0.16	0.87
Sand sagebrush	0.49	0.02	0.41	0.03	-1.62	0.10	0.50	0.15	0.40	0.09	**-2.03**	**0.04**
Mixed grass	0.18	0.01	0.23	0.02	1.76	0.08	0.18	0.08	0.24	0.09	1.86	0.06
Shortgrass/yucca	0.14	0.02	0.17	0.04	0.71	0.47	0.13	0.11	0.18	0.11	1.63	0.10

Table 2. Comparison of vegetation cover within scaled quail selection zones around used (breeding season *n* = 13; non-breeding season *n* = 7) and unused (breeding season *n* = 35; non-breeding season *n* = 29) artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA. Bold denotes significant differences (α = 0.05).

Cover Class	Breeding season						Non-breeding season					
	Used		Unused				Used		Unused			
	Mean	SE	Mean	SE	*Z*	*P*	Mean	SE	Mean	SE	*Z*	*P*
Riparian grassland	0.01	0.01	0.04	0.01	**-2.39**	**0.02**	0.02	0.02	0.03	0.01	-1.00	0.32
Bare Ground	0.01	< 0.01	0.01	< 0.01	-0.97	0.33	0.01	< 0.01	0.02	< 0.01	-0.20	0.84
Exposed soil/sparse vegetation	0.02	0.01	0.01	<0.01	0.63	0.53	0.01	< 0.01	0.03	0.01	-0.64	0.52
Mixed shrub	0.08	0.03	0.10	0.02	-1.00	0.32	0.12	0.05	0.09	0.02	0.84	0.40
Salt cedar	< 0.01	< 0.01	0.03	0.01	**-2.63**	**< 0.01**	< 0.01	< 0.01	0.02	0.01	-0.91	0.36
Sand sagebrush	0.53	0.04	0.44	0.02	**2.00**	**< 0.05**	0.54	0.06	0.40	0.03	1.88	0.06
Mixed grass	0.22	0.03	0.19	0.01	0.91	0.37	0.18	0.04	0.21	0.02	-0.68	0.50
Shortgrass/yucca	0.13	0.03	0.16	0.02	-0.95	0.34	0.11	0.05	0.19	0.03	-1.48	0.14

Table 3. Total cover and use of preferred vegetation types[1] by scaled quail and northern bobwhite during the breeding season (1 April–30 September) from 2012-2013 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

		Scaled quail				Northern bobwhite			
		2012		2013		2012		2013	
Vegetation type	Total cover (%)	Use	CI	Use	CI	Use	CI	Use	CI
Sand sagebrush	36	0.43	0.38 to 0.48	0.42	0.38 to 0.45	0.54	0.52 to 0.57	0.52	0.49 to 0.54
Mixed shrub	8	—[2]	—[2]	—[2]	—[2]	0.29	0.27 to 0.32	0.28	0.26 to 0.31
Salt cedar	2	—[2]	—[2]	—[2]	—[2]	—[2]	—[2]	0.03	0.02 to 0.04
Mixed grass	18	0.25	0.21 to 0.29	0.22	0.19 to 0.25	—[2]	—[2]	—[2]	—[2]

[1] Selection determined by analysis described by Neu et al. (1974).

[2] Dashes indicate the vegetation type was not preferred during a particular year or for a particular species.

Table 4. Total cover and use of preferred vegetation types[1] by scaled quail and northern bobwhite during the non-breeding season (1 October–31 March) from 2012-2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

		Scaled quail				Northern bobwhite			
		2012-2013		2013-2014		2012-2013		2013-2014	
Vegetation type	Total cover (%)	Use	CI	Use	CI	Use	CI	Use	CI
Sand sagebrush	36	0.47	0.43 to 0.52	0.45	0.41 to 0.48	0.47	0.45 to 0.50	0.52	0.50 to 0.54
Mixed shrub	8	—[2]	—[2]	—[2]	—[2]	0.36	0.33 to 0.38	0.31	0.29 to 0.33
Salt cedar	2	—[2]	—[2]	—[2]	—[2]	0.03	0.02 to 0.04	—[2]	—[2]

[1] Selection determined by analysis described by Neu et al. (1974).

[2] Dashes indicate the vegetation type was not preferred during a particular year or for a particular species.

Table 5. Total hectares and proportion of preferred vegetation type (cover[1]) compared to proportion of the total study area and proportion of northern bobwhite locations within and outside the zone of selection surrounding artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

	Breeding season				Non-breeding season			
	Available cover (ha)	% Cover	Total area (%)	Locations (%)	Available cover (ha)	% Cover	Total area (%)	Locations (%)
Within selection buffer	3 372	48	49	62	2 335	33	34	56
Outside selection buffer	3 643	52	51	38	4 680	67	66	44
Total	7 015	100	100	100	7 015	100	100	100

[1] Cover is the total percent cover of selected vegetation types which were determined by methods described by Neu et al. (1974). Selected vegetation types by northern bobwhite during the breeding and non-breeding seasons were sand sagebrush, mixed shrub, and salt cedar.

Table 6. Total hectares and proportion of preferred vegetation type (cover[1]) compared to proportion of the total study area and proportion of scaled quail locations[2] within and outside the zone of selection surrounding artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

	Breeding season				Non-breeding season			
	Available cover (ha)	% Cover	Total area (%)	Locations (%)	Available cover (ha)	Percent Cover (%)	Total area (%)	Locations (%)
Within selection buffer	3 272	47	44	65	296	6	6	9
Outside selection buffer	3 713	53	56	35	4 750	94	94	91
Total	6 985	100	100	100	5 046	100	100	100

[1] Percent cover is the total percent cover of vegetation types being selected for which were determined by methods described by Neu et al. (1974). Selected vegetation types by scaled quail during the breeding season were sand sagebrush and mixed grass and was sand sagebrush during the non-breeding season.

Table 7. Mean standardized resource utilization function coefficients ($\overline{\beta}$)[1] and percentage of birds with positive (+), negative (-), or non-significant (ns) β values[2] indicating the relationship of space use to distance from artificial surface-water sources (m). Data is provided for northern bobwhite and scaled quail during breeding and non-breeding seasons 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

Sample Set	*n*	$\overline{\beta}$	95% CI[1]	+	-	ns	*P*-value[3]
Bobwhite breeding season	80	0.01	-0.04 to 0.06	39	51	10	0.63
Bobwhite non-breeding season	25	-0.06	-0.064 to -0.063	16	44	40	< 0.001
Scaled quail breeding season	10	-0.31	-0.44 to -0.17	0	80	20	< 0.01

[1] Confidence intervals were estimated based on conservative standard errors that include inter-animal variation (Marzluff et al. 2004).

[2] The resource variable being tested is a distance based variable. As such, a negative β value indicates an increase in space use as an individual gets closer to an artificial water source.

[3] The *P*-value indicates a test against a null hypothesis of $\overline{\beta} = 0$ as described by Marzluff et al. (2004; $\alpha = 0.05$).

Table 8. Ranking of *a priori* models based on ΔAIC_c values used to assess the influence of group metrics and surface water source variables on northern bobwhite survival from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

Model	AIC_c	Δ AIC_c	AIC_c Weights	Model Likelihood	No. Parameters.	Deviance
Null	17.8	0.0	0.19	1.00	1	15.8
Water in home range	18.1	0.3	0.16	0.85	2	14.1
Home range size (ha)	18.2	0.4	0.16	0.84	2	14.2
Sex	18.6	0.8	0.13	0.70	2	14.5
Season	18.8	1.0	0.12	0.61	2	14.8
Age	19.1	1.3	0.10	0.53	2	15.1
RUF β	19.8	2.0	0.07	0.38	2	15.8
No. locations by water	19.8	2.0	0.07	0.37	2	15.8
Time	64.7	46.9	0.00	0.00	26	11.3

Table 9. Ranking of *a priori* models based on ΔAIC_c values used to assess the influence of group metrics and surface water source variables on scaled quail survival from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

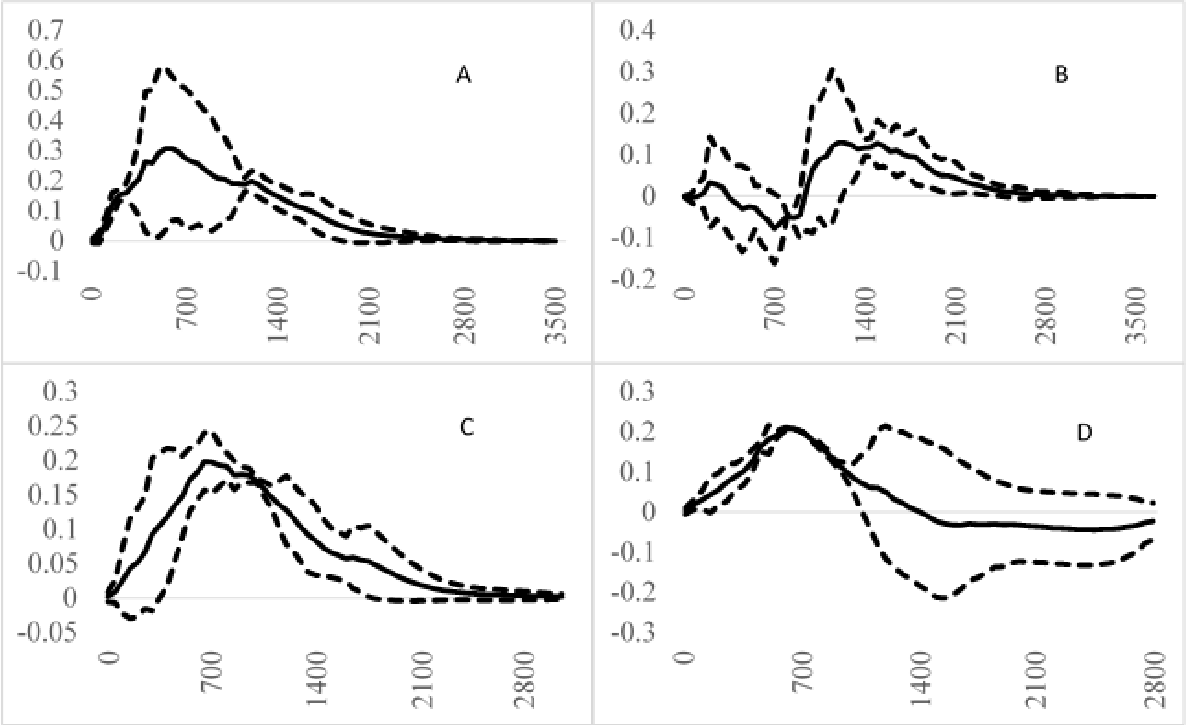
Model	AIC_c	ΔAIC_c	AIC_c Weight	Model Likelihood	No. Parameters	Deviance
Home range size (ha)	29.8	0.0	0.67	1.00	2	25.3
Season	33.9	4.1	0.07	0.13	2	29.4
Null	34.0	4.2	0.08	0.12	1	31.9
No. locations by water	34.2	4.4	0.07	0.11	2	29.8
Sex	35.7	5.9	0.03	0.05	2	31.2
Water in home range	35.9	6.1	0.03	0.05	2	31.4
Age	36.3	6.5	0.03	0.04	2	31.8
Time	73.0	43.2	0.00	0.00	26	13.9

Table 10. Distance (m) of pooled northern bobwhite and scaled quail nests to artificial surface-water sources and random locations from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

		Distance to water sources (m)		Distance to random locations (m)		
Sample	*n*	*x*	SE	*x*	SE	*P*-value[1]
Nests						
Successful	31	755.0	66.0	969.3	52.9	**0.01**
Failed	30	821.8	112.7	1 002.3	69.9	0.18
Total	61	787.9	64.4	985.6	43.3	**0.01**

[1] Bold p-values denote significant differences between distances from nests to water sources compared to distance from nests to random locations ($\alpha = 0.05$).

Figure 1**.** Average selection-avoidance-neutral trends (solid lines) with 95% confidence limits (dashed lines) of scaled quail and northern bobwhite based on distance from artificial surface-water sources (m) from 1 April 2012–31 March 2014, Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA. **A,** Scaled quail breeding season. **B,** Scaled quail non-breeding season. **C,** Northern bobwhite breeding season. **D,** Northern bobwhite non-breeding season.



CHAPTER II

USE OF SPECIES' ABUNDANCE DATA IN INTERPRETATIONS OF CLIMATE-BASED ENSEMBLE FORECASTING OF SPECIES' DISTRIBUTIONAL SHIFTS

ABSTRACT Ecological niche models (ENMs) have increasingly been used to estimate the potential effects of climate change on species' distributions worldwide. Recently, predictions of population demographic variables and species abundance have also been obtained with such models. However, knowledge of specific environmental variables directly affecting species abundance, as well as abundance data itself, is often lacking. We used a widely studied guild (temperate North American quail) and the Maxent modeling algorithm to compare model performance obtained with three variable selection approaches: correlation/variable contribution (CVC), biological (i.e., variables known to affect species abundance), and random. To estimate species' distributional shifts we generated ensemble forecasts using four global circulation models, four greenhouse gas emission scenarios, and two time periods (2050 and 2070). The CVC variable selection approach outperformed our biological approach for four of the six species. Model projections of all species indicated shifts in future distributions, with three species having an overall loss in projected suitable distribution (-3.43% to -61.12%) and three species having an overall gain in projected suitable distribution (1.04% to 50.39%). Our models projected loss of area for the northern bobwhite (*Colinus virginianus*) in the southern and western portion of the distribution, which are stronghold areas of high abundance. Similarly, scaled quail (*Callipepla* squamata) were predicted to lose areas of high abundance within their current distribution. Conversely, California quail (*Callipepla californica*) and mountain quail (*Oreortyx pictus*) were projected to retain population strongholds while still losing significant area of their distributions. Our results suggest mixed effects of climate change on future

distributions of temperate North American quail. Finally, special attention should be given to selecting variables for ENMs, and tests of model performance should be used to validate the choice of variables.

INTRODUCTION

Global climate change may drastically influence species populations worldwide and may have increased negative effects on species that are not able to adapt to changes in climate or to disperse to suitable conditions elsewhere (Walther *et al.*, 2002; Thomas *et al.*, 2004; Guisan, 2014). Climatic conditions are important in determining an organism's geographic distribution because of specific eco-physiological constraints (Grinnell, 1917; Veneir *et al.*, 1999; Thomas *et al.*, 2004; Monahan and Hijmans, 2008). Climate change has already caused shifts in the distribution of many species (Johnson, 1994; Thomas and Lennon, 1999; Parmesan, 2006), and is estimated to continue affecting distributions in the future (Lawler *et al.*, 2009; Thomas, 2010). Ecological niche models (ENMs) can be useful in predicting changes in a species' distribution (Austin and Van Niel, 2010), though such techniques often rely on the availability of a sufficient amount of occurrence and/or abundance data representative of the species' distribution (Elith and Leathwick, 2009). This potential limitation has led to a large number of studies focused on avian species (Jiménez-Valverde *et al.*, 2011; Sohl, 2014) because of the plethora of occurrence data publicly accessible through government monitoring programs (Breeding Bird Survey [BBS]; Pardieck *et al.*, 2014), as well as citizen science programs (eBird; Sullivan *et al.*, 2009).

Though initially ENMs were focused on studying the biogeography of species, more recently research has focused on utilizing such models to help relate probability of occurrence to intrinsic growth rates (Thuiller *et al.*, 2014), population size (Legault *et al.*, 2013), population density (Oliver *et al.*, 2012), reproductive parameters (Brambilla and Ficetola, 2012), and species abundance (Vanderwal *et al.*, 2009*b*; Van Couwenberge *et al.*, 2013; Howard *et al.*, 2014). Combined with population demographic information, these analyses can be used to more accurately target areas of conservation concern (Vanderwal *et al.*, 2009*b*) by identifying potential "species' strongholds". However, an important assumption made about environmental variables incorporated in ENMs is that they are biologically meaningful to the species of interest, and the selection of these variables can greatly affect the performance and resulting ENMs (Peterson and Nakazawa, 2008; Rödder and Lötters, 2009). When incorporating population demographic information to ENMs, inclusion of biologically meaningful variables that directly relate to demographic rates and exclusion of "relaxed" variables (Rödder and Lötters, 2009), or variables that have little importance on such rates, should be taken into consideration (Rödder and Lötters, 2010). Despite this concern, ecological niche modeling studies often use all 19 bioclimatic variables that are freely available (www.worldclim.org) and correlation/variable contribution filtering to dictate the modeling parameters (Dormann *et al.*, 2013).

Here, we investigate model performance differences under three variable selection methods and present an analysis of potential climate induced shifts in the distributions of the temperate North American quail species (California quail [*Callipepla californica*], Gambel's quail [*Callipepla gambelii*], scaled quail [*Callipepla squamata*], northern bobwhite [*Colinus virginianus*], Montezuma quail [*Cyrtonyx montezumae*], and mountain quail [*Oreotyx pictus*]). These species are of conservation concern as they have experienced distribution-wide declines in recent decades (Oberholser 1974; Sauer *et al.*, 2014), which may be exacerbated in future climates because of their low dispersal abilities (Li *et al.*, 2010). Furthermore, many of these species are designated as umbrella species (Caro, 2003) for biodiversity conservation and have been shown to be positive indicators for the occurrence of other avian species of conservation concern (Crosby *et al*., 2015). Thus understanding potential climate induced shifts in the distributions of these species may have conservation implications beyond temperate North American quail. Finally, these species offer an opportunity to relate abundance data to ENMs because extensive knowledge exists on what abiotic variables drive annual abundance and reproduction of most of these species (Table 1). Our objectives were to: 1) test whether ENMs performance improved with using only variables known to directly affect species' abundance, compared to performance of models based on other variable selection approaches and 2) analyze species abundance data in relation to future distribution shift estimates to identify potential critical areas of loss in environmental suitability.

METHODS

Species Occurrence Data

We collated species occurrence data from the BBS (Pardieck *et al.*, 2014) and eBird (Sullivan *et al.*, 2009) databases, similar to other ENMs studies (Hochachka *et al.*, 2012; Hurlbert and Liang, 2012; Sohl, 2014). The BBS is a multi-national bird survey program that has been used to monitor breeding bird population trends in North America since 1966 (Robbins *et al.*, 1986; Link and Sauer, 1998). Its design includes using thousands of observers annually to conduct point count surveys along repeated transects located on roadways throughout much of North America (Robbins *et al.*, 1986). Raw data and trend estimates are made publicly available through the BBS website (https://www.pwrc.usgs.gov/bbs/). A more detailed description of the BBS protocol and analysis techniques are provided by Robbins *et al.* (1986) and Peterjohn (1994). The eBird database is a citizen science program established to archive and share bird observations submitted by the public (Sullivan *et al.*, 2009). Currently, this is considered the largest ecology based citizen science project (Hochachka *et al.*, 2012). Inclusion of eBird records in our occurrence dataset allowed us to consider geographic areas outside the current sampling range of the BBS survey (i.e., Mexico) in which some of our target species occur. The range of dates for occurrence data from the BBS and eBird was 1966-2000 and 1950-2000, respectively, which temporally matched the range in dates for the environmental variables included in the modeling framework discussed below. We note that eBird observations were more abundant in recent decades as opposed to the earlier decades during our study period, however this database was useful in obtaining occurrence information through the entire temporal range that coincided with our environmental data.

Because the species we examined are non-migratory game species, the overall number of occurrence points was much greater than typical sample sizes recommended for ENMs (Wisz *et al.*, 2008). Oversampling and clustering of occurrence data can often lead to overfitting issues in a presence-only modeling framework (Elith *et al.*, 2011; Boria *et al.*, 2014). This relates to models fitting tightly to calibration data, which in turn will limit the ability of the model to predict independent evaluation data (Boria *et al.*, 2014). Spatially rarefying occurrence data in such situations has been shown to improve models by limiting the possibility of over-fitting predictive models (Kramer-Schadt *et al.*, 2013; Boria *et al.*, 2014). Previous studies vary in the spatial rarefication buffer used (10-20km), with justification for these buffer distances based on ecology of the study species (Kramer-Schadt *et al.*, 2013), spatial heterogeneity of vegetation (Boria *et al.*, 2014), or the clustering nature and abundance of data points from a database (Sohl, 2014). Similar to Sohl (2014), we chose a 20 km buffer around points for all six species we examined, a distance within their dispersal range (Campbell and Harris, 1965; Savage, 1974; Lehman, 1984; Pope, 2002). To spatially rarefy occurrence data, we used the Spatially Rarefy Occurrence Data tool in the SDM Toolbox (v1.1b; Brown, 2014) for ArcGIS 10.2.1 (ESRI, Redland, California, USA). Further elimination of points included the removal of occurrence points that represented “introduced” or “stocked” populations, as we were only interested in modeling the distribution of native populations. To eliminate these types of entries, we removed any occurrences outside the known historic distribution of the species and any entries in which observers noted “stocked” or “introduced” individuals in the comments section. We also verified that locations were within the species’ historic distribution by validating our data with range maps downloaded from NatureServe (NatureServe 2015). Finally, as outlined by Sohl (2014), eBird includes different observation protocols that may influence the interpretation of occurrence type. The “exhaustive area counts” protocol can represent single occurrence coordinates for large areas covered by the observer and may not reflect occurrence at a scale relevant to ecological modeling. Likewise, the “traveling count” protocol represents a single occurrence coordinate for a large distance traveled. To account for these potential biases, we eliminated traveling count observations in which the observer traveled >2 km (Fink *et al.*, 2010; Sohl, 2014) and exhaustive area counts in which the observer covered an area >100 ha (Sohl, 2014).

Initial sample sizes and spatially rarefied sample sizes varied across species. Initial sample sizes ranged from 382 (Montezuma quail) to >38,000 (bobwhite) occurrence locations. After spatially rarifying our data, sample sizes were reduced to: 31, 216, 268, 317, 552, and 2,013 for Montezuma quail, mountain quail, Gambel’s quail, scaled quail, California quail, and bobwhite, respectively.

Climate Data

We obtained baseline (1950-2000) climate data at a spatial resolution of five arc minutes (~9 km) from the WorldClim database (Hijmans *et al.*, 2005). We created three unique suites of environmental layers to run three separate models. We used this approach so that we could directly test whether or not a model utilizing environmental variables known to directly affect local abundance performed better than other approaches. The three model suites used were: biological (use of variables known to directly affect local abundance), correlation/variable contribution (CVC; i.e., variable reduction through correlation analysis [Dormann *et al*. 2013] and variable contribution to model accuracy gain), and random (i.e., a selection of random bioclimatic variables equal to the number of variables contained in each biological model). To create the CVC suite, we initially selected 19 bioclimatic variables and eliminated highly correlated variables ($|r^2|>0.7$; Dormann *et al*. 2013), as well as variables contributing $\leq$1% to model accuracy gain (Brambilla and Ficetola, 2012). For the random model suite, we used randomly selected variables from the list of the 19 bioclimatic variables. The number of randomly selected variables was equal to the number of variables used in our biological model. For the biological model, we limited our variable selection to eight climate variables based on previous knowledge of these species' ecological responses to environmental trends (Table 1). These eight variables included: maximum temperature of the warmest month (°C; Bio5), mean annual temperature (°C; Bio1), average maximum temperature for June, July, and August (°C), average annual rainfall (mm; Bio12),cumulative rainfall for winter (mm; December, January, and February), cumulative rainfall for spring (mm; March, April, and May), cumulative rainfall for summer (mm; June, July, and August), and cumulative rainfall for fall (mm; September, October, November). Average maximum summer temperature and cumulative seasonal rainfall variables were calculated using the monthly average environmental data available through WorldClim. For the biological suite, we estimated a Pearson's correlation coefficient for all combinations of variables and used the threshold of $|r^2|>0.7$ to eliminate highly correlated variables (Dormann *et al.*, 2013). We also eliminated variables that had $\leq$1% contribution to accuracy gain of preliminary models that we ran for the six species (Brambilla and Ficetola, 2012). These three approaches left us with a specific set of variables for each species of interest.

For future projections of the models, we used the best performing variable suite (discussed in the next section) as our baseline model for estimating future distributions. Climate data (the same variables) for future projections was also obtained from the WorldClim database at a spatial resolution of five arc minutes, similar to the baseline data. To account for variation in global circulation models (GCMs) on which the future climate datasets are based, we used an ensemble forecasting procedure to estimate future distribution shifts (Araújo and New, 2007). To capture variability across GCMs, we randomly selected four (Domisch *et al.*, 2013) and used data at four representative concentration pathways (RCPs; 2.6, 4.5, 6.0, and 8.5), or scenarios of greenhouse gas emissions, across two time periods (2050 [average for 2041-2060] and 2070 [average for 2061-2080]) in which data were available. The four random GCMs selected were the CCSM4, GISS-E2-R, HadGEM2-ES, and the MRI-CGCM3, all included in the 5th Assessment IPCC report (AR5; IPCC, 2014). In sum, for each species we obtained 32 models and corresponding future projections (4 GCMs X 4 emission scenarios X 2 time periods).

Previous research has emphasized the importance of training ENMs only based on environmental data existing within the known spatial distribution of a study species (Soberón and Peterson, 2005, Elith *et al*. 2010). We therefore trained our models with environmental data that were clipped to the spatial extent of the species' potential study extent. We restricted the study extent to a 500km buffer around "contemporary" locations (Sohl, 2014). Sohl (2014) described contemporary locations as species occurrence points from the year 2001. As our most recent occurrence data was in 2000, we considered these locations to be our contemporary points which were used in creating the species' study extent. In a similar study, a 200km buffer was shown to be too restrictive for many species and their projected future distributions (VanDerWal *et al.*, 2009*a*), thus Sohl (2014) suggested a 500km buffer to encompass potentially large shifts in projected occurrence data. Therefore, we used this buffered range as our study extent for selecting background points and projecting future species' distributions. This buffer ensured that no occurrence points were located outside of our study extent for each species. Study extents after this procedure were: $1.80\text{x}10^{12}$ ha, $2.39\text{x}10^{12}$ ha, $2.63\text{x}10^{12}$ ha, $3.29\text{x}10^{12}$ ha, $3.43\text{x}10^{12}$ ha, and $7.43\text{x}10^{12}$ ha for mountain quail, Montezuma quail, Gambel's quail, scaled quail, California quail, and northern bobwhite, respectively. We projected all of our data into the North American Albers Equal Area Conic projection (Snyder, 1987; Elith *et al.*, 2011) as our study extents covered a large range in latitude (>200 km) based on our criteria (Elith *et al*. 2011). Once we identified the best performing model suite (out of three possible, CVC, biological, and random; see above) for each species, we projected it on future climate data from the GCMs across the entirety of North America.

Maximum Entropy Modeling

Incorporating species occurrence data and climate variables, we estimated quail distributions with the Maximum Entropy algorithm Maxent, version 3.3.3k (Phillips and Dudik, 2008). We chose not to include relative species' abundance models as an environmental variable in our niche modeling process as these data were not available across the entire area of our species' study extents. The Maxent algorithm is considered similar to Poisson regression (Renner and Warton, 2013) and is used for generating ENMs with presence-only data (Elith *et al.*, 2006) and environmental variables. Maxent has been shown to have higher predictive power than many other modeling techniques (Wisz *et al.*, 2008; Elith *et al.*, 2011) by minimizing the entropy between the probability densities of presence data and “background” data (locations without presence information).

The remaining analysis parameters for our distribution modeling were set to Maxent default options (Phillips and Dudik, 2008). This included the use of 10,000 background points, which has been shown to perform similarly when compared to models using all potential background points (Phillips and Dudik, 2008). We used a regularization multiplier of 1, performed 500 iterations per model, and used a convergence threshold of 0.00001 for each model. To test the validity of our models, we held-out 25% of our presence data for testing through random selection and used 75% for training each species model (Bahn and McGill, 2012; Sahlean *et al.*, 2014; Sohl, 2014). We replicated our baseline model 100 times using the bootstrap method. For each species we used 10 percentile training presence as the threshold method to convert the continuous occurrence probability estimates into binary, presence-absence, occurrence maps. This threshold rule has been shown to outperform other threshold rules in Maxent modeling (Liu *et al.*, 2013). This threshold rule resulted in the use of average logistic thresholds of 0.223, 0.288, 0.304, 0.343, 0.374, and 0.374 for Montezuma quail, Gambel’s quail, California quail, mountain quail, northern bobwhite, and scaled quail, respectively. Thus, any cells with logistic values below these individual threshold values were categorized as unsuitable. Finally, we projected Maxent models onto the future climate change scenarios described above.

To evaluate and compare the performance of our three model suites, we used test occurrence data and the binary occurrence maps to calculate omission error, averaged across the 100 replicates for each suite and standardized by mean area predicted present (Wilson *et al*. 2013), as well as the average Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC), a threshold independent method of evaluating models (Fielding and Bell

1997). Since test omission errors are sensitive to the amount of area predicted suitable (Anderson *et al*. 2003), we further assessed the performance of our model suites using the standardized omission error. This is calculated by estimating test omission for each model replicate based on a binary suitability map that has the same percent area of suitability, which was set at the mean percentage of suitable area predicted across all model replications for each species (Wilson *et al*. 2013). This standardized test omission error thus allows for direct comparison of performance between models. The mean percentages of suitable area predicted for each species across replications and model suites were: 21.72%, 22.56%, 23.74%, 29.05%, 30.33%, and 55.76% for mountain quail, Montezuma quail, California quail, Gambel's quail, scaled quail, and northern bobwhite, respectively. For the threshold-independent method of model evaluation (ROC), the AUC value can range from 0-1 and indicates the probability of a presence point having a higher AUC value than a random background point. This means that a value of 1 indicates a completely accurate prediction, whereas a value of 0.5 indicates no difference in the presence and the background point, and values <0.5 indicate predictions that perform worse than a random model (Phillips *et al.*, 2006). The AUC value has been scrutinized for being a poor predictor of model performance (Lobo *et al*. 2007; Peterson *et al*. 2008), thus conclusions based solely on ROC AUC are not recommended.

The importance of the environmental variables to building ENMs was assessed using two methods. First, we calculated in Maxent the average percent contribution of each environmental variable to individual species' models. Second, we analyzed the partial plot response curves (Torres *et al.*, 2010) that indicated the relationship between a single environmental variable and the probability of suitability when all other variables are kept at their average sample value (Phillips *et al.*, 2006). Because we were interested in the variability of partial plot response curves between model replications, we assessed the average partial plot response curves along with their standard deviation (Anadón *et al.*, 2015).

Post-modeling Analysis

To estimate species' potential distribution shifts in future climatic conditions, we used the Raster Calculator tool in ArcGIS 10.2 to compare differences in binary occurrence probabilities of current and future distributions. An ensemble suitability range for current distributions was assigned where all 32 model runs agreed on a binary presence for each species. We then created ensemble future distribution projections across both time periods, at three levels of projection agreement: 75%, 90%, and 100%. We used binary outputs to create our ensemble forecasts as to avoid uncertainty in the appropriateness of averaging different Maxent logistic values across models. We included three levels of agreement to capture variability between climate scenarios that may have altered degree of agreement. Based on these ensemble forecasts, we categorized distribution conditions that raster cells could be classified into 8 conditions (Table 2). We used these distributional conditions to estimate the overall percent gain or loss for future distributions relative to the current estimated distribution.

Finally, we accessed relative abundance data for all species except the Montezuma quail, which were not available (Sauer *et al.*, 2014). For each of the other five species abundance was estimated from BBS data for 2008-2012. These relative abundance values generally predict the average number of individuals for a specific species that can be seen along roadsides in ~2.5 hours (Sauer *et al*., 2014). We conducted a one-way ANOVA of relative abundance among areas of current suitability to areas that are estimated to contract in future climate scenarios using PROC GLM in SAS 9.4 (Statistical Analysis System Institute Inc, Cary, North Carolina, USA) and compared statistical significance between our distribution conditions using the Tukey-Kramer test for unequal samples across 75%, 90%, and 100% ensemble forecasts.

RESULTS

Model Performance

Based on standardized test omission errors, the CVC variable selection approach significantly outperformed the biological variable selection approach for all species except Gambel's quail and Montezuma quail (Fig. 1). For Gambel's quail, the biologically relevant variable suite significantly outperformed the CVC approach. There was no significant difference between these two variable suites when analyzing Montezuma quail data. Models for all species and all variable suites besides the random variable suite for bobwhite performed reasonably well (Swets, 1988), with all test AUCs averaging within 0.72 to 0.91 (Fig. 1). The random variable suite for bobwhite had a test AUC value of 0.67. Test omission rates at the 10% training omission threshold also indicated that our models performed well, with average rates ranging from 0.11 to 0.18 (Fig. 1). Based on the standardized test omission error values, we used the CVC variable suite for California quail, scaled quail, mountain quail, and bobwhite ENMs. We used the biological variable suite to create ENMs for the Gambel's and Montezuma quail.

Average variable contributions to model accuracy gain (averaged across 100 replicates per species) are indicated in Table 3. The Montezuma quail and the northern bobwhite had the least number of contributing variables whereas scaled quail and mountain quail had the most, after adjusting models for initial variable correlations and contributions. At least one bioclimatic variable was included in each species' model set except for the Gambel's quail. Mean temperature of the wettest quarter (BioClim8) was the most frequently included variable and occurred in four of the six species' ENMs. Average partial plot relationships between all contributing models and climate suitability are presented for all species in the supporting material (Fig. S1-S6).

Future Species' Distributions

Based on 90% agreement between all future climate projections, California quail, scaled quail, mountain quail, and Montezuma quail are predicted to have a net loss in areas that are currently environmentally suitable when projecting models to 2070 (Fig. 2). In general, areas of net gains in future distributions occurred across high latitudes whereas distribution contraction occurred across lower latitudes (Figs. 3-5). However, areas that were predicted to remain suitable for mountain quail were not significantly different in elevation ($\bar{x}$ = 919.77 ± 13.37 m) compared to areas that were predicted to contract in suitability ($\bar{x}$ = 891.78 ± 25.59 m). Though disparity existed in estimated losses and gains of future projected distributions for all species between model agreement scenarios, Gambel's quail was predicted to gain more environmentally suitable area in all model agreements when compared to the other five species (Fig. 2). Conversely, scaled quail were predicted to lose the most area of environmental suitability (Fig. 2). It should be noted that 75% model projection agreement (Figs. S8-S10) is likely more liberal and 100% model projection agreement (Figs. S11-S13) is likely a conservative estimate of future distributions and should be interpreted with some caution.

Abundance Trends

We noted important trends for four species when considering BBS relative abundance data in relation to areas predicted to remain suitable versus those that would contract in suitability under 90% model agreement. Northern bobwhite models indicate future loss of suitable areas that currently have high-to-intermediate levels of relative abundance for this species (Table 4). Scaled quail models indicate future loss of areas that currently have the highest levels of relative abundance, suggesting a potential loss in this species' "strongholds" (Table 4). Conversely, the California quail and mountain quail are projected to lose approximately 21% and 17% of their suitable distributions in the 90% agreement of the ensemble future distribution predictions, respectively (Fig. 2). Yet areas that are currently suitable and remain suitable have significantly higher relative abundance than areas that are lost in future climate scenarios (Table 4). There were no general trends with the Gambel's quail data with respect to loss of areas that could be considered strongholds. As noted before, relative abundance data were not available for Montezuma quail. Similar information on relative abundance trends for the 75% and 100% agreement in the ensemble future distribution predictions is presented in supporting material (Tables S1 and S2).

DISCUSSION

Our results indicate that the traditional CVC variable selection approach outperformed a climate-based biological variable selection approach for four of the six species we studied. However, all variable selection approaches produced accurate estimates of current distributions based on three different model performance metrics. The only exception was the random variable selection approach for the northern bobwhite model, in which the average AUC value indicated poor performance (AUC = 0.67). Our ENMs predicted that only three of the six quail species are projected to have overall increases in environmentally suitable area under climate scenarios for 2070, under our most liberal model agreement scenarios. There was generally no significant difference in relative abundance for areas of continued suitability versus areas of future suitability loss in the context of one of our six species (Gambel's quail). Northern bobwhite and scaled quail were predicted to lose areas of suitability that currently support intermediate to high levels of relative abundance (or "species' strongholds") compared to the areas that remain suitable. Conversely, California quail and mountain quail maintain “species’ strongholds” though are predicted to lose large areas of suitability in the southern portion of their current distribution.

The use of a standardized test omission error to assess model performance has only recently been proposed to help eliminate the ambiguity and biases related to AUC and test omission errors (Wilson *et al*., 2013). Interestingly, there were relatively few differences in the results of our test AUC and standardized test omission errors, with the primary difference relating to the performance of our Montezuma and mountain quail data sets and the significance level of our Gambel’s quail data sets (Fig. 1). However, there were significant differences when standardized test omission errors were compared to traditional test omission errors, emphasizing the importance of standardizing this performance metric to better measure differences in model performance across variable suites.

The CVC variable selection approach generally outperformed our abundance-based biological variable selection approach (i.e., for two-thirds of the species), though the magnitude of these difference varied from species to species (Fig. 1). Discrepancy existed between climate variables that influenced local annual abundance and variables that influenced species’ distributions in our study. This was evidenced by the lack of performance for our biological variable suite when compared to the CVC variable suite in the analysis of four of the six species (Fig. 1). The most reasonable explanation for these discrepancies is likely related to scale (Wiens *et al*., 1987), suggesting that factors that influence local species’ abundance do not always scale up to determine species’ distributions. A case in point can be made for the northern bobwhite, in which the broad distribution of this species would lend itself to varying effects of climate variables across latitudinal (i.e., temperature) and longitudinal (i.e., precipitation) gradients. Furthermore, for the two species in which the biological variable suite was used to determine species' distributions (Gambel's quail and Montezuma quail), there was evidence of transmutability (O'Neill 1979) in the relationship of these variables as data were scaled up. For instance, a negative relationship between summer temperatures and productivity of Gambel's quail has been reported (Heffelfinger *et al.*, 1999). However our results indicate that, although maximum average summer temperature contributed most to our ENMs for Gambel's quail (Table 3), there was actually a positive relationship between probability of suitability and maximum average summer temperature (Fig. S2). Transmutation across scales also occurred for the Montezuma quail data, in which the positive relationship between abundance and summer precipitation (Howard, 1979) changed to a unimodal relationship (i.e., an indication of niche breadth) when scaled up to the species' distribution (Fig. S5). These results further emphasize the importance of considering scale when working with species' distribution models.

Based on our analysis of species' relative abundance, scaled quail and northern bobwhite trends indicated the loss of areas with high and/or intermediate relative abundance, respectively (Table 4). Interestingly, a majority of these "strongholds" occur on the periphery of the estimated species' distributions (Sauer *et al.*, 2014). As climate induced shifts in distributions can often affect edge populations disproportionately (Hampe and Petit, 2005), direct loss of these "peripheral strongholds" could have major conservation implications (Steen and Barrett, 2015). Conversely, though California quail and mountain quail are predicted to have a net loss in areas that are environmentally suitable (Fig. 2), areas that are retained under future climate scenarios are currently areas with the highest relative abundance for these species (Table 4) and are centrally located within their current distribution (Sauer *et al.*, 2014). We analyzed these data to help illustrate that even when species' were predicted to have a net gain in areas of environmentally suitability, areas of predicted loss could include some population strongholds and should be of conservation concern. We note that just as distributions are expected to shift, dispersal patterns and species' interactions with biotic and abiotic variables (Davis *et al*. 1998) will likely facilitate a shift in species' abundance as well. Interpretations should take this into consideration and future research attempting to model shifts in the future abundance of these species would be beneficial.

A general outcome in biogeographical studies in the context of future climate change is that non-montane species tend to shift distributions northward while montane species shift distributions towards higher elevations (Pounds *et al.*, 1999; Parmesan and Yohe, 2003; Parmesan 2006; Guralnick, 2007; Beever *et al.*, 2011). This trend has been exhibited in across a wide spectrum of vertebrates and invertebrates. Species endemic to high elevation montane areas may be more vulnerable to a changing climate as they become more restricted to smaller, higher elevation areas termed "sky islands" (Knowles *et al.*, 2007). Geographic restriction of species to these sky islands may be a result of the traditional low elevation/competition vs. high elevation/physiological stress hypothesis (McArthur, 1972), though more recently this pattern has also been attributed to the phylogenetic niche conservatism process (Wiens *et al.*, 2010; Gifford and Kozak, 2012), in which instantaneous niche retention exists (Pyron *et al*., 2014). If indeed niche conservatism determines high elevation distribution restrictions in certain species, they may be highly susceptible to geographic isolation due to climate change (Gifford and Kozak, 2012). In a broad analysis of Galliformes response to climate change in China, species at high elevations were predicted to have greater distribution shifts (Li *et al.*, 2010). Similarly, in our study, mountain quail, which typically occur at elevations of 1,050-2,161 m (Brennan *et al.*, 1987), had predictions of distribution contraction. However, inconsistent with the concept of sky islands, the contraction of this species' distribution did not occur at lower elevations, though did occur at southern latitudes. Although an apparent sky island effect was not evident in our study with this montane species, avian species tend to respond the least with regards to elevational shifts related to climate change (Chen *et al*. 2011) and interspecific phenotypic differences may cause variability in generalized responses (Bestion *et al*. 2015) such as elevational shifts.

All six species indicated general trends of southern latitudinal loss, at varying levels, in environmental suitability of their current distribution (Figs. 3-5). This has been shown in many other Galliformes, in which northward shifts were more common than any other directional shift (Li *et al.*, 2010). These southern edge shifts in future predicted distributions should be viewed with caution. The low latitudinal periphery of a species' distribution could actually have high stability because of heterogeneity in topography and in plant community structure, providing greater opportunities for establishing climatic niches (Parmesan *et al.*, 1999; Hampe and Petit, 2005). The variability in these responses is related to the scale in which most climate change research is focused. Detailed knowledge is becoming increasingly available on how organisms respond to fine-scale heterogeneity in a thermal landscape, particularly in relation to local topography and vegetation structure (Matala *et al.*, 2013; Hovick *et al.*, 2014; Varner and Dearing, 2014; Carroll *et al.*, 2015). These behavioral responses could help to stabilize potential distribution shifts. For instance, a temperature related variable was the highest contributing variable for only half of the species (Table 3), with all relationships indicating the presence of a niche breadth except for the Gambel's quail (Figs. S2-S7). It is likely that temperature was not the best contributor to many broad scale models in our study because many of these species have been known to phenotypically and behaviorally adapt to variation in temperatures at very fine scales (Reyna and Burggren, 2012; Guthery *et al.*, 2001; Guthery *et al.*, 2005), which may slow the rate of low latitudinal distribution contraction beyond that which our models predict.

The use of land cover data in ENMs has produced mixed results with regards to model performance and predicted distributions for many species, and varies species by species (Thuiller *et al.*, 2004; Lee and Jetz, 2011; Mathews *et al.*, 2011; Bucklin *et al.*, 2015). However, there is often high uncertainty in projected future land cover models and these variables are often not included when projecting ENMs into future scenarios (Barbet-Massin *et al.*, 2012). Thus our overall goal was to model the climatic suitability for these species rather than trying to incorporate both climate variables and land cover data under future scenarios. This is not to say that conservation biologists should ignore land cover in future conservation planning and management efforts. Indeed, current and future land cover across species' distributions will likely influence abundance and distribution of Galliformes included in our analysis (Brennan, 1991; Church *et al.*, 1993; Guthery, 1997). Climate based models merely offer one of several tools to aid in decision making and should be viewed as such, with the inherent limitations acknowledged.

Though conservation has historically been considered a crisis discipline with objectives focused on preventing the extinction of rare or threatened species (Soulé, 1985; Gaston and Fuller, 2008), recent arguments suggest conservation biologists should also focus efforts on conservation of more common species, as declines in such species may be representative of changes in ecological structure and functions (Gaston and Fuller, 2008). For instance, recent research indicates that across 144 European avian species, common species are declining the most whereas rarer species are generally increasing in abundance, a trend attributed to landscape scale deterioration in environmental quality (Inger *et al.*, 2015). A benefit to modeling common species is that occurrence data and knowledge of biologically meaningful environmental variables can often be easily accessible, as we have demonstrated here. These data may give conservation biologists insight into broad temporal and spatial trends related to at risk ecosystems. We suggest, as did Crosby *et al.* (2015), that relatively common species, in addition to rare species, should receive attention if maintaining biodiversity is a goal.

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Table 1 Climate variables known to affect abundance and/or reproduction of temperate quail species in North America.

Common name	Scientific name	Climate variable	Reference(s)
California quail	*Callipepla californica*	Fall-Spring precipitation	(Francis, 1970)
		Winter precipitation	(Botsford *et al.*, 1988)
Gambel's quail	*Callipepla gambelii*	Winter-Spring precipitation	(Gullion, 1954; Hungerford, 1960; Raitt and Ohmart, 1966; Heffelfinger *et al.*, 1999)
		Maximum July temperature	(Heffelfinger *et al.*, 1999)
Scaled quail	*Callipepla squamata*	Winter precipitation	(Giuliano and Lutz, 1993)
		Summer precipitation	(Campbell, 1968; Campbell *et al.*, 1973; Leyva-Espinosa, 2000)
		Spring precipitation	(Campbell, 1968; Campbell *et al.*, 1973)
		Annual precipitation	(Bridges *et al.*, 2001)
		Modified Palmer Drought Severity Index[1]	(Bridges *et al.*, 2001)
Northern bobwhite	*Colinus virginianus*	Maximum July temperature	(Lusk *et al.*, 2001; Lusk *et al.*, 2002)
		Spring precipitation	(Guthery *et al.*, 2002)
		Summer precipitation	(Guthery *et al.*, 2002)
		Fall precipitation	(Lusk *et al.*, 2002)
		Modified Palmer Drought Severity Index[1]	(Bridges *et al.*, 2001, Perez *et al.*, 2002)
		Annual precipitation	(Perez *et al.*, 2002)
Montezuma quail	*Cyrtonyx montezumae*	Summer precipitation	(Brown, 1979)
Mountain quail	*Oreortyx pictus*	N/A[2]	N/A[2]

[1] Not included in our analysis.

[2] Information not available.

Table 2 Possible distribution conditions occurring within species' distribution maps produced by the Maxent algorithm under future climate scenarios.

Condition	Description
1	distribution expansion from current to 2050 and remaining suitable from 2050 to 2070
2	suitable at current and through all time periods
3	unsuitable from current to 2050 but expanding from 2050 to 2070
4	distribution contraction from current to 2050 but expanding from 2050 to 2070
5	distribution expansion from current to 2050 but contracting from 2050 to 2070
6	suitable from current to 2050 but contracting from 2050 to 2070
7	unsuitable at current and through all time periods
8	distribution contraction from current to 2050 and remaining unsuitable from 2050 to 2070

Table 3 Variables used[1] in the Maxent algorithm for training niche models of temperate North American quail species and average variable contribution to model accuracy gain. Standard errors are in parentheses.

Variable	*Callipepla californica*	*Callipepla gambelii*	*Callipepla squamata*	*Colinus virginianus*	*Cyrtonyx montezumae*	*Oreortyx pictus*
BioClim[2] 1	0.00	0.00	0.00	49.62 (0.17)	26.83 (0.74)	0.00
BioClim 3	24.22 (0.43)	0.00	24.32 (0.52)	0.00	0.00	11.39 (0.56)
BioClim 4	0.00	0.00	0.00	0.00	0.00	27.32 (0.95)
BioClim 8	16.84 (0.46)	0.00	12.35 (0.43)	1.55 (0.06)	0.00	10.79 (0.36)
BioClim 9	2.25 (0.14)	0.00	0.00	0.00	0.00	0.00
BioClim 11	0.00	0.00	12.64 (0.47)	0.00	0.00	0.00
BioClim 14	0.00	0.00	0.00	0.00	0.00	9.47 (0.36)
BioClim 15	0.00	0.00	9.0509 (0.40)	36.54 (0.16)	0.00	16.80 (0.96)
BioClim 16	0.00	0.00	35.26 (0.54)	0.00	0.00	0.00
BioClim 18	40.46 (0.45)	0.00	0.00	12.29 (0.20)	0.00	0.00
BioClim 19	16.22 (0.52)	0.00	6.38 (0.18)	0.00	0.00	24.23 (0.65)
Cumulative fall precipitation	0.00	7.17 (0.36)	0.00	0.00	0.00	0.00
Cumulative spring precipitation	0.00	21.11 (0.62)	0.00	0.00	25.11 (0.70)	0.00
Cumulative summer precipitation	0.00	13.48 (0.26)	0.00	0.00	30.86 (0.73)	0.00
Cumulative winter precipitation	0.00	15.47 (0.26)	0.00	0.00	17.20 (0.80)	0.00
Maximum average summer temperature	0.00	42.78 (0.68)	0.00	0.00	0.00	0.00

[1] Variables with 0% contribution to model accuracy gain were not used in model training.

[2] BioClim variables are estimated from Hijmans *et al*. (2005) and are described at www.worldclim.org.

Table 4 Mean relative abundance (RA) estimates[1] and standard errors (SE) of temperate North American quail species[2] and associated conditions[3] of distributions, based on ENMs using the Maxent algorithm, at 90% ensemble forecasting agreement. Significant difference in RA estimates indicated by Tukey-Kramer test results[4] from a one-way ANOVA.

Species	Condition	Mean RA	SE	Tukey-Kramer grouping
Callipepla californica	2	7.79	0.09	A
	4	6.92	0.59	A
	6	5.07	0.29	B
	8	4.78	0.15	B
Callipepla gambelii	2	10.18	0.14	A
	4	3.80	1.83	BA
	6	5.11	1.33	BA
	8	1.57	0.49	B
Callipepla squamata	2	3.12	0.04	B
	4	2.09	0.24	C
	6	3.70	0.13	A
	8	2.46	0.08	C
Colinus virginianus	2	6.99	0.05	C
	4	21.47	0.74	A
	6	14.19	0.40	B
	8	14.63	0.29	B
Oreortyx pictus	2	2.45	0.04	A
	4	1.75	0.28	B
	6	1.60	0.10	B
	8	1.60	0.08	B

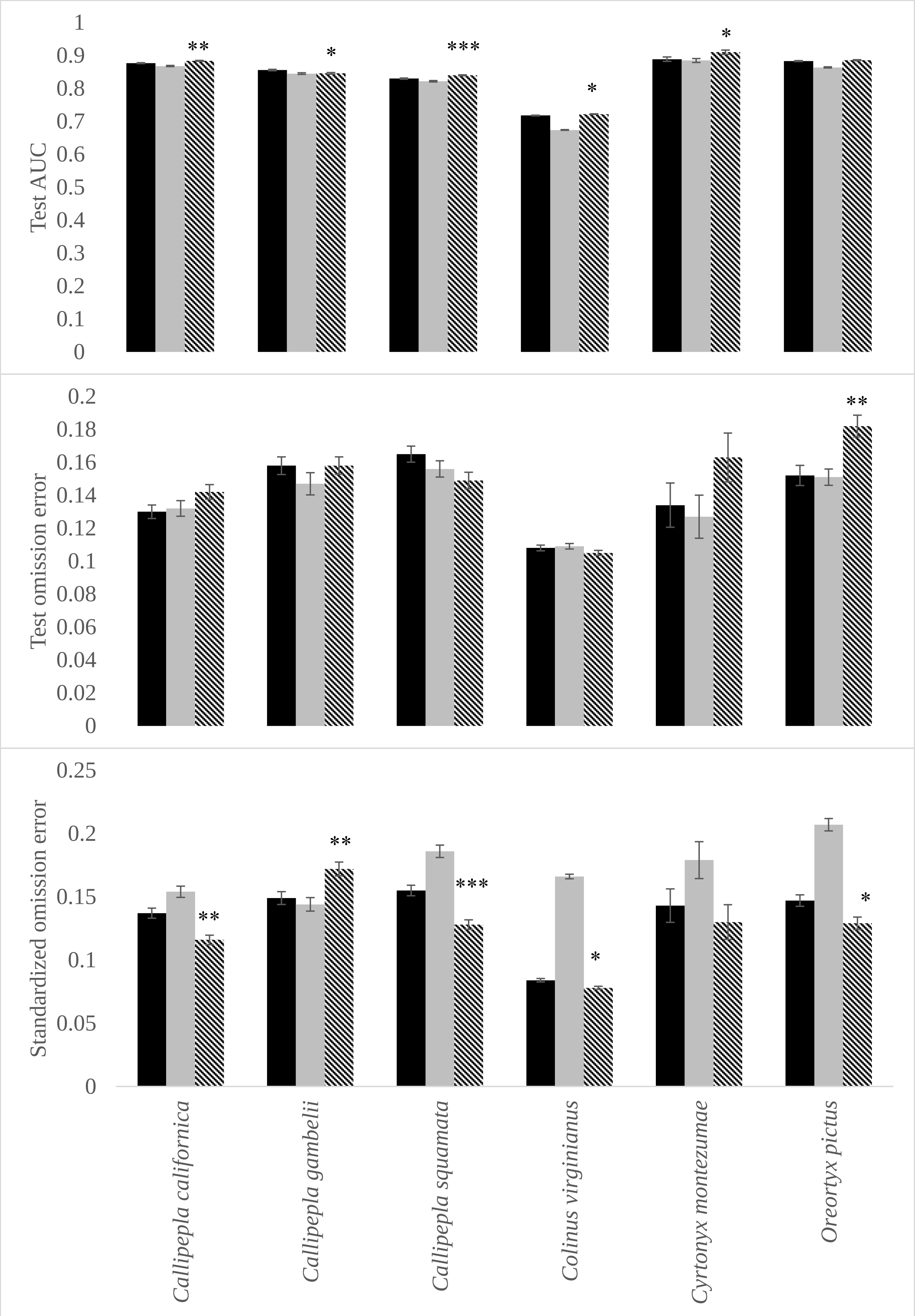
[1] Estimate from Sauer et al. (2014). Values generally predict the average number of birds for a species that can be seen along roadsides in ~2.5 hours.

[2] Data not available for *C. montezumae*.

[3] Descriptions for possible distribution conditions are given in Table 2.

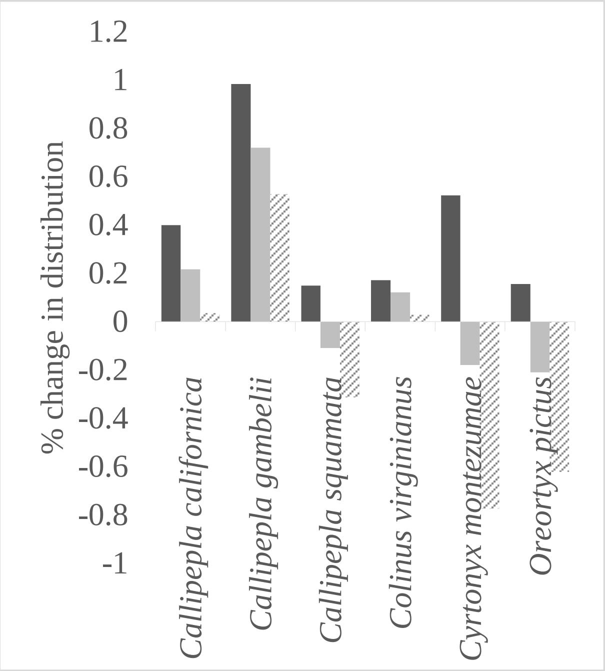
[4] Letter categories represent significant differences between relative abundance values between scenarios at α = 0.05 level.

Figure 1. Model performance metrics[1] used in determining the best variable selection approach to estimate distribution shifts for temperate North American quail through the Maxent algorithm. Variable selection approaches included a biologically relevant (black bar), a random (grey bar), and a correlation/variable contribution (striped bar) approach.

Test AUC
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
**
*
***
*
*
Test omission error
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
**
Standardized omission error
0.25
0.2
0.15
0.1
0.05
0
**
**
***
*
*
Callipepla californica
Callipepla gambelii
Callipepla squamata
Colinus virginianus
Cyrtonyx montezumae
Oreortyx pictus

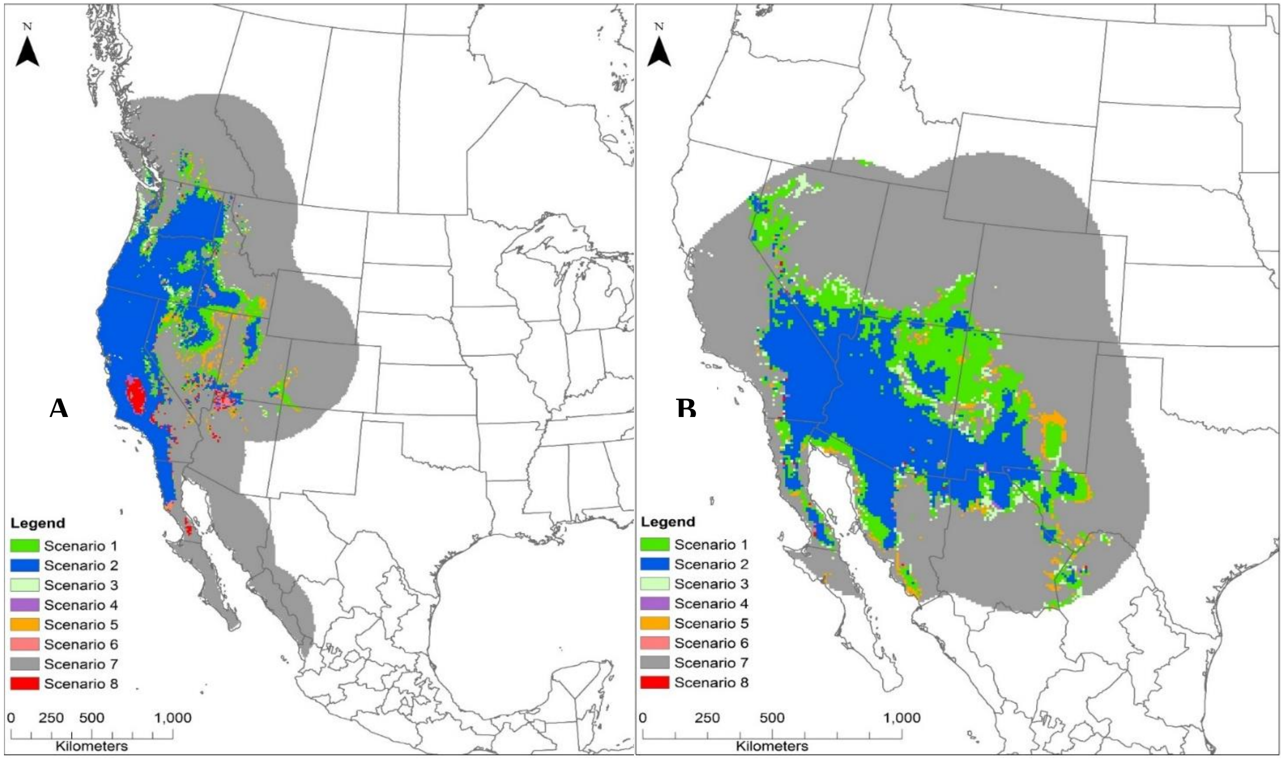
[1] Asterisks indicate different levels of significance between the CVC and biological variable selection approach. * indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$.

Figure 2. Estimated percentages of distribution shifts[1] for temperate North American quail based on ensemble projections of Maxent models into 2070.



[1] Ensemble forecast agreement is indicated as followed: 75% (black), 90% (gray), and 100% (striped).

Figure 3. Future predicted changes[1] in distributions of California quail (*Callipepla californica*; **A**) and Gambel's quail (*Callipepla gambelii*; **B**) projected to 2070 and based on ensemble forecasts (estimated through Maxent) at 90% agreement.



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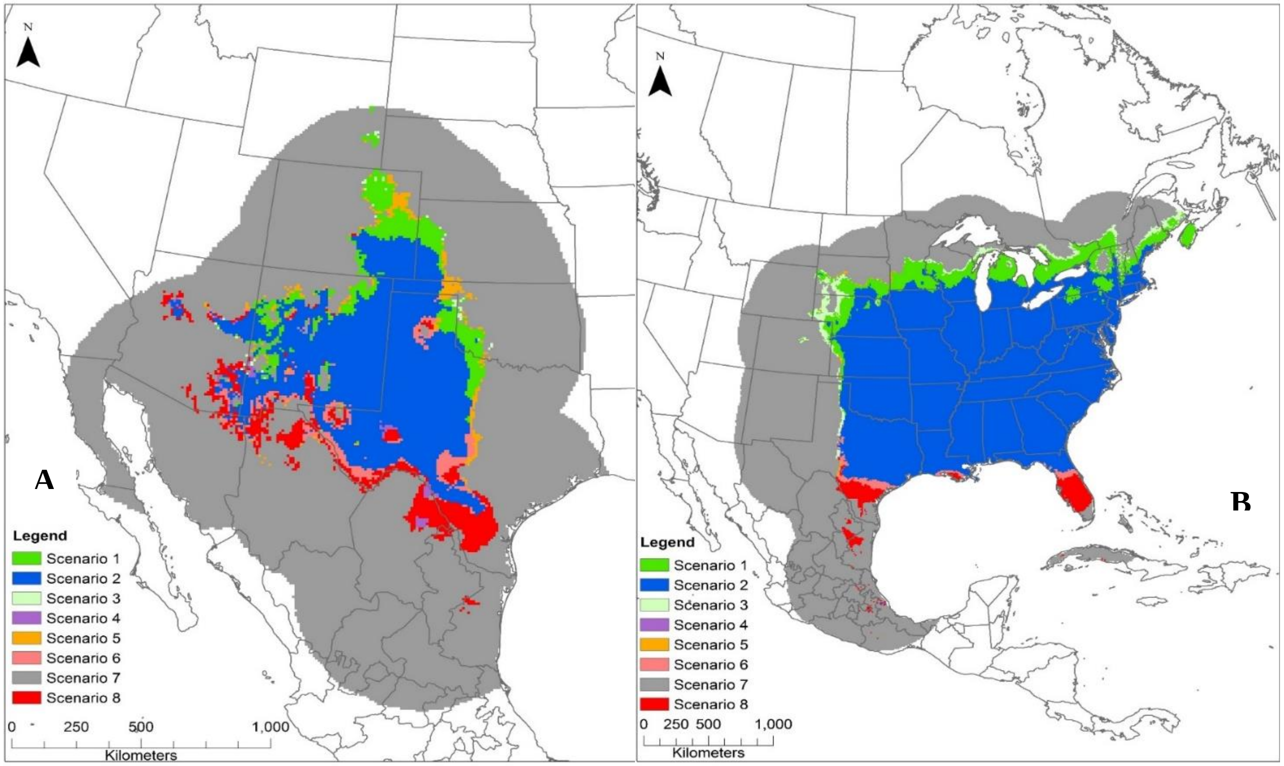
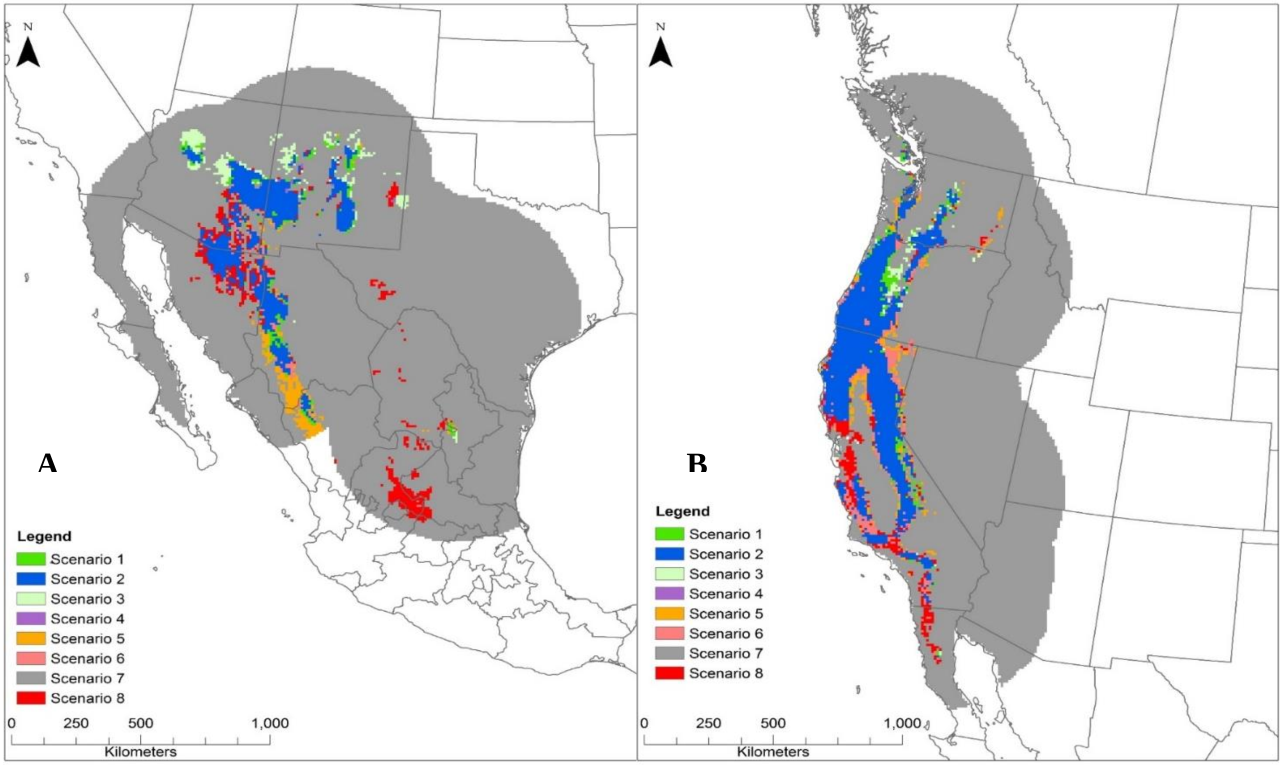
[1] Descriptions for possible distribution conditions are given in Table 2.

Figure 4. Future predicted changes[1] in distributions of scaled quail (*Callipepla squamata*; **A**) and northern bobwhite (*Colinus virginianus*; **B**) projected to 2070 and based on ensemble forecasts (as estimated through Maxent) at 90% agreement.



[1] Descriptions for possible distribution conditions are given in Table 2.

Figure 5. Future predicted changes[1] in distributions of Montezuma quail (*Cyrtonyx montezumae*; **A**) and mountain quail (*Oreortyx pictus*; **B**) projected to 2070 and based on ensemble forecasts (estimated through Maxent) at 90% agreement.



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[1] Descriptions for possible distribution conditions are given in Table 2.

CHAPTER III

ECOLOGICAL PINCH POINTS RESTRICT USABLE SPACE OF A GROUND-NESTING BIRD

ABSTRACT Habitat use has often been viewed as a means of improving fitness of individual organisms. However, these behavioral patterns have typically been considered within the context of predatory avoidance or foraging patterns. Recently a growing body of literature has identified thermal stress as a potential mechanism in determining habitat use. We sought to determine how extreme thermal conditions affect the habitat use and alter the amount of usable space for a ground-nesting shrub-obligate quail (northern bobwhite [hereafter bobwhite; *Colinus virginianus*]). We used radio-telemetry data collected from 2012-2015 to estimate usable space for bobwhite across an ambient temperature gradient (ranging from -20 °C to 38.33 °C). Occurrence data and 39 vegetation cover environmental variables (at 2 x 2 m and 30 x 30 m grains) were used to model usable space through a Maxent algorithm. Estimated usable space ranged from 18.55% to 57.13% of the landscape. However, the coldest and hottest ambient temperature categories (<15°C and >35 °C, respectively) were estimated as having the least amount of usable space (18.55% and 24.59% respectively). Range overlap analysis using ENMTools indicated that areas where birds were restricted during these times of thermal extremes were not highly similar (range overlap = 0.37) indicating that habitat under a given condition is not necessarily habitat under alternative conditions. Future

climate projections indicate that summer months may encounter a ~20% increase in the amount of time with ambient temperatures in the hottest temperature category, likely resulting in more frequent thermal “pinch points”. Our results demonstrate that habitat is often in a non-equilibrium state and that managers and ecologists should consider ecological pinch points when evaluating space use and habitat.

INTRODUCTION

Climate change is a ubiquitous pattern that affects the conservation of organisms (Walther et al. 2002, Gaston and Fuller 2008, Guisan 2014). Overall climate patterns throughout the world are expected to change (Houghton et al. 1990, Williams et al. 2007) with a continual increase in annual global temperatures predicted by climate models (IPCC 2014). Species that are unable to adapt or that exhibit strong niche conservatism face threats of declines or possible extinction (Parmesan 2006, Wiens et al. 2012).

Inter and intraspecific phenotypic differences (Chen et al. 2011, Bestion et al. 2015) may cause variability in species’ responses to climate change through different tolerance levels in thermal niches (Bestion et al. 2015). Time lag effects can also lead to high variability among species’ response to changing climate conditions, in which habitat specialists or species with high niche conservatism may respond at different rates compared to habitat generalists (Thomas 2010, Chen et al. 2011, Wiens et al. 2012).

It has been suggested that heterogeneity in topography and in biotic factors such as the structure of the plant community play a role in the stabilization of populations through increased opportunities in establishing climatic niches (Parmesan et al. 1999, Hampe and Petit 2005). However, despite thermal tolerances being a long understood ecological driver of species distributions (Begon et al. 2006), it was only recently that studies began to scale down to assess how organisms respond to fine scale patterns of thermal heterogeneity that are driven by landscape structure and heterogeneity (Hovick et al. 2014, Melin et al. 2014, Carroll et al. 2015, Marchand et al. 2015). Structural patterns in a landscape can drive ecological processes and functions (Turner 1989), and moderation of thermal conditions is an important aspect of landscape patterns that may be vital during important life history stages for organisms (Hovick et al. 2014, Carroll et al. 2015, Marchand et al. 2015). If habitat selection is to be considered a function of an organism ultimately seeking to increase their fitness (Roseberry and Klimstra 1984, Rosenzweig 1991, Block and Brennan 1993), certain extreme thermal conditions could decrease fitness levels. This would result in an organisms' available habitat being "pinched" if only small amounts of the landscape provided adequate refuge from these stressful abiotic conditions.

Within the context of landscapes moderating thermal conditions, recent research has often focused on heat as the abiotic stressor driving species' behavioral patterns. Likely, this is an artifact related to increasing risk of climate change, potential losses in reproductive opportunities (Hovick et al. 2014, Silva et al. 2015), or because events occurring during the breeding season (when extreme heat events typically occur) have been suggested as having a large influence on a species throughout the annual cycle (Pulliam and Milikan 1982). While there is obvious importance in understanding how heat events alter or constrain animal behavior, assessing the potential effects of thermal extremes on the opposite end of the spectrum (i.e., extreme cold events) or throughout the entire annual cycle may be equally as important when considering potential carryover effects that could ultimately impact the following reproducing population (Harrison et al.

2011). Further, recent discussions have argued for a better balance to be stricken with regards to seasonally-biased research, in which more attention should be given to full annual cycles (Marra et al. 2015). Thus, by studying how organisms respond to a complete gradient of abiotic variables (i.e., ambient temperature), we may better incorporate full annual cycles to determine if certain thresholds may exist across the spectrum of an environmental variable.

To better understand how available habitat may exist in a non-equilibrium state with regards to extreme thermal conditions, we studied a population of northern bobwhite (*Colinus virginianus*; hereafter "bobwhite") on the western periphery of their distribution. The bobwhite is a ground-nesting Galliforme that has generally experienced distribution-wide declines (Sauer et al. 2014) due to habitat loss and fragmentation (Hernández et al. 2013). However, along the western periphery of their distribution, habitat is often not a limiting factor and local abundance is typically driven by stochasticity in weather patterns (Lusk et al. 2001, Guthery et al. 2002, Lusk et al. 2002, Perez et al. 2002). As ground-nesting avifauna tend to be more susceptible to extreme thermal conditions (Albright et al. 2010), and studies have suggested loss of usable space (Guthery et al. 2000) and temporally variable habitat availability (Carroll et al. 2015) with regards to extreme heat events, we sought to determine if available habitat can become restricted during periods of thermal extremes across the entire ambient temperature gradient. Specifically, our objectives were to: (1) determine if space use was "pinched" at thermal extremes (i.e., habitat availability was much less during thermal extremes), (2) determine how space use varied or was similar across a temperature gradient, and (3) use climate change projections to understand the implications of thermal extremes on future potential space use for bobwhite.

METHODS

Study Area

We conducted our research on the Beaver River Wildlife Management Area (WMA), located in Beaver County, Oklahoma (lat 36°50'21.62"N, long 100°42'15.93"W), which consists of approximately 11 315 ha managed by the Oklahoma Department of Wildlife Conservation (ODWC). A majority of the WMA consists of upland rangelands and the floodplain of the Beaver River. Much of the upland areas are dominated by tivilo fine sand soils, while the floodplain is dominated by lesho silty clay loam. Dominant grasses on upland sites consist of buffalograss (*Buchloe dactyloides*), little bluestem (*Schizachyrium scopariu)*, and bromes (*Bromus* spp.; non-native). Dominant forbs on upland sites include western ragweed (*Ambrosia psilostachya*), queen's delight (*Stillingia sylvatica*), and Texas croton (*Croton texensis*). Dominant shrubs on upland sites include yucca (*Yucca glauca*), sand sagebrush (*Artemisia filifolia*), sand plum (*Prunus angustifolia*), and fragrant sumac (*Rhus aromatica*). Dominant grasses in the floodplain areas include weeping lovegrass (*Eragrostis curvala*; non-native), little bluestem, and switchgrass (*Panicum virgatum*). Dominant woody plants in the floodplain include fragrant sumac, sand plum, salt cedar (*Tamarix spp*; non-native), eastern cottonwood (*Populus deltoides*), and sugarberry (*Celtis laevigata*). Western ragweed is the dominant forb in the floodplain areas.

During the course of the study, annual precipitation was 34.44, 50.29, and 39.42 cm in 2012, 2013, and 2014 respectively, while long term (1895-2014) average annual precipitation for this region is 49.63 cm. Average summer temperatures ranged from 19.56-22.28, 25.72-27.22, and 25.32-30.06 °C during May, June, and July, respectively. The long-term regional average during this period was 25.28 °C. Average winter temperatures ranged from -0.83 to 2.61, 1.28 to 1.83, and -0.33 to 2.39 °C during December, January, and February, respectively. The long-term regional average during this period was -3.78 °C. Climate data were obtained from the Beaver Mesonet station (Brock et al. 1995, McPherson et al. 2007). However, at no time was our study area drought free (The National Drought Mitigation Center, Lincoln, Nebraska, USA).

Field Methods

Radio-telemetry

We captured bobwhite between 2012-2015 using walk-in funnel traps as described by Stoddard (1931). Necklace-style radio transmitters weighing 6 g (Advanced Telemetry Systems, Isanti, Minnesota, USA) were attached to captured individuals if they met a minimum body mass requirement of 130 g. We located radio-marked individuals a minimum of three times per week using a receiver and Yagi antenna. Locations of individuals were determined through the homing method (White and Garrot 1990) by homing within ~15 m of each bird. The distance and azimuth to the bird location was recorded and the Universal Transverse Mercator (UTM) coordinates of the observer were used to estimate the true location of the radio-marked individuals. We also recorded the time (to the nearest minute) that a bird was located. Individuals and coveys were located at different times on subsequent days to capture any variability of diurnal patterns throughout the non-breeding season, as described by Tanner et al. (2015). All trapping and handling methods complied with the protocol determined by the Oklahoma State University's Institutional Animal Care and Use Committee Permit (no. AG-11-22).

Data Analysis

Occurrence Data

We used bobwhite locations obtained from our telemetry efforts as known presence points in our space-use analysis. Telemetry collection occurred throughout the entirety of our study, resulting in an inherently large amount of presence locations for our analysis (i.e., >18,000 locations). For many research questions, a concern when incorporating such a large sample size in a presence-only modeling framework is that there is an increased possibility of over-estimation of usable space (Elith et al. 2011, Boria et al. 2014). However, because our research objectives were to determine if birds were restricted to condensed areas during potential periods of environmental stress, we did not spatially filter our occurrence locations as this would have potentially eliminated any such relationship. Only identical occurrence locations (i.e., same coordinates for individuals occurring in a covey) were removed in our dataset to eliminate any spatial autocorrelation associated with covey associations (Janke and Gates 2013, Brooke et al. 2015). We also eliminated any locations that occurred outside of the WMA so that no occurrence locations occurred outside the extent of environmental data included in our analysis (discussed below).

Bird locations were split into categories representing varying ranges of temperatures. Temperature (°C) values were obtained from the nearest Mesonet weather station (~2 km from nearest WMA boundary; Brock et al. 1995, McPherson et al. 2007) and were recorded every five minutes. All bird locations were matched with weather data corresponding to the nearest minute. Temperature categories were arbitrarily split by every 5°C. This resulted in a range of temperatures from -20°C to 38.33 °C. Our highest and lowest temperature categories were represented with the least amount of observations (Table 1). However, these samples sizes are within the range of necessary observations needed to provide useful Maxent models (Hernandez et al. 2006, Wisz et al. 2008).

Environmental Data

To quantify vegetation cover on our study site, we used an unsupervised max combined vegetation classification method from 2 meter resolution satellite imagery using ArcMap 10.1 (ESRI, Redlands, California, USA). Satellite imagery was collected in July 2013 when cloud cover was minimized. This method resulted in 65 different classes which were reclassified into 10 ecologically meaningful cover types based on field observations and 214 ground-truthed points. The primary cover types that comprised both units were: mixed shrub (consisting of sand plum [*Prunus angustifolia*], fragrant sumac [*Rhus aromatic*], sand sagebrush (*Artemisia filifolia*), mixed grass (little bluestem [*Schizachyrium scopariu*], switchgrass [*Panicum virgatum*], bromes [*Bromus* spp.; non-native]), short-grass/yucca (*Yucca glauca*), sparse vegetation/exposed soil, bare ground, salt cedar (*Tamarix spp.*; non-native), open water, developed housing, and crop (primarily winter wheat [*Triticum aestivum*]).

We used Fragstats 4.2.1.603 (McGarigal et al. 2012) to incorporate class and landscape metrics based on our vegetation classification into our assessment of bobwhite space use. To eliminate redundancy and narrow our selection of variables included in our analysis, we used results from Ritters et al. (1995) to help with our initial variable selection (Fuhlendorf et al. 2002). Furthermore, because we included two different grain sizes (2 m and 30 m) in our analysis, we also limited Fragstats variable selection to those variables least affected by changes in spatial resolution as indicated by results from Lustig et al. (2015). We chose these two grain sizes based on two criteria: 2 m resolution was used as it was the finest resolution data available for our study site; 30 m resolution was used to represent the resolution size of open-source data available to researchers (i.e., Landsat imagery). Finally, if there was a biologically meaningful reason to include a Fragstats variable within the analysis, these specific variables were also included. For instance, we included the contagion index in our initial suite of variables (which is a measure of interspersion and dispersion of a landscape) which has been shown to be a useful predictor of bobwhite presence (Roseberry and Sudkamp 1998). A list of variables initially included in our analysis are listed in Table 2. To account for collinearity of variables within our models, we estimated a Pearson’s correlation coefficient for all combinations of variables and used a threshold of $|r| \geq 0.70$ to eliminate highly correlated variables (Dormann et al. 2013). Finally, we eliminated variables that had $\leq 5\%$ contribution to accuracy gain (Sahlean et al. 2014) of preliminary models that we ran for each weather category to further increase the robustness of our space-use models.

Beyond the Fragstats metrics, we also included the categorical vegetation cover variable and the 2013 normalized difference vegetation index (NDVI) in our analysis. We calculated the NDVI using the equation ($NDVI = \frac{NIR-VIS}{NIR+VIS}$) in which VIS represents the spectral reflectance in the visible region and NIR represents the spectral reflectance in the near-infrared region. All environmental variables were clipped to the extent of the study area boundary to maintain consistency throughout our analysis and because we were not interested in projecting a species distribution model (SDM) to other regions.

To incorporate the 2 m and 30 m grain sizes, we used the Block Statistics and Resample tools in ArcGIS 10.2 (ESRI 2011). A majority rule was used to scale up our 2 m vegetation raster to a 30 m raster. Both 2 m and 30 m resolution layers were used as the base layers for all subsequent Fragstats analysis. We reclassified all “no data” cells for Fragstats layers within the extent of our study area to 0 before incorporating them into our modeling procedures (Foley et al. 2008).

Maximum Entropy Modeling

A maximum entropy algorithm, Maxent version 3.3.3 (Phillips and Dudik 2008), was used to model bobwhite space use in relation to our environmental variables at both grain sizes. Though this algorithm has been traditionally used for species distribution modelling and large geographic scales (Elith et al. 2011), Maxent is considered similar to a generalized linear model (Renner and Warton 2013) and can be used to estimate space use or habitat selection at smaller extents using presence-only data. This tool has been shown to have higher predictive power than other similar modeling techniques (Wisz et al. 2008, Elith et al. 2011) by minimizing the entropy between the probability of presence data and “background” data (locations without presence information; i.e., telemetry locations). Presence information used in our modeling approach was seperated into the 5 °C categories (12 total categories), resulting in 12 separate Maxent models with idiosyncratic environmental variables used for each model run.

We used the default options of the analysis parameters for our Maxent modeling (Phillips and Dudik 2008). This included the use of 10,000 background points, which has been shown to perform similarly when compared to models using all potential background points (Phillips and Dudik 2008). We used a regularization multiplier of 1, performed 500 iterations per model, and used a convergence threshold of 0.00001 for each model. To test the validity of our models, we used a boostrap method with 100 replicates (Araújo et al. 2014), in which 25% of our data was held-out for testing through random selection and 75% of our data was used for training our models (Bahn and McGills 2012, Sahlean et al. 2014, Sohl 2014). We used 10 percentile training presence as the threshold method to convert the continuous occurrence probability estimates into binary, presence-absence maps (Sahlean et al. 2014).

Model complexity and variable selection can affect Maxent performance during the model building process (Warren and Seifert 2011). Indeed, model complexity was a concern when incorporating Fragstats metrics and vegetation variables into our Maxent modeling approach, as the number of variables that could be included can easily exceed 100 unique variables (Lustig et al. 2015). There may have inevitably been variables that could have contributed better to our models. However, we used previous published literature and detailed knowledge of bobwhite ecology to help narrow the breadth of variables to decrease our model complexity.

To evaluate our model results, we assessed the average Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) and the average omission error which was calculated using test occurrence data and the binary occurrence maps. The AUC value can range from 0-1, and indicates the probability of a presence point having a higher AUC value than a random background point. This means that a value of 1 indicates a completely accurate prediction, whereas a value of 0.5 indicates no difference in the presence and the background point, and values <0.5 indicate predictions that perform worse than a null model (Phillips et al. 2006).

Post-hoc Analysis

To determine similarities between predicted areas of space-use across temperature gradients, we used ENMTools v1.4.4 (Warren et al. 2010) to calculate range overlap between temperature categories using an overall average logistic threshold value to determine binary "presence-absence" categories. We compared overlap between the two thermal extreme categories (35°C to 40°C; -20°C to -15°C), the temperature category predicting the highest amount of space use, and the category containing the freezing point of water (0°C to 5°C), as bobwhite have been shown to behaviorally respond to freezing weather events to increase fitness levels (Janke et al. 2015). The values of this metric range from 0 (no overlap) to 1 (complete overlap).

Finally, we incorporated future climate change projections to evaluate the difference in the percentage of time occurring within each temperature category during the course of our study (current) versus 2050 and 2080. We used ensemble model predictions from high, medium, and low emission scenarios (A2, A1B, and B1 scenarios, respectively) using data provided by ClimateWizard (www.climatewizard.org). Future climate projections were based on downscaling methods as described by Maurer et al. (2007) and indicated projected changes in temperatures to future decades (2040-2069 and 2070-2099) compared to baseline climate data (1951-2006). All future climate data was approximately 12 km resolution and values for the WMA were obtained by selecting the cell within the very center of our WMA shapefile. Models were obtained for each month to capture potential variability in ensemble models across months.

RESULTS

During the course of our study, we captured a total of 958 bobwhite (477 males, 470 females, and 11 unknown; 496 adults and 462 juveniles), of which 700 received a radio-transmitter based on minimum weight requirements. After censoring location data to remove brooding and nesting locations, as well as locations beyond the boundary of our WMA, we recorded a total of 16,467 unique bobwhite locations across years and seasons for use in subsequent analysis. However, since the "remove duplicate presence records" option was used during our Maxent analysis, not all locations were retained for our modeling procedure. Table 2 indicates the sample sizes of occurrence data used for each Maxent analysis.

After examining the results of correlation analysis and after removing variables that contributed ≤5% to our Maxent models we retained 15 and 21 variables for the 2 m and 30 m analysis respectively of the original 39 variables. A complete list of variables used for each model run and the average variable contribution are listed in supplementary material (Tables S3 and S4).

We found that usable space significantly decreased during periods of extreme heat and cold events when compared to intermediate temperatures. Although this trend was shown across both the 30 m and 2 m grain sizes, the magnitude of this relationship was strongest when using 30 m resolution data. The overall trend generally indicated a bimodal relationship of usable space across temperature gradients at the 30 m grain (Figure 1) and a multimodal relationship with the 2 m grain (Figure 2). Across both grains, the least amount of usable space available was during the coldest temperature category (18.55% and 29.41%; 30 m and 2 m grains, respectively). The maximum amount of usable space was estimated within the 15-20 °C temperature category, with a total of 57.13% and 52.60% of the landscape predicted as suitable using 30 m and 2 m resolution data, respectively (Tables 3 and 4). Though the two temperature extreme categories had the highest AUC values, these two categories also had the highest test omission values (Table 3). Overall, all AUC values indicated useful model predictions across temperature categories (AUC >0.70; Swets 1988), while test omission values also indicated good performance for most models (test omission <0.20; Tables 3 and 4). Only the -20 to -15 °C, 30 to 35 °C, and >35 °C temperature categories had test omission >0.20.

Figure 3 (A-D) illustrates discrete suitable-unsuitable rasters of estimated usable space for bobwhite across four temperature categories (-20 to -15 °C, 0 to 5 °C, 15 to 20 °C, and >35 °C). Larger proportions of usable space are estimated at intermediate temperature categories (0 to 5 °C and 15 to 20 °C) when compared to thermal extreme categories. These figures correspond to the average amount of usable space indicated in Table 3 across 100 Maxent replications. Using the discrete rasters illustrated in Figure 3, we determined the amount of range overlap for each pairwise comparison of these temperature categories (Table 5). The average logistic threshold across these four temperature categories was used to determine the suitability threshold for bobwhite presence ($\bar{x}$ = 0.299). Range overlap values at a 30 m resolution between our hottest and coldest temperature categories indicate that the overlap of space usable to bobwhite during these temperatures events is not highly comparable (0.37; Figure 4A). This trend was similar when analyzed at the 2 m resolution (range overlap = 0.36). However, the hottest temperature category (>35 °C) and the coldest temperature category (<15 °C) both overlapped considerably with the intermediate temperature categories (0.76 to 0.88; Figure 4B).

Figures 4 and 5 indicate potential shifts in the percent of time per month occurring within each temperature category, compared between actual observed values during our study (solid line) and future ensemble climate model predictions (dashed line). Data in Figure 5 only illustrates future climate data from the 2080 A2 (high emissions) model for simplicity. Data indicating potential changes across the remaining five scenarios (2050 A2, A1B, B1; 2080 A1B and B1) are presented in the supplementary material (Tables S5 through S16). Overall trends show a distinct shift in the frequency of time occurring in each temperature category (i.e., a shift to hotter temperature categories). However, an increase in the percent of time occurring within our hottest temperature category (>35 °C) is evident beginning in May and continuing through October. The future predicted percent of time occurring during the coldest temperature category (<15 °C) does not reflect any major increases when compared to the hottest temperature category, as would be expected with climate change trends.

DISCUSSION

Extreme temperature events can negatively affect fitness levels which can affect habitat selection of terrestrial vertebrates (Rosenzweig 1991). Our data suggests that bobwhite begin to be “pinched” into smaller areas of usable space when extreme temperature events occur. Usable space was most limited during extreme periods of cold, however similar patterns of space loss occured during extreme heat events. Taking into account potential changes in temperature patterns due to climate change, the implications of space loss related to extreme heat events will likely be more important than space loss related to cold events, at least within the southern Great Plains. Furthermore, range overlap analysis suggests that there is dissimilarity between usable space during periods of extreme heat versus extreme cold. This indicates that bobwhite require heterogeneity of vegetation types and vegetation structure to help alleviate potential stress from environmental conditions across an entire gradient.

Progress in research continues to illustrate the importance of landscape patterns on the process of habitat selection in response to changes in the thermal environmental (Sears et al. 2012, Hovick et al. 2014, Mellin et al. 2014, Carroll et al. 2015). Landscape patterns that include heterogeneity of vegetation, topography, and/or geology (Chen et al. 1999, Sears et al. 2012) can alter the thermal environment and create microclimates (Begon et al. 2006) that allow individuals to thermoregulate (Kearney et al. 2009, Sears et al. 2012, Briscoe et al. 2014). The distribution of thermal refugia available to organisms during times of thermal stress influences their activity patterns and ability to behaviorally thermoregulate (Huey and Slatkin 1976, Sears et al. 2012). Our data suggests that, based on observed bobwhite space-use, the distribution of these refuge areas may be more limiting during extreme temperature events, as suitable space was predicted to significantly decrease during times of extreme heat and cold (Figure 3A and D; Table 3). This suggests that available habitat is in a non-equilibrium state for bobwhite, and that useable space is variable depending on environmental conditions.

During periods of extreme heat, ground-nesting avifauna have been shown to be more susceptible to stress compared to other avifauna (Albright et al. 2010) and are known to behaviorally moderate thermal conditions that they experience during different life history stages (Hovick et al. 2014, Carroll et al. 2015). This behavior has also been shown to occur when decoupled from the potential influence of predation risk (Hiller and Guthery 2005). Furthermore, ground-foraging avifauna have been shown to alter their use of habitat in response to extreme heat events, and in fact may begin to select space that are typically avoided when they were not thermally stressed (Martin et al. 2015). Such behavioral responses to extreme heat conditions can result in space loss for individuals (Forrester et al. 1998, Guthery et al. 2005).

For extreme cold events, avifauna may have behavioral or physiological traits that help with thermoregulation and fitness (Swanson 2010, Carr and Lima 2014) which could result in variable space use during these temperature events as a result of species' specific traits (Lima 1990, Carrascal et al. 2001). Details on how ground-nesting avifauna respond to discrete events of extreme cold temperatures is lacking and offers an opportunity for future research. However, Janke et al. (2015) recently described how bobwhite increase selection of woody cover during snow events to increase their over-winter survival. Typically the selection of vegetation during the non-breeding season has been viewed through the lens of trade-offs between predation risk and foraging opportunities (Grubb and Greenwald 1982, Caraco et al. 1990, McNamara et al. 1994, Watson et al. 2007). We argue that the process of fine-scale selection of micro-climates to improve individual fitness during extreme cold events must be considered beyond the scope of predator avoidance for ground-nesting and ground-foraging birds. Although the predicted general increase in future temperatures throughout much of the Great Plains has possibly resulted in a major focus of hot thermal constraints on organisms, our data suggests that cold thermal constraints may also restrict space and warrants further investigation.

Disparity in the range overlap value between our hottest and coldest temperature categories (0.37) helps emphasize the importance of heterogeneity in vegetation structure and arrangement to facilitate tolerance of extreme thermal events. Furthermore, the greater range overlap values of the intermediate temperature categories (range: 0.76-0.88) indicate that these areas potentially act as “thermally neutral” areas when birds are not thermally stressed. However, our data suggest that when bobwhite are thermally stressed, space use is restricted at both ends of the temperature spectrum, though restricted in uniquely different ways. This illustrates that managers and researchers should not view cover as a stable or stagnant component of habitat. Instead, management of cover should account for spatiotemporal variation in behavioral patterns across an organism’s annual cycle. Moreover, an increased emphasis on managing cover for thermal refugia should be considered within the context of both weather variability and climate change, as temperatures within and beyond the hottest thermal category are predicted to become more common within the Great Plains in future decades.

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Table 1. List of variables used in Maxent analysis for northern bobwhite (*Colinus virginianus*) locations during 2012-2015 at Beaver River WMA, Beaver County, Oklahoma, USA.

Metric	Fragstats category (C/L)	Description	Number of variables
Area CV (vegetation type)	C	Coeffecient of variation in vegetation type patch sizes	6
Area Mean (vegetation type)	C	Mean area of vegetation type patches (m^2)	6
Edge density (vegetation type)	C	Total length (meters [m]) of vegetation type edge (m) divided by total area (m^2) multiplied by 10,000	6
Perimeter-area fractal dimension of vegetation type patch	C	Shape complexity across all patches of a vegetation type. Range $1 \leq x \leq 2$.	6
Shape mean (vegetation type)	C	Mean of shape index (complexity of patch shape compared to a square) of a vegetation type across all patches	6
Area CV	L	Coeffecient of variation of patch area across all classes	1
Area Mean	L	Mean area of all patches across all classes (m^2)	1
Contagion index	L	Measure of patch-type interspersion and overall patch dispersion (1 = no interspersion, 0 - max interspersion)	1
Edge density	L	Total length (m) of edge in the landscape divided by the total area of the landscape (m^2) multiplied by 10,000	1
Perimeter-area fractal dimension	L	Identical to class metric except includes all patches across vegetation types	1
Patch richness	L	Number of different patches within the landscape	1
Shape mean	L	Mean of shape index (complexity of patch shape compared to a square) across all patches	1
2013 normalized difference vegetation index	N/A	$NDVI = \frac{NIR - VIS}{NIR + VIS}$	1
Vegetation type	N/A	Categorical variable of vegetation types	1

[1] C indicates a class variable and L indicates a landscape variable.

Table 2. Number of training and testing locations used for Maxent analysis of northern bobwhite (*Colinus virginianus*) space use across 12 temperature categories from 2012-2015 at Beaver River WMA, Beaver County, Oklahoma, USA.

Temperature category (°C)	Training locations (*n*)	Test locations (*n*)	Training locations (*n*)	Test locations (*n*)
	30 m resolution		2 m resolution	
>35	35	5	35	5
30 to 35	109	36	135	15
25 to 30	612	204	803	90
20 to 25	1356	452	1854	206
15 to 20	1513	504	2097	234
10 to 15	1004	334	1345	150
5 to 10	728	242	947	106
0 to 5	626	208	803	90
-5 to 0	512	57	531	60
-10 to -5	373	42	389	44
-15 to -10	90	11	93	11
-20 to -15	33	5	33	5

Table 3. Predicted percent usable area[1] for northern bobwhite (*Colinus virginianus*), suitable area standard errors (S.E.), lower and upper confidence intervals (L.C.I. and U.C.I.), and model performance metrics as determined through Maxent on northern bobwhite observations located from 2012-2015 at Beaver River WMA, Beaver County, Oklahoma, USA. Environmental data used in analysis was 30 m.

Temperature category (°C)	Suitable Area (%)	Suitable Area S.E.	Suitable Area L.C.I.	Suitable Area U.C.I.	Test A.U.C.	Average test omission
>35	24.59	0.008	0.23	0.26	0.84	0.25
30 to 35	35.59	0.006	0.34	0.37	0.81	0.19
25 to 30	49.18	0.003	0.49	0.50	0.77	0.13
20 to 25	54.75	0.002	0.54	0.55	0.75	0.11
15 to 20	57.13	0.002	0.57	0.57	0.73	0.11
10 to 15	54.51	0.002	0.54	0.55	0.74	0.12
5 to 10	52.59	0.002	0.52	0.53	0.76	0.11
0 to 5	44.28	0.002	0.44	0.45	0.79	0.14
-5 to 0	38.07	0.003	0.38	0.39	0.81	0.16
-10 to -5	38.56	0.003	0.38	0.39	0.81	0.15
-15 to -10	44.17	0.005	0.43	0.45	0.76	0.17
-20 to -15	18.55	0.007	0.17	0.20	0.84	0.29

[1] Discrete suitable areas were determined based on logistic thresholds using the 10% training presence threshold rule.

[2] Area under the curve of the receiver operating characteristic.

Table 4. Predicted percent usable area[1] for northern bobwhite (*Colinus virginianus*), suitable area standard errors (S.E.), lower and upper confidence intervals (L.C.I. and U.C.I.), and model performance metrics as determined through Maxent on bobwhite observations located from 2012-2015 at Beaver River WMA, Beaver County, Oklahoma, USA. Environmental data used in analysis was 2 m.

Temperature category (°C)	Suitable Area (%)	Suitable Area S.E.	Suitable Area L.C.I.	Suitable Area U.C.I.	Test A.U.C.	Average test omission
>35	30.27	0.010	30.25	30.29	0.84	0.19
30 to 35	35.66	0.006	35.65	35.67	0.80	0.20
25 to 30	42.10	0.002	42.10	42.10	0.80	0.14
20 to 25	51.04	0.002	51.04	51.04	0.77	0.11
15 to 20	52.60	0.001	52.60	52.60	0.75	0.11
10 to 15	50.74	0.002	50.73	50.74	0.76	0.12
5 to 10	43.55	0.002	43.55	43.56	0.77	0.15
0 to 5	49.10	0.002	49.09	49.10	0.76	0.13
-5 to 0	38.57	0.003	38.57	38.57	0.81	0.15
-10 to -5	37.65	0.003	37.64	37.66	0.81	0.17
-15 to -10	51.13	0.007	51.12	51.15	0.77	0.13
-20 to -15	29.41	0.012	29.39	29.43	0.82	0.23

Table 5. Range overlap[1] of discrete usable space for northern bobwhite (*Colinus virginianus*) compared between four temperature categories (°C) during 2012-2015 at Beaver River WMA, Beaver County, Oklahoma, USA. Discrete presence rasters were obtained from Maxent (v3.3.3) using 30 m resolution environmental data. Range overlap was estimated through ENMTools v1.4.4.

Temperature Category (°C)	>35	15 to 20	0 to 5	-20 to -15
>35	1.00	0.87	0.76	0.37
15 to 20	0.87	1.00	0.88	0.86
0 to 5	0.76	0.88	1.00	0.88
-20 to -15	0.37	0.86	0.88	1.00

[1] Range overlap values are estimated from 0 to 1 in which 0 represents no overlap and 1 represents complete range overlap.

Figure 1. Percent usable space (+/- 1 standard deviation) for northern bobwhite (*Colinus virginianus*) across a temperature gradient (°C) as determined through Maxent. Observations were collected during 2012-2015 at Beaver River WMA, Beaver County, OK, USA. Environmental data was analyzed at 30 m resolution.

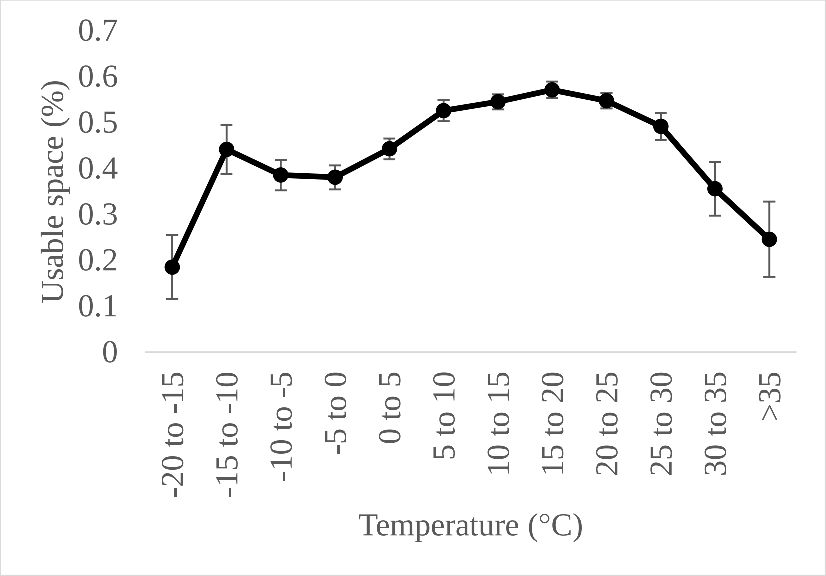


Figure 2. Percent usable space (+/- 1 standard deviation) for northern bobwhite (*Colinus virginianus*) across a temperature gradient (°C) as determined through Maxent. Observations were collected during 2012-2015 at Beaver River WMA, Beaver County, OK, USA. Environmental data was analyzed at 2 m resolution.

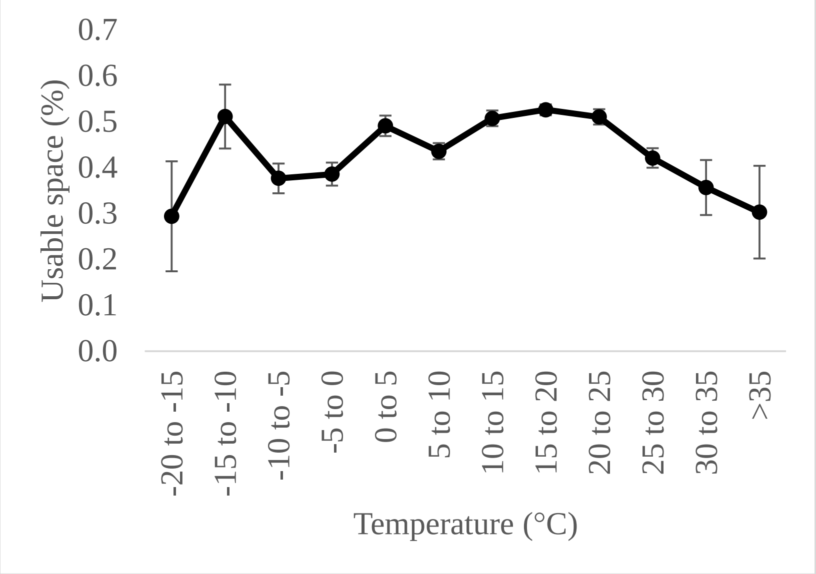


Figure 3. Illustration of usable space for northern bobwhite (*Colinus virginianus*) as predicted through a Maxent algorithm at four temperature (°C) categories: >35 (A), 15 to 20 (B), 0 to 5 (C), and -20 to -15 (D). Observations were collected from 2012-2015 at Beaver River WMA, Beaver County, OK, USA. Data was analyzed using 30 m resolution environmental data.

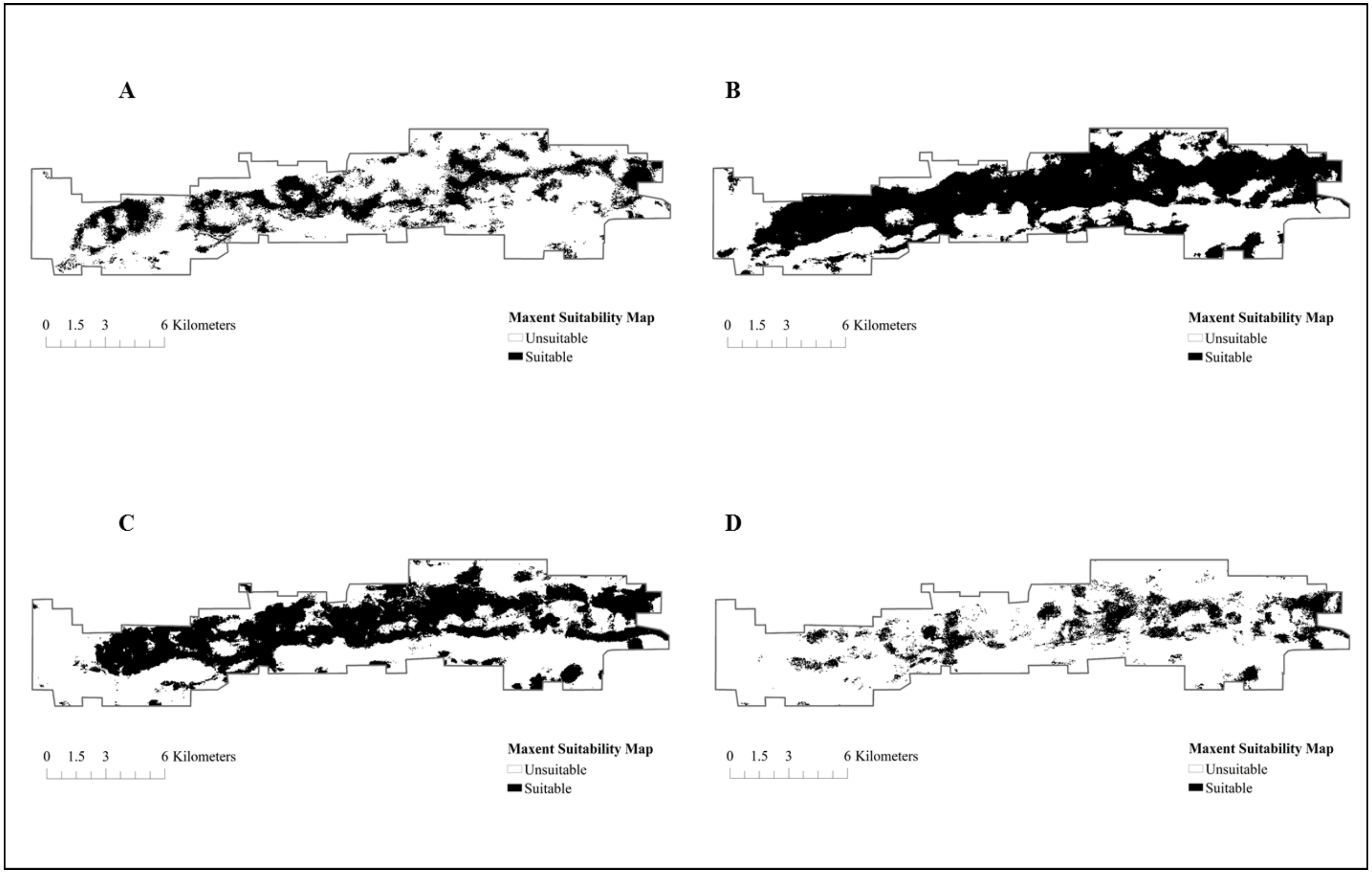


Figure 4. Disparity in usable space for northern bobwhite (*Colinus virginianus*) across high (>35 °C) and low (<15 °C) temperature categories as predicted through a Maxent algorithm (A). Inset B indicates the disparity between these two temperatures categories along with an intermediate temperature category (0 to 5 °C and 15 to 20 °C combined), which is outlined with a solid black line. Observations were collected from 2012-2015 at Beaver River WMA, Beaver County, OK, USA. Data was analyzed using 30 m resolution environmental data.

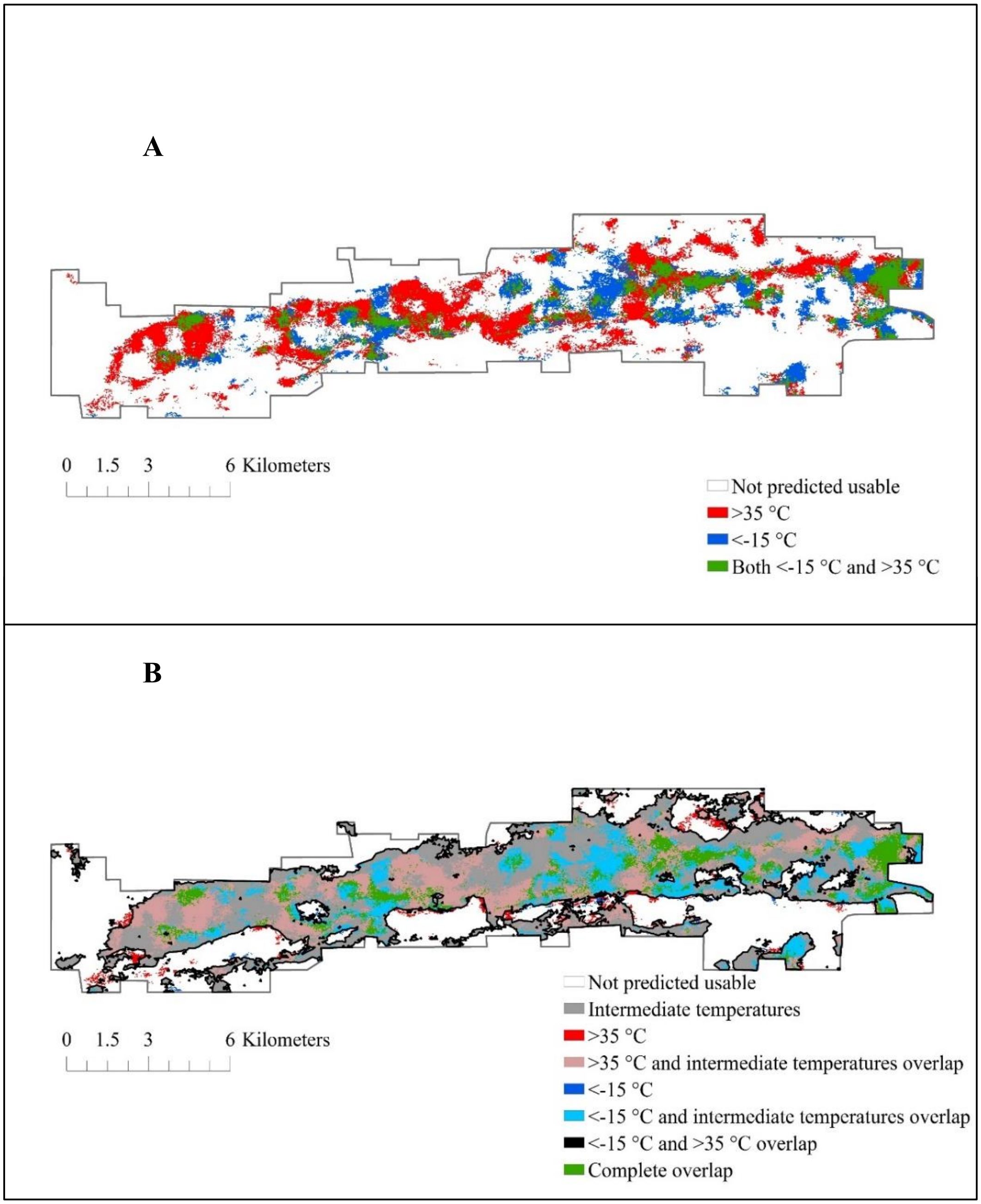
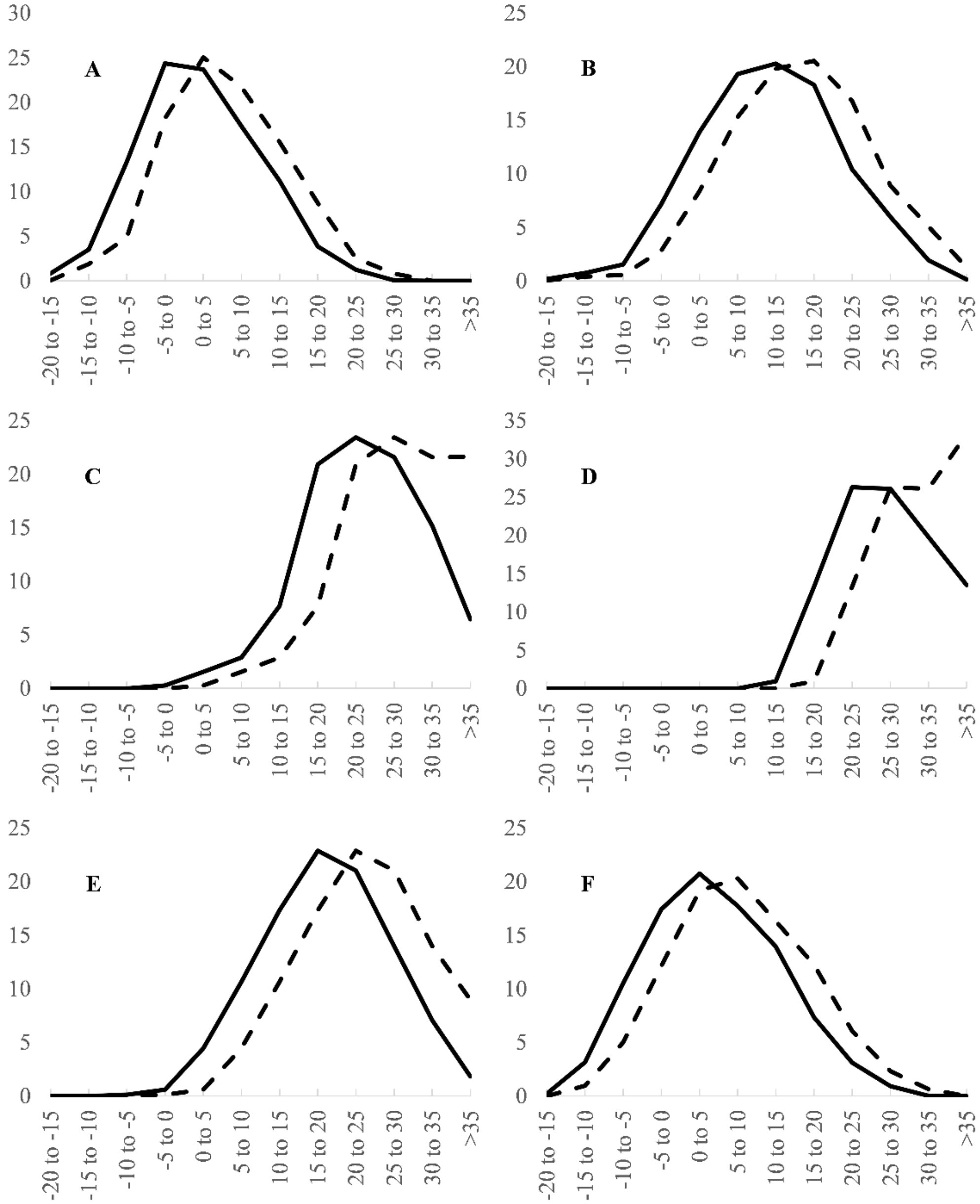


Figure 5. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 (black line) compared to future climate conditions (dashed line) at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high emission scenario (A2) and projected to the year 2080. Data is presented for: Jan-Feb (A), Mar-Apr (B), May-Jun (C), Jul-Aug (D), Sep-Oct (E), and Nov-Dec (F).



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[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

CHAPTER IV

DOES THE PRESENCE OF ANTHROPOGENIC FEATURES POTENTIALLY INCREASE RISK OF HARVEST IN NORTHERN BOBWHITE?

ABSTRACT As anthropogenic development and disturbance continues to grow throughout North America, it has become increasingly important to understand how organisms may respond to this disturbance. Beyond organisms experiencing direct impacts from the presence of anthropogenic features (mortality), interactive relationships may exacerbate the effects of anthropogenic disturbance within the context of these features. For example, hunting pressure may be positively influenced by the infrastructure paired with energy development by facilitating easier access via road and energy pad networks. To assess these relationships, we conducted research on northern bobwhite (*Colinus virginianus*; hereafter bobwhite) across a hunted and non-hunted area of Beaver River Wildlife Management Area, Oklahoma, using radio-telemetry from 2012-2015. We found that bobwhite mortality risk increased as the distance from primary roads (m) decreased across weeks (hazard ratio [HR] = 1.007, P = <0.001) yet this relationship was detected in both hunted and non-hunted units. Additionally, mortality risk was greater for juveniles (HR = 1.39, P = 0.04). Bobwhite on the hunted unit avoided exposed soil/sparse vegetation more than bobwhite on the non-hunted unit ($\overline{\beta}$ = -0.01, CI = -0.02 to -0.0001), however this was a weak relationship. Based on our results, bobwhite

did not alter their space use or movement patterns in response to anthropogenic features or hunting but did have differential survival associated with primary roads.

INTRODUCTION

The effects of human activity on ecosystems has been so prominent that the late 18th century marked the beginning of what is known as the Anthropocene (Crutzen 2002, Ellis 2011). During recent decades, empirical evidence indicates that conservation of biodiversity is falling short for many ecosystems (Butchart et al. 2010, Kareiva et al. 2011). Sih et al. (2011) synthesized five major types of human-related impacts affecting such natural systems: habitat loss, exotic species, harvesting, pollutants, and climate change. As a result of these impacts, researchers have focused on monitoring and describing potential effects of these human impacts on wildlife populations worldwide.

Specifically, habitat loss has been suggested as the primary contributor to biodiversity loss in North America (Pimm and Raven 2000). Increases in energy development (Kuvlesky et al. 2007, Gilbert and Chalfoun 2011) and long-term impacts of agricultural development (Barnes 1993, Manning 1995) are significant changes that have left the North American prairie the most altered biome in North America (Samson and Knopf 1994, Askins et al. 2007). Such extensive losses of these native ecosystems have resulted in extensive declines in avian guilds (Sauer et al. 2014).

Although energy development and its related infrastructure has existed in much of North America within the context of recent history (Braun et al. 2002), technological advances and increased demand in local and global markets may lead to wildlife coping with unprecedented levels of this development (Arnett et al. 2007, Johnson and Lefebrve 2013). Potential effects of energy development on wildlife are complex and extensive, and could be related to increases in noise and light pollution (Barber et al. 2010, Blickley et al. 2012, Shannon et al. 2015, Swaddle et al. 2015), direct mortality from collisions (Kunz et al. 2007, Reese and Connelly 2011, Loss et al. 2013), and behavioral changes from activity and habitat fragmentation (Slater and Smith 2010, Winder et al. 2013, Hovick et al. 2014, Ludlow et al. 2015, Mutter et al. 2015).

With regard to energy development impacts on prairie species, particular attention has been given to resident ground nesting birds (i.e., Galliformes) as their life history strategies could make them more vulnerable to human development when compared to migratory species (Storch 2007, Hovick et al. 2014). With regards to grouse species, oil and gas structures have been shown to have the largest impact on behavioral responses, while roads associated with these structures were also shown to influence grouse behavior (Pitman et al. 2005, Hagen et al. 2011, Blickley, et al. 2012). Furthermore, wind energy development has been shown to alter behavioral patterns and nesting/brooding success of prairie grouse species (Winder et al. 2013, Lebeau et al. 2014). Most other Galliformes have received little attention with regards to responses to anthropogenic development. A notable exception, Dunkin et al. (2009) reported that northern bobwhite (*Colinus virginianus*; hereafter: bobwhite) tended to avoid fences and be attracted to roads, while exhibiting no behavioral response to oil and power line structures.

Northrup and Wittemyer (2013) characterized the observed and potential impacts of energy development on wildlife species, identifying the importance of understanding confounding factors that can lead to wildlife impacts when increased development occurs. More specifically, they listed increased hunting pressure and increased illegal hunting as identified and potential impacts, respectively, of oil/gas development on wildlife populations. Though increased hunting pressure was listed as an identified impact, it was ranked the lowest in frequency of occurrence among research to date. The interaction between anthropogenic development and hunting pressure could also exacerbate impacts on wildlife if game species are attracted to roads or linear features (Dunkin et al. 2009) or if development is focused on wildlife management areas (WMAs) where public hunting is focused. For instance, the infrastructure that comes with energy development on public hunting lands (roads, well pads, etc.) could increase access for hunters which in turn may increase the potential for harvest-induced mortality. Though harvest may be partially compensatory at times (Burnham et al. 1984), increases in harvest rates eventually can cause harvest-induced mortality to become additive rather than compensatory (Sandercock et al. 2011, Péron 2013). Thus, anthropogenic development on public lands such as WMAs could have unintended negative consequences related to hunting that may ultimately affect population levels.

In this study, we sought to determine if anthropogenic structures and associated infrastructure affected non-breeding season ecology of bobwhite on hunted and non-hunted areas. By incorporating data from both hunted and non-hunted areas, we hoped to determine if there were confounding effects between hunting impacts and anthropogenic development. Our objectives were to: 1) determine if weekly mortality risks differed between hunted and non-hunted bobwhite in relation to anthropogenic features across the non-breeding season, 2) determine if bobwhite space use was influenced by anthropogenic features and/or hunting, and 3) determine if bobwhite covey movement was influenced by hunting.

METHODS

Study Area

We conducted our research at the Beaver River Wildlife Management Area (WMA) which is located in Beaver County, OK (lat 36°50'21.62"N, long 100°42'15.93"W). The total area of the WMA is approximately 11,315 ha, however for our research, the WMA was split into two separate units (Beaver River unit 6823.94 ha; McFarland Unit 4501.26 ha). Both units primarily consists of upland areas dominated by tivilo fine sand soils and a floodplain dominated by lesho silty clay loam.

An unsupervised max combined vegetation classification method was used to develop our vegetation map from 2 meter resolution satellite imagery using ArcMap 10.1 (ESRI, Redlands, California, USA). Satellite imagery was collected in July 2013 when cloud cover was minimized. This method resulted in 65 different classes which were reclassified into 10 ecologically meaningful cover types based on field observations and 214 ground-truthed points. The primary cover types that comprised both units were: mixed shrub (consisting of sand plum [*Prunus angustifolia*], fragrant sumac [*Rhus aromatic*], sand sagebrush (*Artemisia filifolia*), mixed grass (little bluestem [*Schizachyrium scopariu*], switchgrass [*Panicum virgatum*], bromes [*Bromus* spp.; non-native]), short-grass/yucca (*Yucca glauca*), sparse vegetation/exposed soil, bare ground, salt cedar (*Tamarix spp.*; non-native), open water, developed housing, and food plots (primarily winter wheat [*Triticum aestivum*]). A more detailed description of plants found within these cover types on these sites is described in Tanner et al. (2015).

During the course of the study, annual precipitation was 34.44, 50.29, and 39.42 cm in 2012, 2013, and 2014 respectively, while long term (1895-2014) average annual precipitation for this region is 49.63 cm. Climate data were obtained from the Beaver

Mesonet station (Brock et al. 1995, McPherson et al. 2007). However, at no time were our two study units out of drought conditions (The National Drought Mitigation Center, Lincoln, Nebraska, USA).

Anthropogenic features on the WMA that were used in our analysis consisted of roads (four categories described below), buildings, and oil/gas structures. Power lines were not included as a feature as very few of these features existed within our study area and most birds were not exposed to their presence. Overall density of roads was 21.2 m/ha. Additionally, there were 6 buildings (1885.8 ha/building) and 95 oil/gas structures (119.1 ha/structure) on the WMA.

Radio-telemetry

Bobwhite were capture between 2012-2015 using walk-in funnel traps (Stoddard 1931). We attached a necklace-style radio transmitter weighing 6 g (Advanced Telemetry Systems, Isanti, Minnesota, USA) if a bird met a minimum body mass requirement of 130 g. We located radio-marked individuals a minimum of three times per week using a receiver and Yagi antenna. Locations of individuals were determined using the homing method (White and Garrot 1990). We homed in on individuals to within 15 m and recorded the distance and azimuth to the actual bird location while recording the Universal Transverse Mercator (UTM) coordinates of the observer with a Garmin GPS (Garmin International, Inc, Olathe, Kansas, USA). Individuals and coveys were located at different times on subsequent days to capture any variability of diurnal patterns throughout the non-breeding season. A detailed explanation is described in Tanner et al. (2015). All trapping and handling methods complied with the protocol determined by the

Oklahoma State University's Institutional Animal Care and Use Committee Permit (no. AG-11-22).

Andersen-Gill Models

We used Andersen-Gill (AG) models to estimate hazard rates for quail across both units (Andersen and Gill 1982) using the survival package in Program R (ver. 3.1.1, R Foundation for Statistical Computing, Vienna, Austria) due to monitoring gaps and left-truncated entry data for individuals (based on staggered entry design [Pollock et al. 1989]). This model is similar to a Cox proportional hazard model (CPHM), however it allows for time-varying covariates when estimating hazard rates (Fleming and Harrington 1991, Therneau and Grambsch 2000, Murray 2006, Fieberg and DelGiudice 2009). To estimate bobwhite hazard rates, we left-censored individuals if they entered the population after our initial time interval (Oct 1) and right-censored individuals if their fate was unknown (Johnson et al. 2004).

Our dataset consisted of 26 time intervals, which were the number of weeks during the non-breeding season (1 Oct-31 Mar). To estimate the effects of anthropogenic features on bobwhite survival, we estimated the mean weekly Euclidean distance (m) to a feature for each individual. This consisted of distance to: oil and gas well pads, buildings, and the four different road types (county road, primary WMA roads, restricted access WMA roads [truck and all-terrain vehicle {ATV} traffic], and restricted access WMA roads [ATV traffic only]). To determine if the presence of hunting affected survival in our population, we also included a categorical variable based on the unit in which an individual was located in. If an individual changed units during our study, it became a new individual in our dataset corresponding to the other management unit (hunted or non-hunted). Other categorical variables included in our analysis were age (adult or juvenile) and year (2012-2013 [year 1], 2013-2014 [year 2], and 2014-2015 [year 3]). Sex (male or female) of individuals was not included as a covariate in our survival analysis as we expected no difference in harvest rates (Shupe et al. 1990) or survival (Cox et al. 2004, Seckinger et al. 2008, Tanner et al. 2012) between sexes for the nonbreeding season. We stratified our third road category (restricted access roads [truck and ATV traffic]) values into three distance categories (<500 m, 500-1499 m, and $\geq$1500 m) as this variable did not meet the proportional hazard assumption (Fox 2002). The primary assumption of the AG model, like the CPHM, is that hazards from covariates are proportional over time (Johnson et al. 2004). To test this assumption, we plotted Schoenfeld residuals and assessed significant deviances of residual plots from 0 (Therneau et al. 1990, Fox 2002). Finally, we included a global model in our survival analysis, which included the additive effects of all variables of interest.

We used Akaike's information criterion adjusted for small sample sizes (AIC_c) to rank models relating covariates to hazard rates for quail over the non-breeding season. We considered models with a ΔAIC_c <2 plausible models and determined the most parsimonious based on model weights (w_i) and ΔAIC_c values (Burnham and Anderson 2002). We built models that we found biologically meaningful or models that specifically addressed our research questions. We considered parameters with confidence intervals overlapping 0 to be statistically uninformative to our survival analysis.

Resource Utilization Functions

We used resource utilization functions (RUFs; Marzluff et al. 2004, Millspaugh et al. 2006) to estimate the relationships between covey space use and environmental variables.

We estimated RUFs for coveys rather than individuals as space use by individuals within coveys has been shown to be non-independent (Janke and Gates 2013). We estimated 95% fixed-kernel densities (Worton 1989, Seaman et al. 1999) for coveys having ≥20 radio-telemetry location (Tanner et al. 2015) using the Geospatial Modelling Environment (GME; Spatial Ecology LLC, USA). Because we were interested in differences of space use between coveys during the hunting season, we only incorporated coveys having ≥20 (Taylor et al. 1999, Peters et al. 2015, Tanner et al. 2015) locations during the hunting season in our analysis. We did not incorporate locations in our analysis that occurred during the non-breeding season but were outside of the hunting season, as our location sample sizes would not have been large enough to estimate RUFs for these time periods. A likelihood cross-validation bandwidth estimator was used to obtain kernel density estimates (KDEs; Horne and Garton 2006).

Along with the distance-based anthropogenic feature variables included in our survival analysis, we also incorporated vegetation cover types and theoretical hunting pressure variables into our RUF analysis. As we did not have a direct measure of hunting pressure within our hunting unit over the course of the study, we incorporated hunter behavior data discussed in Richardson et al. (2008) to estimate areas of potentially high, medium, low, and no hunting pressure. The data presented by Richardson et al. (2008) incorporated vegetation cover, distance from roads (<500 m, 500-<1,500 m, 1,500-<2,500 m, and ≥2,500 m), and % slope (≤3% and >3%) data and used GPS data from hunters at Packsaddle WMA (Ellis County, Oklahoma, USA) to determine selection indices for quail hunters. They separated slope categories so that both categories contained ~50% of the WMA (Richardson 2006). We used these data to model potential hunting pressure on our study site because road density (Packsaddle WMA: 18.6 m/ha [Dunkin et al. 2009]; Beaver River WMA 21.2 m/ha) and slope ($\leq$3% slope: 50.76% of the area; >3% slope: 49.24% of the area) were similar between WMAs. We incorporated these data into a model of potential hunting pressure on our study site through the use of the weighted overlay tool in ArcGIS 10.2. Taking into consideration the selection indices of hunters provided by Richardson et al. (2008), we used vegetation cover, distance from roads, and % slope in our model, with each variable having equal weight. We assigned values (1-4) to each category within these variables, where 1 represented the highest level of theoretical hunting pressure and 4 represented the lowest. Table 1 indicates the values assigned to all categories within our variables.

We extracted values for space use and all environmental variables to points centered on every cell within each coveys home range. We then used the Ruf.fit package in Program R (ver. 3.1.1) to estimate coefficients of resource use for each variable and for every covey. All values of space use were $\log_e$-transformed to meet the linearity assumption for multiple regression models. Because the variables related to vegetation cover type and theoretical hunting pressure were categorical variables, we removed a class in each variable to serve as a reference class in our analysis (Jachowski et al. 2014). Therefore, we used the sand sagebrush cover type and the highest level of theoretical hunting pressure as the reference class for the vegetation cover and hunting pressure variables, respectively. The sand sagebrush class was used as a reference because it is the most abundant vegetation type on our study site (Jachowski et al. 2014). To directly address the question of whether bobwhite were altering their space use in relation to higher hunting pressure, we used the highest theoretical hunting pressure class as a reference class to compare bobwhite space use of other hunting pressure categories. Mean standardized β coefficients ($\bar{\beta}$) and conservative estimates of variance were calculated for each environmental variable to estimate overall population responses to these variables across the hunted and non-hunted units (Marzluf et al. 2004). Standardized coefficients with confidence intervals overlapping 0 were considered non-significant. Standardized coefficients for distance-based variables would indicate a positive relationships between space use and the variable if a negative value was estimated (i.e., space use increases with a decrease in distance from a feature). Finally, we estimated the number of individual coveys that had significant positive, negative, or non-significant relationships to our environmental variables to indicate differences among coveys.

Movement Analysis

To compare estimates of covey movement across hunted and non-hunted units, we calculated average daily movement across the non-breeding season for coveys with ≥10 locations (Brøseth and Pedersen 2010). Coveys with ≥10 locations, rather than those with ≥20 locations, were used in movement analysis because we were not estimating KDEs for this stage of our analysis. We considered average daily movement to be the Euclidean distance between a covey's locations across consecutive days (Williams et al. 2000, Brøseth and Pedersen 2010, Unger et al. 2012). Linear mixed effect models (Pinheiro and Bates 2000) were used to assess the influence of units, years, weekly time, and all possible interactions between these variables on covey movement. To meet the assumption of data normality, we used a CoxBox transformation (Box and Cox 1964) approach to determine the most appropriate transformation for our movement data. Based on this approach, we used $x^{0.101}$ to transform our data. A covey identity was included as a random effect to account for interdependence of movement data within each covey (Brøseth and Pedersen 2010). We used an AIC_c approach and used model weights (w_{i}) and a ΔAIC $\leq$2 to determine the most parsimonious model (Burnham and Anderson 2002). Finally, we used a restricted maximum likelihood (REML) approach to obtain parameter estimates for fixed effects in our models (Brøseth and Pedersen 2010) and considered any parameters with confidence intervals overlapping 0 to be non-significant in explaining average daily movement between coveys.

RESULTS

The quail hunting season began on November 10, 9, and 8 in 2012, 2013, and 2014 respectively and ended on February 15 of the following year for all three years. A total of 85, 62, and 45 bobwhite were alive and actively being monitored at the beginning of hunting season in 2012, 2013, and 2014 respectively. However, because we trapped periodically throughout the non-breeding season on both units, a total of 225, 211, and 249 bobwhite were captured and radio-collared during the 2012, 2013, and 2014 non-breeding seasons, respectively. This resulted in a total of 59, 62, and 42 unique bobwhite coveys during the 2012, 2013, and 2014 non-breeding seasons, respectively. Finally, a total of 16 and 14 unique coveys with $\geq$20 locations were located on the hunted and non-hunted units, respectively

Bobwhite survival

Based on AIC_c values, the global model was the most parsimonious model when explaining bobwhite survival in relation to anthropogenic features and disturbance during the non-breeding season (Table 2). However, of all the variables retained in this model, only three variables were considered significant within this model. These included a year effect on the year 2 season (year 2 season hazard rate [HR] = 0.60, SE = 0.22, *P* = 0.02), age (juvenile HR = 1.39, SE = 0.16, *P* = 0.04), and distance to primary WMA roads (HR = 1.0007, SE = 0.0002, *P* = 0.0009). Individuals alive during the year 2 non-breeding season were 40% less likely to experience mortality compared to birds during the year 1 non-breeding season, while only 9% less likely to experience mortality when compared to individuals alive during the year 3 non-breeding season (Figure 2A; year 3 season HR = 0.71, SE = 0.26, *P* = 0.17). Furthermore, juvenile bobwhite were 39% more likely to experience mortality compared to adults during the non-breeding season (Figure 2B) across all years. Finally, every 10 m decrease in distance from primary WMA roads was associated with a 0.07% increase in probability of mortality.

There were no differences in survival for individuals on hunted versus non-hunted units in our top model (*P* = 0.26) nor in our model selection results (Unit model ΔAIC_c = 4.83). Furthermore, based on our hazard rate curves, there is no indication that once the hunting season started, hazard rates for birds increased significantly (Figure 2C). However, survival did consistently decrease across weeks for both hunted and non-hunted units during the non-breeding season with ~20% of individuals surviving through the season (Figure 2C).

Covey resource selection

Across all three years, a total of 30 coveys representing 65 birds were used in estimating RUFs with locations occurring only during the quail hunting season. Salt cedar vegetation cover, low hunting pressure, and no hunting pressure variables were not contained within the KDEs for all possible coveys in our analysis, resulting in lower sample sizes for these variables as denoted in Tables 3 and 4.

Generally speaking, there was little difference in space use of hunted versus non-hunted coveys in relation to our variables of interest. Furthermore, almost all variables included in our analysis had a non-significant relationship to covey space use based on ($\overline{\beta}$) estimates with confidence intervals that overlapped 0. Of all the variables analyzed, only the exposed soil/sparse vegetation class had a significant difference between hunted and non-hunted coveys (Tables 3 and 4) when compared to use of sand sagebrush. Coveys on the hunted unit avoided this vegetation cover type significantly when compared to non-hunted coveys (($\overline{\beta}$) = -0.01, CI = -0.02 to -0.0001), however if pooled across all coveys (both hunter and non-hunted coveys), this relationship was not consistent (pooled ($\overline{\beta}$) = -0.005, CI = -0.012 to 0.002).

Covey movement

There were no differences in covey average daily movement between hunted and non-hunted units across all three seasons during our study (Table 5). Time-related variables (week and year) were the best explanatory variables included in our analysis. However, the parameter estimate for the week variable ($\beta = 0.001$, SE = <0.001) was not significantly different from 0 and thus was not considered a strong explanatory variable for covey average daily movement. When compared to year 1, only year 3 was significantly different based on parameter estimate confidence intervals ($\beta = -0.08$, SE = <0.001) indicating that average daily movement for coveys during year 3 was lower than years 1 and 2.

DISCUSSION

We found no evidence that the presence of oil/gas pads or buildings increased the risk of mortality or affected space use of bobwhite coveys regardless of hunting. However, risk of mortality increased as the distance between coveys and primary WMA roads decreased, yet this relationship was not different between hunted and non-hunted units. Furthermore, bobwhite coveys did not select areas categorized with lower theoretical hunting pressure when compared to areas with higher theoretical hunting pressure, and distance-based variables related to anthropogenic features had no significant effect on covey space use for either hunted or non-hunted units. Finally, bobwhite on the hunted unit did avoid exposed soil/sparse vegetation more than expected when compared to birds on the non-hunted unit. However, significant relationships of survival and space use to anthropogenic features and vegetation were weak overall.

Understanding the influence of anthropogenic development in landscapes is becoming increasingly important as energy development continues to increase. For some ground nesting birds there are documented negative behavioral responses to this development (Winder et al. 2013, Hovick et al. 2014). However, neutral effects of space use by bobwhite in relation to anthropogenic features has been shown in similar vegetation communities previously (Dunkin et al. 2009). Our data further support that bobwhite are not negatively responding to the presence of anthropogenic features based on space use and movement patterns. It is evident that bobwhite have some level of tolerance to anthropogenic features (Errington and Hamerstrom 1936, Rosene 1969, Dunkin et al. 2009, Unger et al. 2012, Unger et al. 2015). Yet, if usable space is a measure of an area’s potential to sustain bobwhite populations (Guthery 1997), at some density these anthropogenic features will eventually detract significant amounts of usable space (Masden et al. 2009, Pruett et al. 2009). As an example, oil and gas well development in North America ultimately results in a loss of net primary productivity, which also indicates the loss of vegetation cover in an area (Allred et al. 2015). Additive effects of this development could remove a significant amount of usable space within a finite area. It is likely that we, along with Dunkin et al. (2009), did not detect an overwhelmingly negative response of space use by bobwhite to such features because feature densities were relatively low throughout our study sites.

Beyond differences in survival between age classes and years, the average weekly distance (m) to primary WMA roads was significant in explaining non-breeding season survival during our study. The increased risk of mortality associated with these primary WMA roads could be attributed to an increase in exposure to meso-predators which often use these roads as travel corridors (Frey and Conover 2006). Other causes for this relationship may be related to increased exposure to vehicle traffic when approaching these primary roads. For instance, the presence of roads can increase mortality in greater sage-grouse (*Centrocercus urophasianus*) through risk of collision mortalities (Connelly et al 2000). However, we expect this is unlikely on our site as only 1 bird was suspected of a vehicle collision related mortality and because traffic was generally limited to researchers, hunters, and occasional commercial traffic related to energy pad maintenance. We predicted that if the presence of anthropogenic features increased the risk of harvest mortality for bobwhite, an interactive relationship would exist between these features and the unit (hunted versus non-hunted). Yet, our model including the interaction between distance to primary WMA roads and unit was not considered a plausible model (ΔAIC = 4.02). Furthermore, the singular model with only the unit variable was also a poor performing model, and no difference in survival between our hunted and non-hunted individuals was detected.

Bobwhite have been shown to be attracted to roads during both breeding and non-breeding seasons (Dunkin et al. 2009, Unger et al. 2015, Brooke et al. 2015) while quail hunters also tend to hunt in areas ≤1,500 m from roads (Richardson et al. 2008). Therefore, if hunting were to have a significant effect on bobwhite survival on our study site, we would expect this interactive term to be significant with a larger effect size on our hunting unit. The lack of support for the interactive effect between distance to primary WMA roads and units could be attributed to a low amount of hunting pressure on our study site. Generally speaking, Oklahoma quail hunter numbers tend to decrease as quail densities decrease (Guthery et al. 2005). Based on August and October quail roadside surveys conducted by the Oklahoma Department of Wildlife Conservation (ODWC), 2012, 2013, and 2014 quail numbers were down 70%, 72.5%, and 5% respectively compared to 25 year averages in northwest Oklahoma (ODWC, unpublished data). If hunter numbers followed the trend of quail densities, hunting pressure should have been greatest during the 2014-2015 hunting season. However, 2013-2014 non-breeding season survival was the highest during our study, when quail densities were estimated the lowest by roadside surveys within the northwest Oklahoma region. All indications from ODWC staff on site indicate that hunting pressure was in fact low but present throughout the study period (W. R. Storer, personal communication).

It is evident based on our results that there is some amount of slack (Guthery 1999) in bobwhite requirements of usable space on Beaver River WMA. This is illustrated by the general lack of significance in space us for all anthropogenic features during our study. However, there is undoubtedly a threshold in which anthropogenic features and or disturbance will begin to negatively influence bobwhite space use and survival. This has been shown in populations occupying areas with higher urban and industrial development (Lohr et al. 2011). The lack of significance of bobwhite response during our study should be considered within the context of the low anthropogenic feature density and large amount of usable space across our study sites. Yet, if bobwhite are to be managed as an umbrella species (Crosby et al. 2015), consideration of faunal response to these features should be given beyond just the single species. For instance, the presence of many anthropogenic features (such as oil/gas features) are known to alter behavioral patterns of songbirds, such as song characteristics and territory sizes, which can potentially increase predatory exposure (Machtans 2006, Francis et al. 2011). Furthermore, many other Galliformes that occupy similar vegetation communities as bobwhite are known to respond negatively to these structures (Hovick et al. 2014), thus implications of introducing anthropogenic features across a landscape should consider the full suite of species that occupy the landscape. Despite the broader implications, it appears that bobwhite are resilient to anthropogenic development as long as adequate useable space exists on the landscape.

IMPLICATIONS

Relatively low levels of harvest pressure appear to have no negative impact on bobwhite populations, as illustrated by our results. There is also no evidence that anthropogenic features increased hunting pressure across our study site, however primary WMA roads appeared to increase mortality risk due to some unknown cause. Possible explanations are potential increased exposure to meso-predators or disturbance from vehicle traffic.

We emphasize that low densities of anthropogenic features such as roads and oil/gas structures are compatible with bobwhite management within the context of landscapes already providing large areas of usable space. However, negative confounding impacts related to interactions between anthropogenic features and hunting pressure may exist in other regions within the bobwhite distribution. Therefore, as Williams et al. (2004) discussed, regional efforts should be made to assess whether anthropogenic development may be increasing hunting pressure so that harvest management is scaled appropriately based on local landscape configuration.

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Table 1. Variable weights[1] and assigned values given to vegetation cover types, distance from road categories, and slope (%) categories in estimating potential hunting pressure for northern bobwhite across the hunted unit of Beaver River WMA, Beaver County, Oklahoma, USA, 2012-2015. Values were derived from data presented by Richardson et al. (2008) where 1 represents the highest potential hunting pressure and 4 represents the lowest, and were incorporated into a weighted overlay analysis in ArcGIS 10.2.

Variable	Assigned value
Vegetation cover class	
Sand sagebrush	1
Mixed shrub	2
Mixed grass	2
Shortgrass/yucca	2
Exposed soil/sparse vegetation	3
Bare ground	3
Food plot	3
Salt cedar	4
Distance from roads (m)	
<500	1
500-<1,500	2
1,500-<2,500	3
≥2, 500	4
Slope (%)	
≤3	1
>3	2

[1] All three variables received equal (33.33%) weights in the weighted overlay analysis.

Table 2. Model selection of Andersen-Gill hazard models of survival for northern bobwhite during the non-breeding season at Beaver River WMA, Beaver County, Oklahoma, 2012-2015.

Model	K	AICc	ΔAICc	w_i	Model likelihood
Global	11	1622.81	0	0.31	-800.36
Year + age + unit	4	1624.49	1.67	0.13	-808.24
Primary WMA roads x unit + age	3	1624.67	1.86	0.12	-809.33
Age	1	1624.69	1.88	0.12	-811.34
Year	2	1624.82	2.01	0.11	-810.41
Primary WMA roads	1	1626.13	3.32	0.06	-812.07
Primary WMA roads*unit	2	1626.83	4.02	0.04	-811.41
Gas wells	1	1626.85	4.04	0.04	-812.42
Unit	1	1627.64	4.83	0.03	-812.82
Buildings	1	1627.91	5.1	0.02	-812.95
All roads	5	1629.15	6.34	0.01	-809.57
All anthropogenic features	7	1630.67	7.86	0.01	-808.32

Table 3. Mean standardized resource utilization function coefficients ($\overline{\beta}$)[1], lower and upper confidence intervals (LCI and UCI), and number of coveys with positive (+), negative (-), or non-significant (ns) β values indicating the relationship of space use to distance to anthropogenic features (m), theoretical hunting pressure[2], and vegetation covey types[3]. Data is provided for northern bobwhite coveys during the quail hunting season[4] (2012-2015) on a hunted unit of Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

Variable	*n*	($\overline{\beta}$)	LCI	UCI	+	-	ns
Medium hunting pressure	16	0.02	-0.006	0.04	3	1	12
Low hunting pressure	5	0.01	-0.01	0.03	0	0	5
No hunting pressure (safety zones)	5	0.02	-0.11	0.15	2	2	1
Distance to buildings	16	-0.70	-1.90	0.50	5	5	6
Distance to gas/oil wells	16	0.07	-0.25	0.38	6	6	4
Distance to county roads	16	0.38	-0.21	0.98	6	5	5
Distance to primary WMA roads	16	0.13	-0.38	0.63	6	5	5
Distance to restricted (truck/ATV) WMA roads	16	0.06	-0.16	0.29	8	5	3
Distance to restricted (ATV only) WMA roads	16	-0.17	-0.75	0.41	5	6	5
Mixed shrub	16	-0.002	-0.02	0.01	0	0	16
Mixed grass	16	-0.001	-0.01	0.01	0	0	16
Shortgrass/yucca	16	-0.003	-0.02	0.01	0	1	15
Exposed soil/sparse vegetation	16	-0.01	-0.02	-0.0001	0	1	15
Bare ground	16	-0.01	-0.02	0.0006	0	1	15
Salt cedar	8	-0.01	-0.05	0.02	0	2	6

[1] Confidence intervals were estimated based on conservative standard errors that include inter-animal variation (Marzluff et al. 2004).

[2] Variable coefficients are relative to bobwhite covey space use in areas of highest theoretical hunting pressure.

[3] Variable coefficients are relative to bobwhite covey space use in sand sagebrush.

[4] The Oklahoma quail hunting season began on November 10, 9, and 8 in 2012, 2013, and 2014 respectively and ended on February 15 during all three years.

Table 4. Mean standardized resource utilization function coefficients ($\overline{\beta}$)[1], lower and upper confidence intervals (LCI and UCI), and number of coveys with positive (+), negative (-), or non-significant (ns) β values indicating the relationship of space use to distance to anthropogenic features (m) and vegetation covey types[2]. Data is provided for northern bobwhite coveys during the quail hunting season[3] (2012-2015) on a non-hunted unit of Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA.

Variable	*n*	($\overline{\beta}$)	LCI	UCI	+	-	ns
Distance to buildings	14	-0.60	-1.66	0.47	4	7	3
Distance to gas/oil wells	14	-0.21	-0.57	0.16	6	5	3
Distance to county roads	14	-0.07	-0.70	0.57	5	4	5
Distance to primary WMA roads	14	-0.17	-0.50	0.15	3	7	4
Distance to restricted (truck/atv) WMA roads	14	-0.21	-0.78	0.36	3	7	4
Distance to restricted (atv only) WMA roads	14	-0.30	-0.67	0.08	3	4	7
Mixed shrub	14	0.006	-0.005	0.018	1	0	13
Mixed grass	14	-0.004	-0.024	0.016	1	1	12
Shortgrass/yucca	14	0.01	-0.004	0.02	0	0	14
Exposed soil/sparse vegetation	14	0.002	-0.007	0.011	1	0	13
Bare ground	14	0.01	-0.01	0.02	1	0	13
Salt cedar	5	0.001	-0.018	0.021	0	0	5

[1] Confidence intervals were estimated based on conservative standard errors that include inter-animal variation (Marzluff et al. 2004).

[2] Variable coefficients are relative to bobwhite covey space use in sand sagebrush.

[3] The Oklahoma quail hunting season began on November 10, 9, and 8 in 2012, 2013, and 2014 respectively and ended on February 15 during all three years.

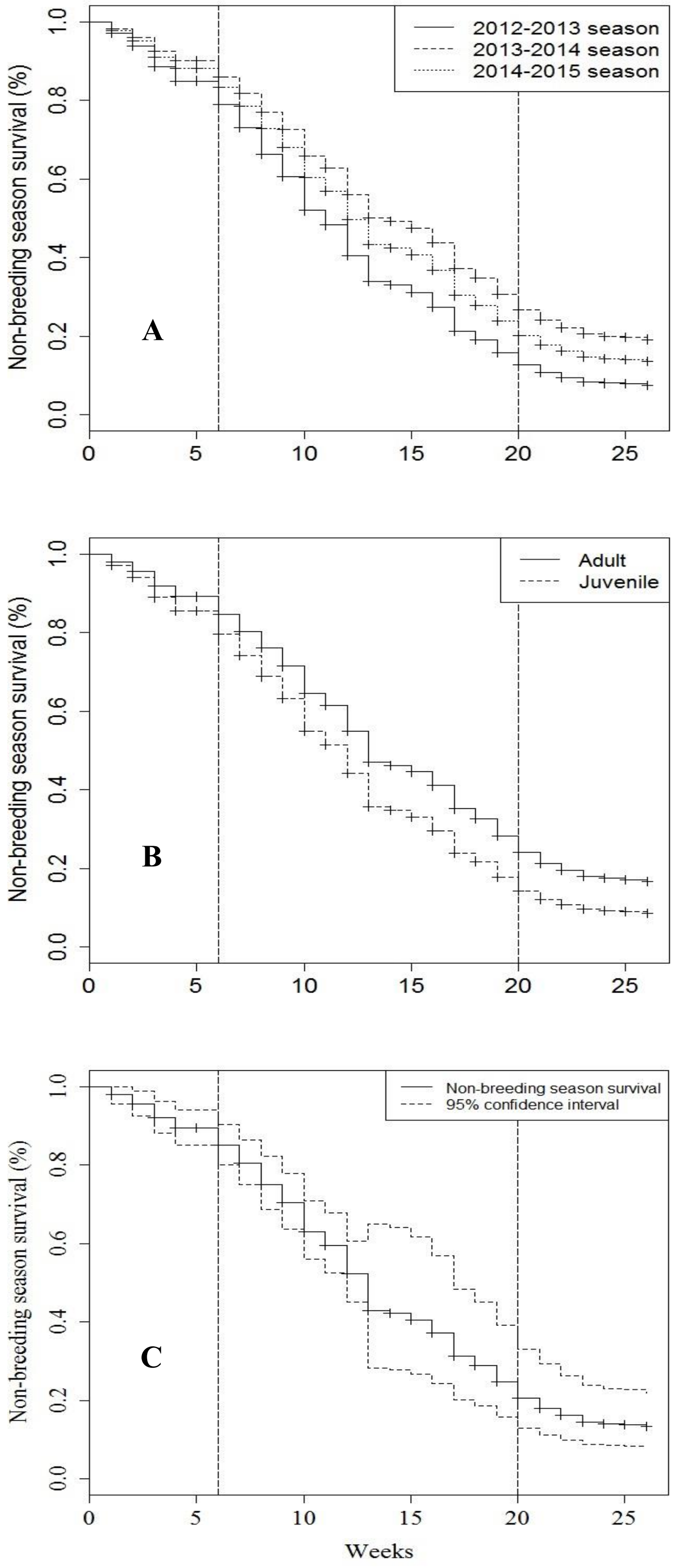
Table 5. Akaike Information Criterion (AIC) model selection results of mixed effect models[1] explaining effects of time (week), year, and hunting (unit) on average daily movement of northern bobwhite during the non-breeding season 2012-2015 on Beaver River WMA, Beaver County, Oklahoma.

Model	K	AIC_c	ΔAIC_c	w_i	Model Likelihood
Intercept + Week + Year	6	-587.58	0	0.21	299.88
Intercept + Week + Year + Unit + Week*Year	9	-587.33	0.26	0.19	302.86
Global	14	-587.29	0.3	0.18	308.1
Intercept + Week + Year + Unit + Year*Unit	9	-587.2	0.39	0.17	302.79
Intercept + Year	5	-586.18	1.41	0.1	298.15
Intercept + Week + Year + Unit	7	-585.53	2.06	0.08	299.88
Intercept + Year + Unit	6	-584.12	3.46	0.04	298.15
Intercept + Week + Year + Unit + Week*Unit	8	-583.47	4.11	0.03	299.89
Intercept + Week	4	-568.85	18.73	0	288.47
Intercept	3	-568.39	19.19	0	287.22
Intercept + Week + Unit	5	-567.9	19.68	0	289.02
Intercept + Week*Unit	5	-567.14	20.45	0	288.63
Intercept + Unit	4	-567.05	20.53	0	287.57

[1] Covey identity was included as a random effect in all models.

Figure 1. Northern bobwhite (*Colinus virginianus*) non-breeding season survival as determined from Andersen-Gill hazard models. Survival curves are broken out by year (A), age (B), and our overall best performing model (C) for bobwhite on Beaver River WMA, Beaver County, Oklahoma, USA, 2012-2015. Week numbers correspond to the non-breeding season beginning on October 1 of each year. Vertical lines indicate the beginning and end of the quail hunting season in Oklahoma.

Figure 1 continued.



CHAPTER V

SUPPLEMENTARY MATERIAL

Table S1 Mean relative abundance (RA) estimates[1] and standard errors (SE) of temperate North American quail species[2] and associated conditions[3] of distributions, based on ENMs using the Maxent algorithm, at 75% ensemble forecasting agreement. Significant difference in RA estimates indicated by Tukey-Kramer test results[4] from a one-way ANOVA.

Species	Condition	Mean RA	SE	Tukey-Kramer grouping
Callipepla californica	2	7.52	0.09	A
	4	4.87	0.55	B
	6	5.19	0.37	B
	8	4.55	0.20	B
Callipepla gambelii	2	10.09	0.14	A
	4	5.29	2.05	BA
	6	0.37	0.06	B
	8	1.72	0.71	B
Callipepla squamata	2	3.20	0.04	A
	4	1.13	0.35	B
	6	3.47	0.18	A
	8	1.78	0.07	B
Colinus virginianus	2	7.41	0.05	D
	4	16.40	1.76	A
	6	12.17	0.39	C
	8	14.34	0.35	B
Oreortyx pictus	2	2.37	0.04	A
	4	0.99	0.24	B
	6	1.50	0.12	B
	8	1.64	0.11	BA

[1] Estimate from Sauer et al. (2014). Values generally predict the average number of birds for a species that can be seen along roadsides in ~2.5 hours.

[2] Data not available for *C. montezumae*.

[3] Descriptions for possible distribution conditions are given in Table 2.

[4] Letter categories represent significant differences between relative abundance values between scenarios at α = 0.05 level.

Table S2 Mean relative abundance (RA) estimates[1] and standard errors (SE) of temperate North American quail species[2] and associated conditions[3] of distributions, based on ENMs using the Maxent algorithm, at 100% ensemble forecasting agreement. Significant difference in RA estimates indicated by Tukey-Kramer test results[4] from a one-way ANOVA.

Species	Condition	Mean RA	SE	Tukey-Kramer grouping
Callipepla californica	2	8.05	0.10	A
	4	5.45	0.29	BC
	6	6.38	0.26	B
	8	5.09	0.13	C
Callipepla gambelii	2	10.38	0.14	A
	4	3.89	0.50	B
	6	4.94	0.45	B
	8	2.37	0.48	B
Callipepla squamata	2	3.00	0.05	B
	4	4.65	0.20	A
	6	3.02	0.07	B
	8	2.81	0.07	B
Colinus virginianus	2	6.94	0.05	C
	4	19.14	0.39	A
	6	5.82	0.11	D
	8	15.60	0.25	B
Oreortyx pictus	2	2.65	0.05	A
	4	2.09	0.23	B
	6	1.76	0.07	BC
	8	1.54	0.06	C

[1] Estimate from Sauer et al. (2014). Values generally predict the average number of birds for a species that can be seen along roadsides in ~2.5 hours.

[2] Data not available for *C. montezumae*.

[3] Descriptions for possible distribution conditions are given in Table 2.

[4] Letter categories represent significant differences between relative abundance values between scenarios at α = 0.05 level.

Table S3. Percent variable contribution of variables used to estimate northern bobwhite (*Colinus virginianus*) space use across temperature categories using Maxent and 30 m resolution. Observations were collected from 2012-2015 at Beaver River WMA, Beaver County, OK, USA.

	Variable contribution (%)											
	Temperature Category (°C)											
Variable	>35	30 to 35	25 to 30	20 to 25	15 to 20	10 to 15	5 to 10	0 to 5	-5 to 0	-10 to -5	-15 to -10	-20 to -15
Area C.V.[1] (mixed grass)	22.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.71	9.66	18.81	0.00
Edge density	28.81	17.35	25.34	47.20	31.45	11.30	12.20	0.00	0.00	0.00	0.00	0.00
Edge density (bare ground)	0.00	0.00	11.16	0.00	0.00	5.83	0.00	8.12	11.24	8.80	14.31	22.48
Edge density (mixed shrub)	14.14	0.00	0.00	0.00	0.00	0.00	0.00	18.59	10.48	11.46	28.03	14.73
Edge density (sagebrush)	12.34	19.05	24.28	9.14	15.98	9.62	0.00	0.00	13.04	0.00	0.00	0.00
Edge density (salt cedar)	0.00	11.71	13.30	13.12	19.45	21.62	19.67	9.31	8.32	9.29	0.00	0.00
Edge density (shortgrass/yucca)	12.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mean area	0.00	27.12	20.71	21.28	33.12	51.63	44.64	26.73	25.34	32.60	0.00	0.00
Mean area (bare ground)	0.00	6.39	0.00	0.00	0.00	0.00	0.00	6.31	0.00	0.00	0.00	0.00
Mean area (mixed grass)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.37	0.00	0.00	0.00	0.00
Mean area (mixed shrub)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.84	7.30	20.78	14.26	33.09
Mean area (sagebrush)	3.76	0.00	0.00	9.26	0.00	0.00	0.00	6.92	0.00	0.00	16.12	0.00
Mean shape index (mixed shrub)	0.00	0.00	0.00	0.00	0.00	0.00	15.52	0.00	0.00	0.00	0.00	0.00
Perimeter-area fractal dimension	0.00	0.00	5.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Perimeter-area fractal dimension (bare ground)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.07
Perimeter-area fractal dimension (mixed grass)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.91	0.00	0.00	0.53

[1] C. V. stands for coefficient of variation.

	Variable contribution (%)											
	Temperature Category (°C)											
Variable	>35	30 to 35	25 to 30	20 to 25	15 to 20	10 to 15	5 to 10	0 to 5	-5 to 0	-10 to -5	-15 to -10	-20 to -15
Perimeter-area fractal dimension (mixed shrub)	0.00	10.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Perimeter-area fractal dimension (sagebrush)	0.00	8.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Perimeter-area fractal dimension (salt cedar)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00
Perimeter-area fractal dimension (shortgrass/yucca)	0.00	0.00	0.00	0.00	0.00	0.00	7.97	8.54	8.65	7.40	8.46	15.19
Vegetation type	5.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.90

Table S3. Continued.

Table S4. Percent variable contribution of variables used to estimate northern bobwhite (*Colinus virginianus*) space use across temperature categories using Maxent and 2 m resolution. Observations were collected from 2012-2015 at Beaver River WMA, Beaver County, OK, USA.

	Variable contribution (%)											
	Temperature Category (°C)											
Variable	>35	30 to 35	25 to 30	20 to 25	15 to 20	10 to 15	5 to 10	0 to 5	-5 to 0	-10 to -5	-15 to -10	-20 to -15
2013 N.D.V.I.	5.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.47
Area C.V.[1]	10.67	13.17	8.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.69
Area C.V.[1] (bare ground)	6.01	18.27	11.44	13.24	12.82	10.31	13.92	19.05	15.85	16.03	21.21	30.82
Area C.V.[1] (mixed grass)	0.00	0.00	0.00	0.00	0.00	0.00	6.53	0.00	5.05	7.45	0.00	0.00
Area C. V.[1] (shortrass/yucca)	0.00	0.00	0.00	0.00	0.00	0.00	6.65	0.00	6.85	9.08	0.00	0.00
Edge density	0.00	42.97	31.16	47.87	48.55	35.86	15.64	11.47	0.00	0.00	0.00	0.00
Edge density (bare ground)	0.00	0.00	0.00	0.00	0.00	12.99	10.91	14.35	16.87	17.50	6.66	0.00
Edge density (mixed grass)	33.67	18.43	15.54	17.35	8.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Edge density (mixed shrub)	0.00	0.00	14.65	12.45	21.09	27.02	30.41	55.13	36.64	39.76	47.49	35.22
Edge density (sagebrush)	23.49	0.00	8.96	0.00	0.00	0.00	11.49	0.00	17.62	9.33	0.00	0.00
Edge density (salt cedar)	0.00	7.56	8.89	7.79	7.97	13.82	7.41	0.00	0.00	0.00	0.00	0.00
Edge density (shortgrass/yucca)	6.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Perimeter-area fractal dimension (bare ground)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.92	5.09
Perimeter-area fractal dimension (mixed shrub)	7.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vegetation type	9.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.72	14.69

[1] C. V. stands for coefficient of variation.

Table S5. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for January.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015	2050			2080		
		A2	A1B	B1	A2	A1B	B1
>35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30 to 35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25 to 30	0.00	0.20	0.20	0.20	0.68	0.68	0.20
20 to 25	1.34	1.73	1.73	1.73	2.43	2.43	1.73
15 to 20	3.48	6.09	6.09	6.09	8.90	8.90	6.09
10 to 15	11.25	13.57	13.57	13.57	15.33	15.33	13.57
5 to 10	17.43	20.01	20.01	20.01	21.90	21.90	20.01
0 to 5	23.80	24.17	24.17	24.17	25.16	25.16	24.17
-5 to 0	25.31	23.18	23.18	23.18	18.74	18.74	23.18
-10 to -5	13.24	8.67	8.67	8.67	5.62	5.62	8.67
-15 to -10	3.29	1.60	1.60	1.60	0.59	0.59	1.60
-20 to -15	0.29	0.21	0.21	0.21	0.07	0.07	0.21
N/A[2]	0.58	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S6. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for February.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015	2050			2080		
		A2	A1B	B1	A2	A1B	B1
>35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30 to 35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25 to 30	0.14	0.54	0.62	0.54	0.96	0.75	0.62
20 to 25	1.15	1.57	1.92	1.57	2.68	2.20	1.92
15 to 20	4.25	6.71	7.19	6.71	8.56	8.04	7.19
10 to 15	11.19	13.00	14.31	13.00	15.78	14.83	14.31
5 to 10	17.23	19.94	20.01	19.94	21.57	21.10	20.01
0 to 5	23.55	24.71	25.09	24.71	24.91	24.87	25.09
-5 to 0	23.39	20.89	19.69	20.89	17.68	19.04	19.69
-10 to -5	13.49	8.23	7.04	8.23	4.19	5.18	7.04
-15 to -10	3.77	3.70	3.49	3.70	3.19	3.44	3.49
-20 to -15	1.38	0.26	0.19	0.26	0.03	0.09	0.19
N/A[2]	0.45	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S7. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for March.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015		2050			2080	
		A2	A1B	B1	A2	A1B	B1
>35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30 to 35	0.76	2.49	2.49	1.98	3.95	3.48	2.49
25 to 30	4.84	5.50	5.50	5.38	6.42	6.10	5.50
20 to 25	7.80	11.25	11.25	10.12	13.31	12.58	11.25
15 to 20	14.29	16.89	16.89	16.59	19.00	18.71	16.89
10 to 15	19.55	19.93	19.93	19.58	20.47	20.45	19.93
5 to 10	20.74	20.19	20.19	20.63	18.93	19.32	20.19
0 to 5	17.62	14.15	14.15	14.90	11.27	11.55	14.15
-5 to 0	9.89	7.05	7.05	8.17	4.39	5.46	7.05
-10 to -5	2.42	0.79	0.79	0.87	1.13	0.70	0.79
-15 to -10	1.50	1.33	1.33	1.33	0.79	1.26	1.33
-20 to -15	0.35	0.18	0.18	0.22	0.09	0.14	0.18
N/A[2]	0.25	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S8. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for April.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015	2050			2080		
		A2	A1B	B1	A2	A1B	B1
>35	0.29	1.46	1.46	1.15	2.56	0.02	1.46
30 to 35	3.10	4.17	4.17	3.70	6.20	0.06	4.17
25 to 30	7.13	9.43	9.43	8.80	11.35	0.11	9.43
20 to 25	13.01	18.55	18.55	17.29	20.25	0.20	18.55
15 to 20	22.29	22.62	22.62	22.87	22.09	0.23	22.62
10 to 15	21.01	19.85	19.85	20.04	19.15	0.19	19.85
5 to 10	17.88	12.87	12.87	14.24	11.67	0.12	12.87
0 to 5	10.17	8.71	8.71	8.98	5.49	0.06	8.71
-5 to 0	4.43	2.33	2.33	2.89	1.25	0.02	2.33
-10 to -5	0.68	0.02	0.02	0.03	0.00	0.00	0.02
-15 to -10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-20 to -15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	0.00	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S9. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for May.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015		2050			2080	
		A2	A1B	B1	A2	A1B	B1
>35	3.20	9.14	9.14	7.31	15.29	12.18	9.14
30 to 35	12.09	14.21	14.21	14.43	15.73	14.64	14.21
25 to 30	15.73	18.86	18.86	18.07	22.72	21.43	18.86
20 to 25	22.72	25.26	25.26	25.12	25.04	25.26	25.26
15 to 20	25.04	19.04	19.04	20.18	11.97	15.25	19.04
10 to 15	11.97	8.23	8.23	9.00	5.56	6.84	8.23
5 to 10	5.56	3.32	3.32	3.65	3.11	3.21	3.32
0 to 5	3.11	1.85	1.85	2.10	0.54	1.14	1.85
-5 to 0	0.54	0.07	0.07	0.09	0.00	0.02	0.07
-10 to -5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-15 to -10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-20 to -15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	0.04	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S10. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for June.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015	2050			2080		
		A2	A1B	B1	A2	A1B	B1
>35	9.71	19.19	21.34	16.93	27.97	23.36	19.19
30 to 35	18.26	23.56	24.70	23.05	27.42	25.48	23.56
25 to 30	27.42	26.49	26.01	26.22	24.16	25.68	26.49
20 to 25	24.16	22.77	21.59	24.04	16.79	20.34	22.77
15 to 20	16.79	7.20	5.94	8.36	3.41	4.75	7.20
10 to 15	3.41	0.78	0.40	1.35	0.22	0.37	0.78
5 to 10	0.22	0.00	0.00	0.02	0.00	0.00	0.00
0 to 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-5 to 0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-10 to -5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-15 to -10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-20 to -15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	0.02	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S11. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for July.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015	2050			2080		
		A2	A1B	B1	A2	A1B	B1
>35	17.51	27.02	27.02	24.97	35.72	31.15	27.02
30 to 35	18.20	22.58	22.58	21.75	27.40	25.47	22.58
25 to 30	27.40	27.42	27.42	27.07	23.07	26.04	27.42
20 to 25	23.07	18.33	18.33	20.83	12.50	14.29	18.33
15 to 20	12.50	4.44	4.44	5.10	1.13	2.88	4.44
10 to 15	1.13	0.04	0.04	0.10	0.00	0.00	0.04
5 to 10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0 to 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-5 to 0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-10 to -5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-15 to -10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-20 to -15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	0.18	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S12. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for August.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015		2050			2080	
		A2	A1B	B1	A2	A1B	B1
>35	9.50	20.42	20.42	18.19	30.83	28.32	20.42
30 to 35	21.33	22.73	22.73	22.89	24.76	24.21	22.73
25 to 30	24.76	29.98	29.98	27.59	29.53	30.04	29.98
20 to 25	29.53	23.34	23.34	26.48	14.08	16.29	23.34
15 to 20	14.08	3.46	3.46	4.76	0.77	1.13	3.46
10 to 15	0.77	0.03	0.03	0.06	0.00	0.00	0.03
5 to 10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0 to 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-5 to 0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-10 to -5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-15 to -10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-20 to -15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	0.02	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S13. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for September.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015		2050			2080	
		A2	A1B	B1	A2	A1B	B1
>35	3.64	10.67	9.11	9.11	15.69	14.02	10.67
30 to 35	11.86	19.15	18.43	18.43	20.40	19.77	19.15
25 to 30	20.40	24.09	23.05	23.05	27.53	26.81	24.09
20 to 25	27.53	27.12	27.67	27.67	22.98	24.16	27.12
15 to 20	22.98	14.38	16.27	16.27	10.54	11.95	14.38
10 to 15	10.54	4.46	5.07	5.07	2.82	3.24	4.46
5 to 10	2.82	0.10	0.37	0.37	0.00	0.00	0.10
0 to 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-5 to 0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-10 to -5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-15 to -10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-20 to -15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	0.04	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S14. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for October.

	Percent time (minutes/month)						
Temperature category (°C)	2012-2015		2050			2080	
		A2	A1B	B1	A2	A1B	B1
>35	0.00	1.02	1.02	0.67	2.26	1.57	1.02
30 to 35	2.26	5.09	5.09	4.46	7.53	6.29	5.09
25 to 30	7.53	11.38	11.38	10.51	14.53	12.78	11.38
20 to 25	14.53	19.98	19.98	19.69	22.77	21.88	19.98
15 to 20	22.77	23.46	23.46	22.61	24.11	23.87	23.46
10 to 15	24.11	21.92	21.92	22.58	18.50	20.18	21.92
5 to 10	18.50	12.97	12.97	14.45	8.90	10.68	12.97
0 to 5	8.90	3.72	3.72	4.53	1.17	2.48	3.72
-5 to 0	1.17	0.43	0.43	0.45	0.22	0.27	0.43
-10 to -5	0.22	0.00	0.00	0.04	0.00	0.00	0.00
-15 to -10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
-20 to -15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	0.01	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S15. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for November.

Percent time (minutes/month)							
Temperature category (°C)	2012-2015	2050			2080		
		A2	A1B	B1	A2	A1B	B1
>35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30 to 35	0.01	0.40	0.40	0.19	1.27	1.10	0.40
25 to 30	1.82	3.06	3.06	2.80	4.37	3.77	3.06
20 to 25	5.44	7.64	7.64	6.86	9.66	8.94	7.64
15 to 20	11.01	14.24	14.24	13.85	15.90	15.74	14.24
10 to 15	17.19	18.79	18.79	18.42	17.83	17.97	18.79
5 to 10	16.94	15.04	15.04	15.30	15.93	15.83	15.04
0 to 5	16.29	18.21	18.21	17.25	16.69	17.18	18.21
-5 to 0	14.83	9.48	9.48	11.44	7.25	7.91	9.48
-10 to -5	6.19	3.26	3.26	3.87	1.35	1.78	3.26
-15 to -10	0.55	0.16	0.16	0.29	0.03	0.06	0.16
-20 to -15	0.02	0.00	0.00	0.00	0.00	0.00	0.00
N/A[2]	9.73	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Table S16. Percent time (minutes/month) occurring within temperature categories (°C) during 2012-2015 compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Climate projections[1] are based on an ensemble model under a high, medium, and low emission scenarios (A2, A1B, B1 respectively) and projected to the years 2050 and 2080. Data is presented for December.

Percent time (minutes/month)							
Temperature category (°C)	2012-2015	2050			2080		
		A2	A1B	B1	A2	A1B	B1
>35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30 to 35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25 to 30	0.00	0.04	0.01	0.04	0.26	0.26	0.01
20 to 25	0.81	2.03	1.64	1.31	2.49	2.49	1.64
15 to 20	3.64	6.51	6.00	4.97	8.61	8.61	6.00
10 to 15	10.72	13.18	12.30	12.05	14.80	14.80	12.30
5 to 10	18.54	22.55	21.55	19.89	24.68	24.68	21.55
0 to 5	25.21	23.77	24.52	25.38	21.63	21.63	24.52
-5 to 0	19.99	17.18	17.69	18.23	16.99	16.99	17.69
-10 to -5	14.88	11.55	12.61	13.81	8.65	8.65	12.61
-15 to -10	5.78	3.14	3.59	4.16	1.87	1.87	3.59
-20 to -15	0.41	0.02	0.06	0.13	0.00	0.00	0.06
N/A[2]	0.02	-	-	-	-	-	-

[1] Climate data obtained on Sep 25th, 2015 from www. Climatewizard.org.

[2] N/A represents periods in which the Beaver Mesonet station was not recording temperatures.

Figure S1**.** Map of artificial surface water locations on Beaver River Wildlife Management Area, Beaver County, Oklahoma from 1 April 2012-31 March 2014.

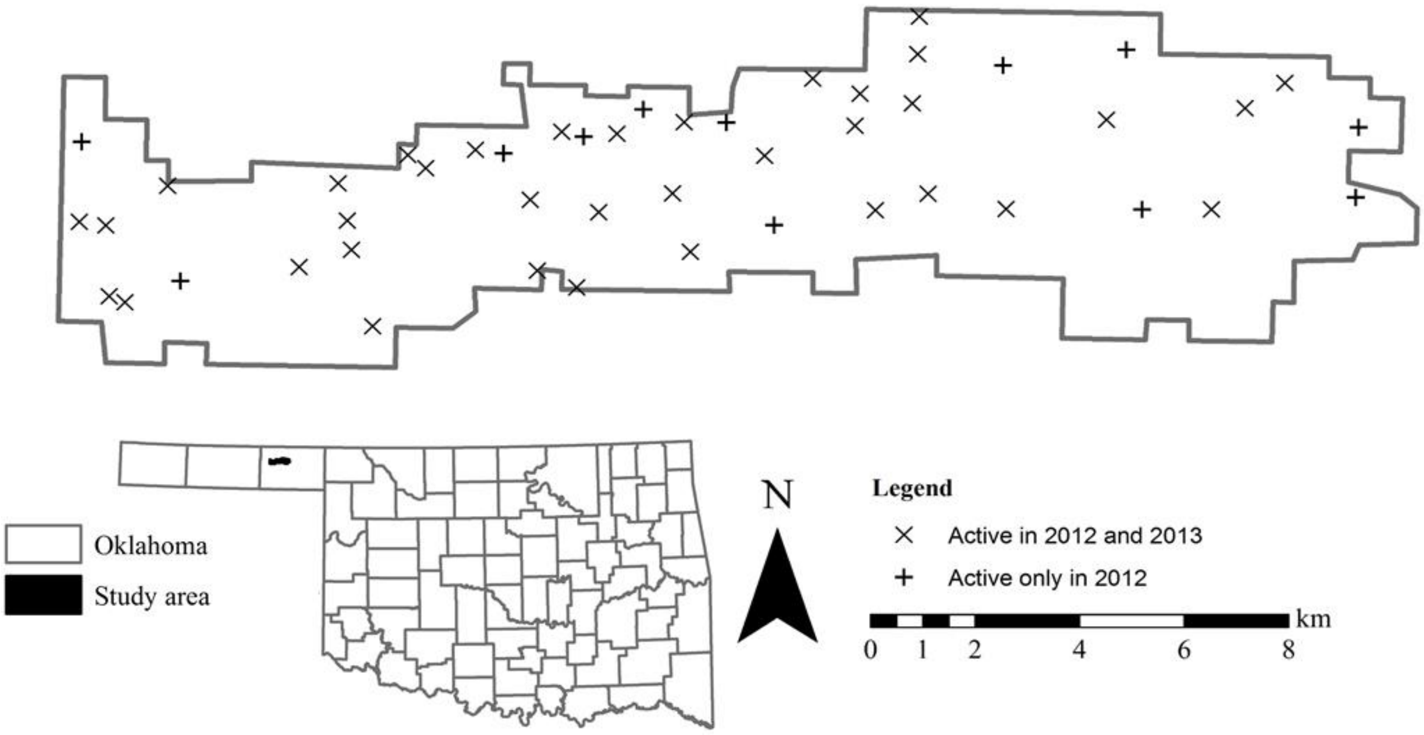


Figure S2. Relationship between environmental variables and probability of climate suitability for California quail (*Callipepla californica*). Response curves indicate mean response of 100 replicated Maxent runs and the +/- one standard deviation (grey).

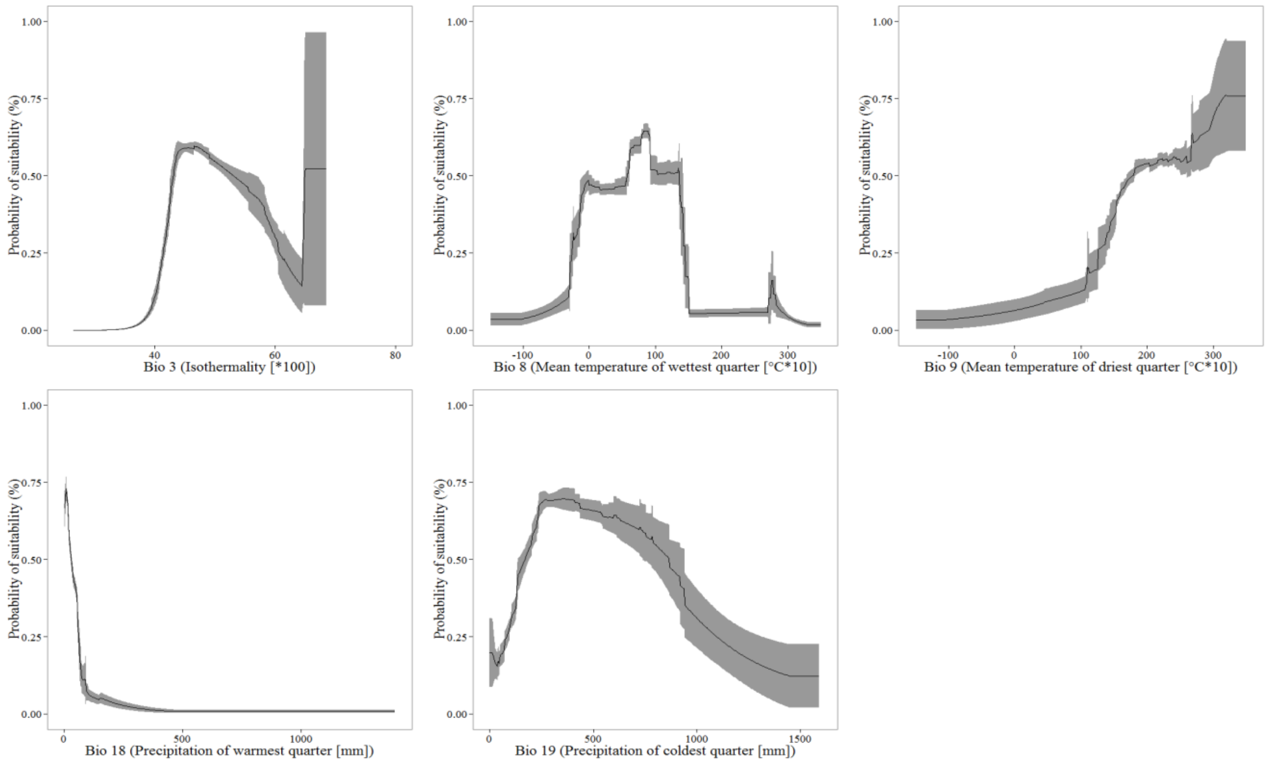


Figure S3. Relationship between environmental variables and probability of climate suitability for Gambel's quail (*Callipepla gambelii*). Response curves indicate mean response of 100 replicated Maxent runs and the +/- one standard deviation (grey).

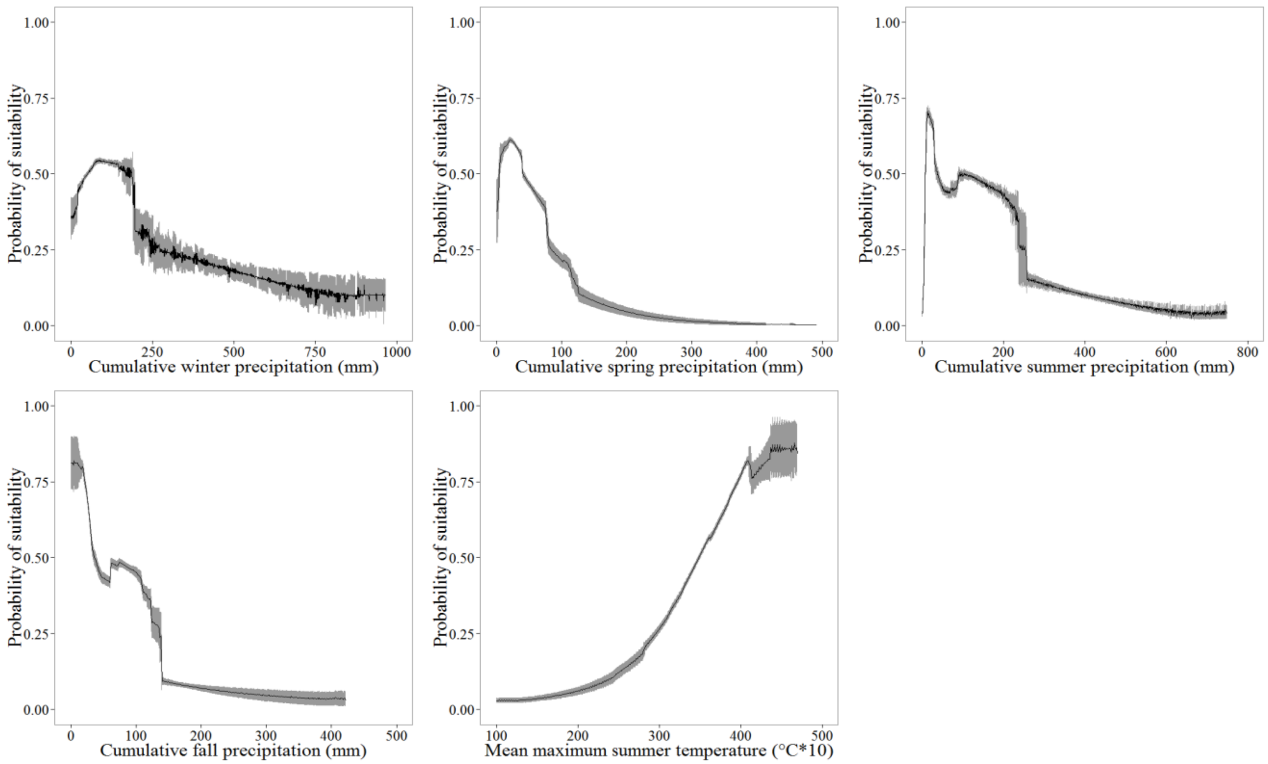


Figure S4. Relationship between environmental variables and probability of climate suitability for scaled quail (*Callipepla squamata*). Response curves indicate mean response of 100 replicated Maxent runs and the +/- one standard deviation (grey).

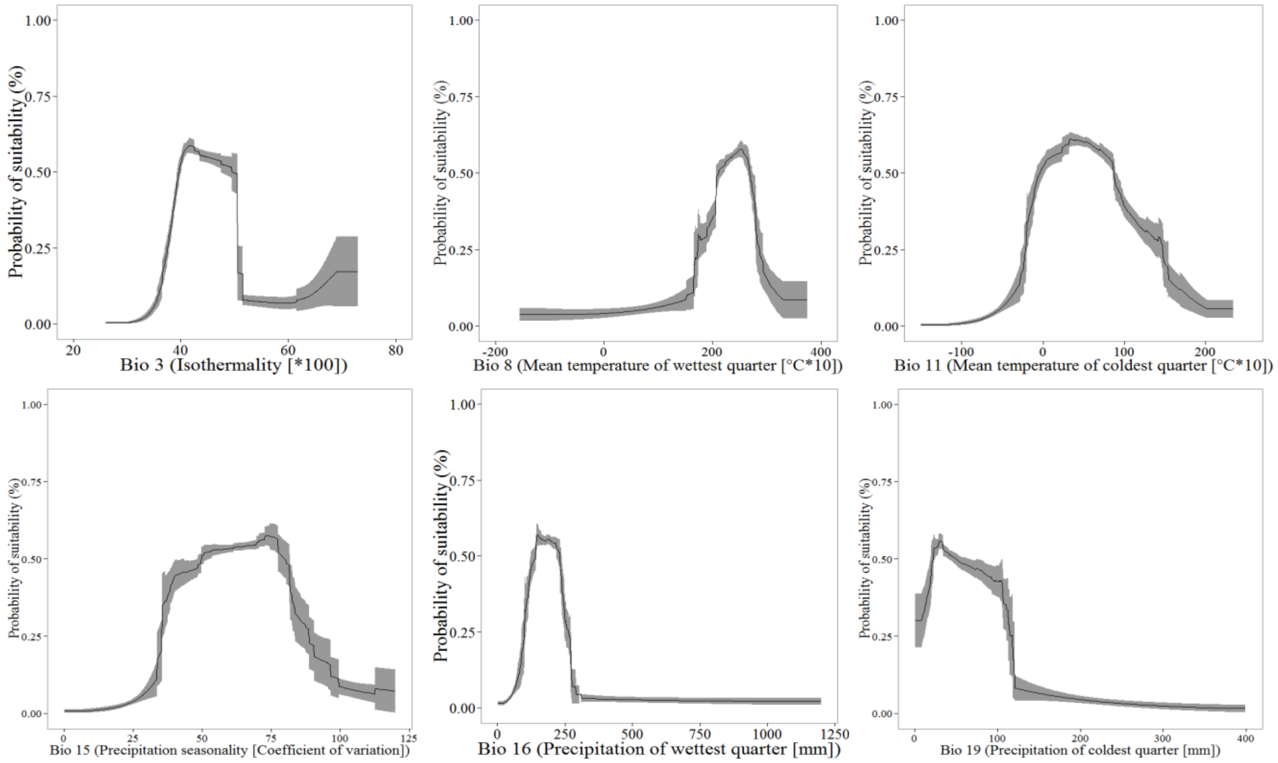


Figure S5. Relationship between environmental variables and probability of climate suitability for northern bobwhite (*Colinus virginianus*). Response curves indicate mean response of 100 replicated Maxent runs and the +/- one standard deviation (grey).

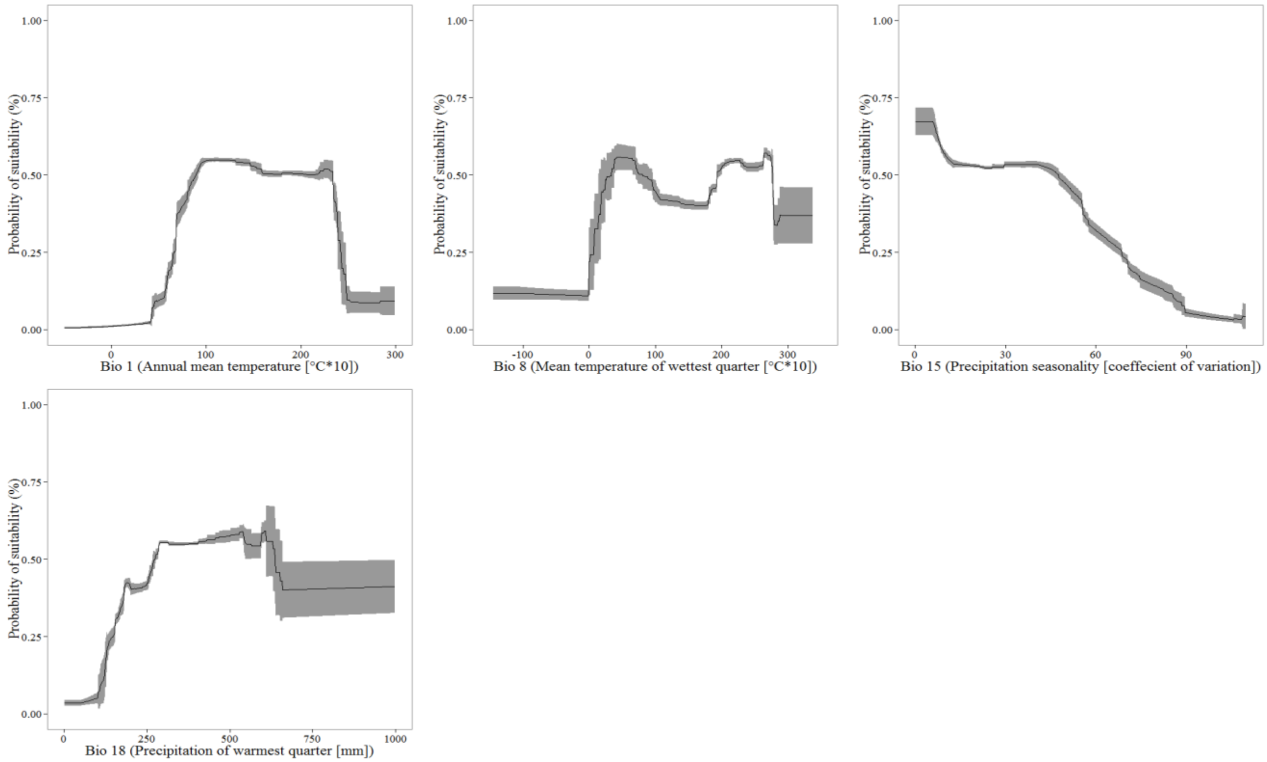


Figure S6. Relationship between environmental variables and probability of climate suitability for Montezuma quail (*Cyrtonyx montezumae*). Response curves indicate mean response of 100 replicated Maxent runs and the +/- one standard deviation (grey).

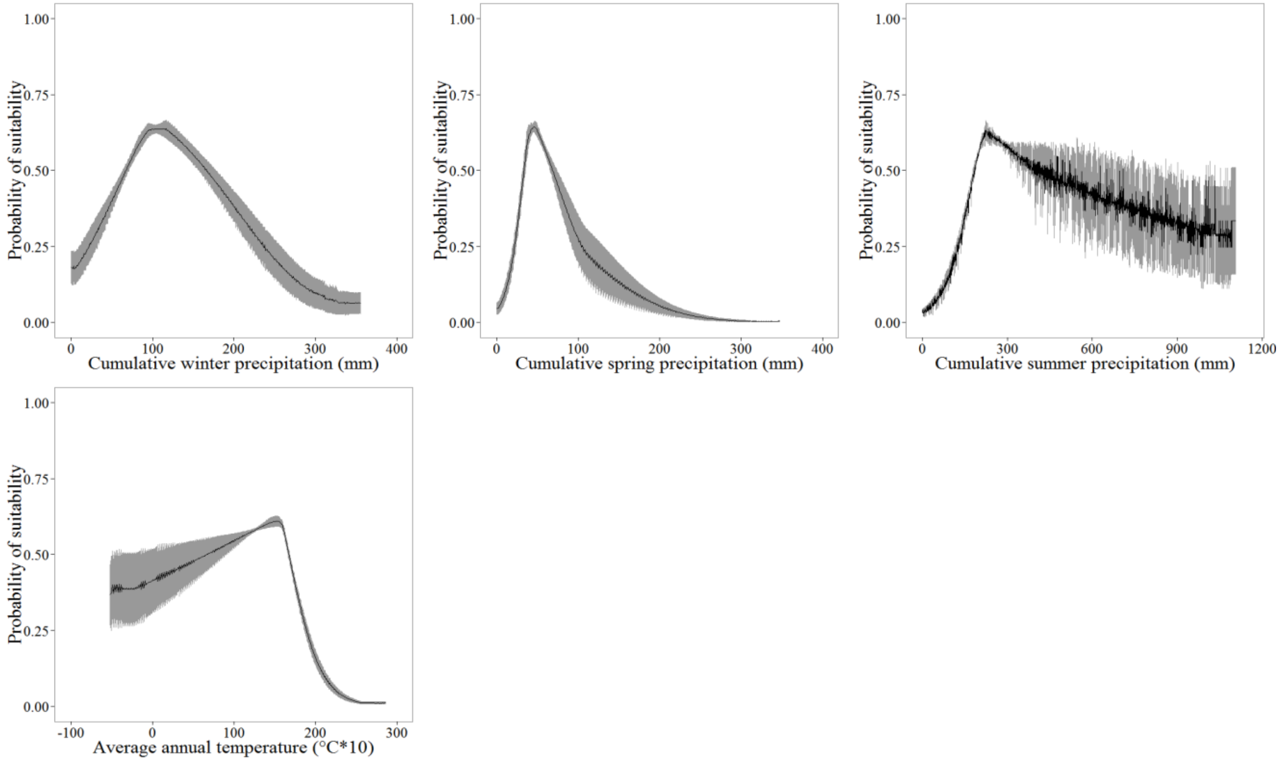


Figure S7. Relationship between environmental variables and probability of climate suitability for mountain quail (*Oreortyx pictus*). Response curves indicate mean response of 100 replicated Maxent runs and the +/- one standard deviation (grey).

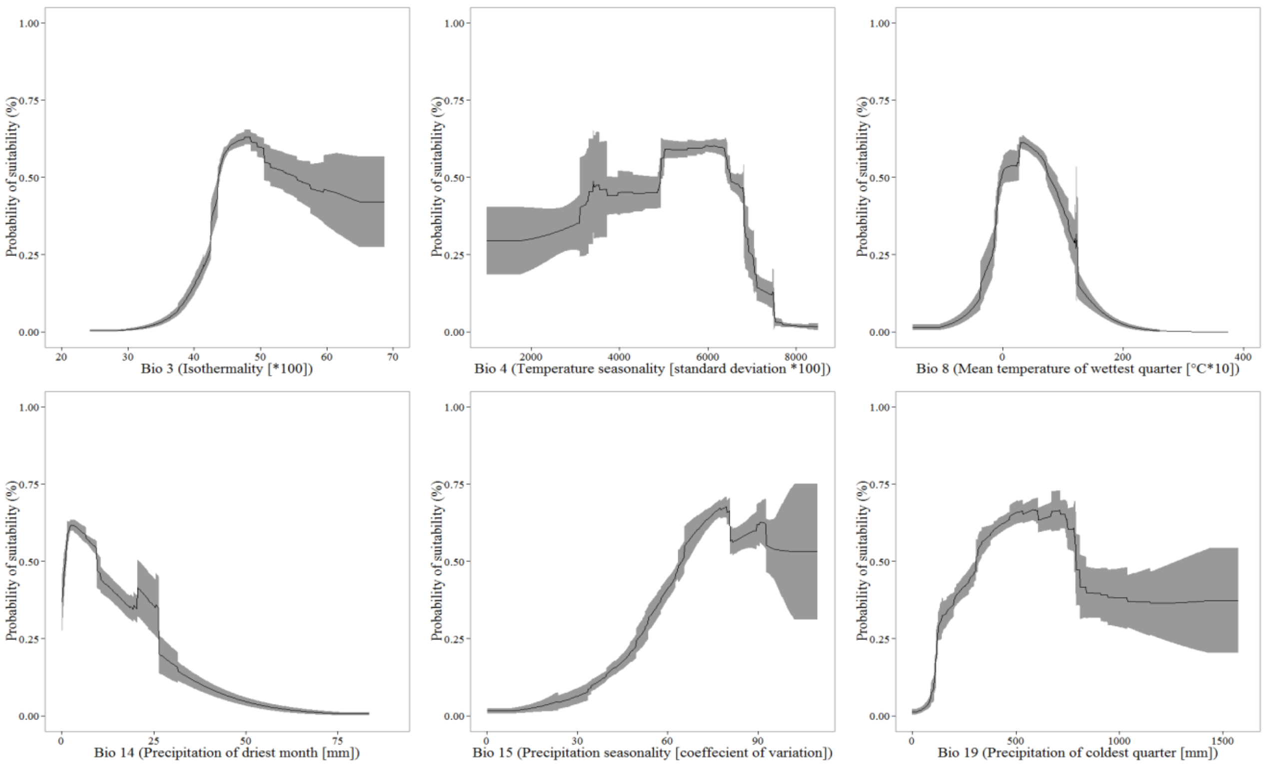
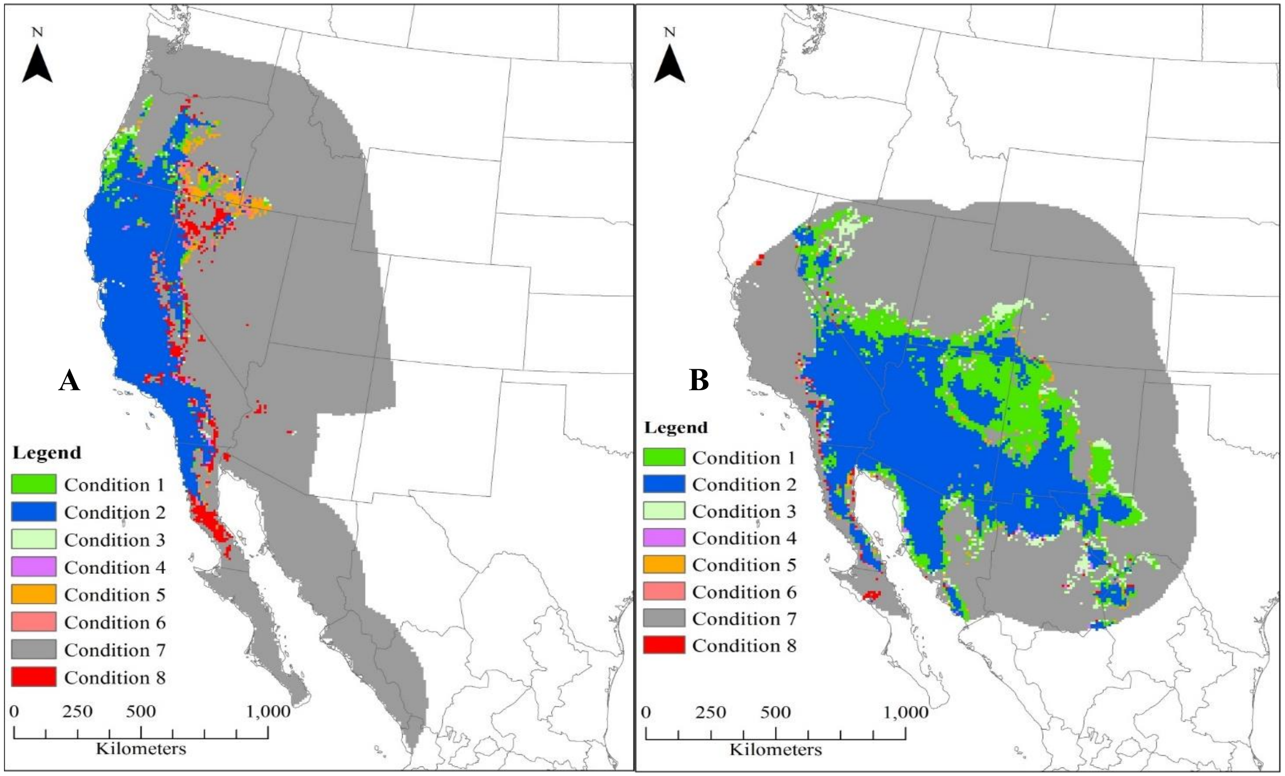


Figure S8. Future predicted changes[1] in distributions of California quail (*Callipepla californica*; **A**) and Gambel's quail (*Callipepla gambelii*; **B**) projected to 2070 and based on ensemble ecological niche models at 75% model agreement as estimated through Maxent.



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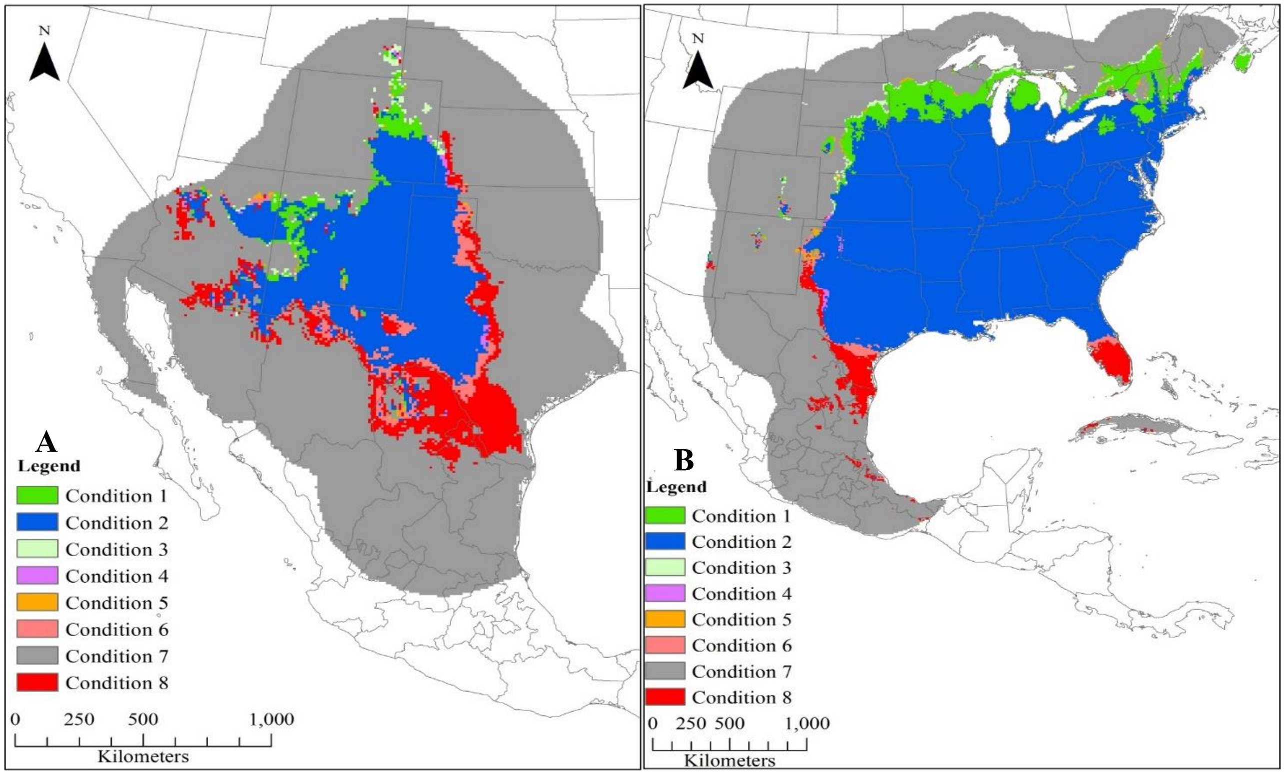
[1] Descriptions for possible distribution conditions are given in Table 2.

Figure S9. Future predicted changes[1] in distributions of scaled quail (*Callipepla squamata*; **A**) and northern bobwhite (*Colinus virginianus*; **B**) projected to 2070 and based on ensemble ecological niche models at 75% model agreement as estimated through Maxent.



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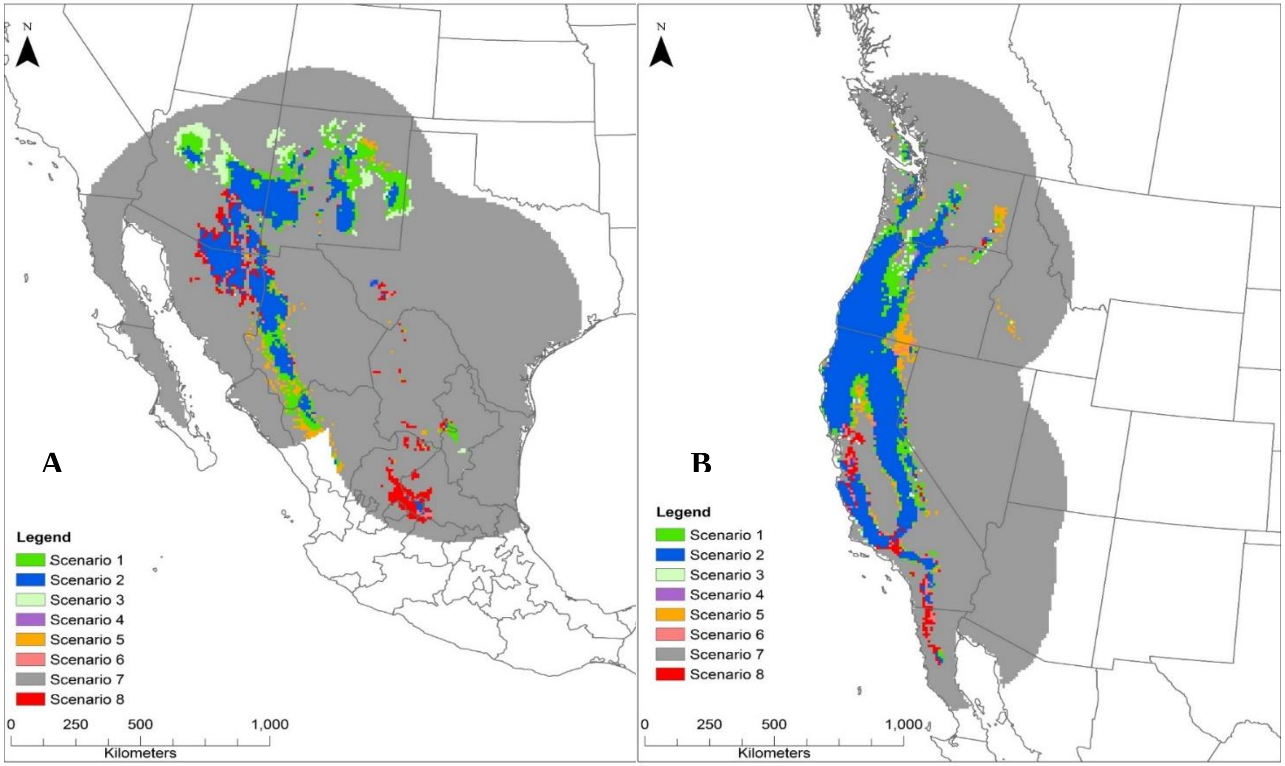
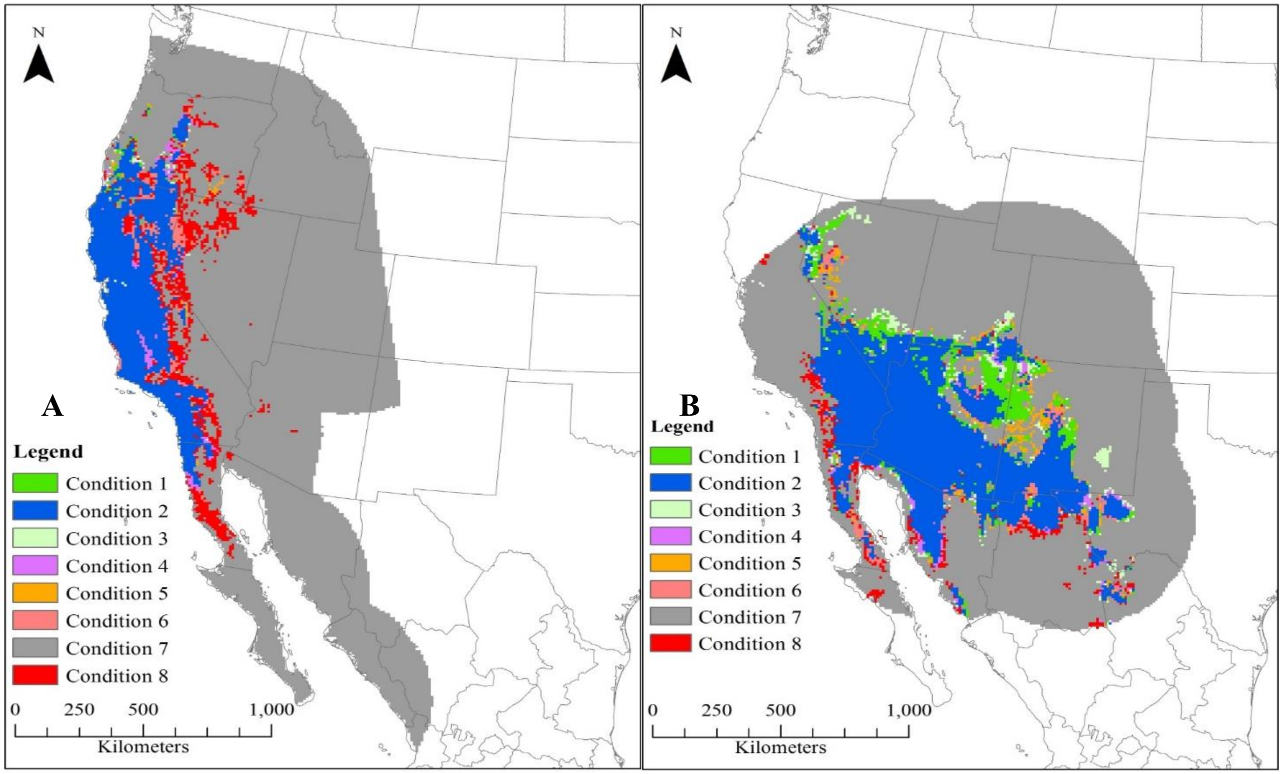
[1] Descriptions for possible distribution conditions are given in Table 2.

Figure S10. Future predicted changes[1] in distributions of Montezuma quail (*Cyrtonyx montezumae*; **A**) and mountain quail (*Oreortyx pictus*; **B**) projected to 2070 and based on ensemble ecological niche models at 75% model agreement as estimated through Maxent.



[1] Descriptions for possible distribution conditions are given in Table 2.

Figure S11. Future predicted changes[1] in distributions of California quail (*Callipepla californica*; **A**) and Gambel's quail (*Callipepla gambelii*; **B**) projected to 2070 and based on ensemble ecological niche models at 100% model agreement as estimated through Maxent.



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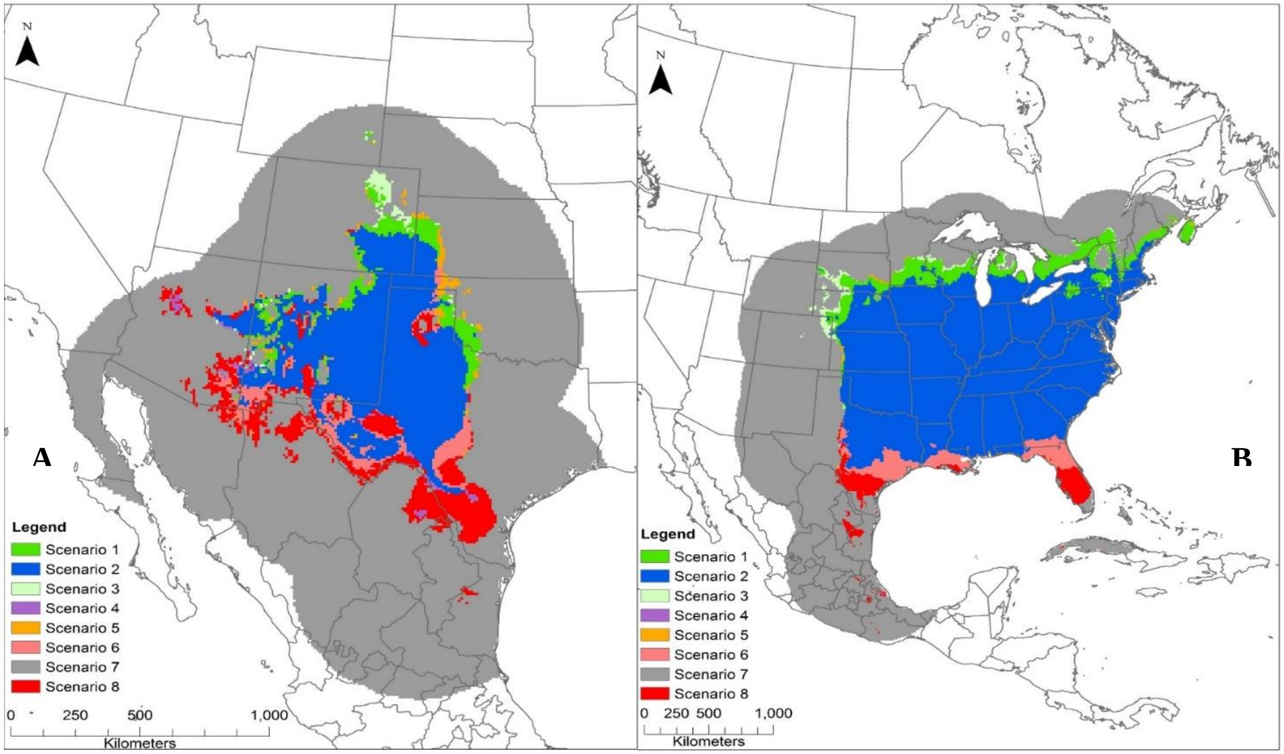
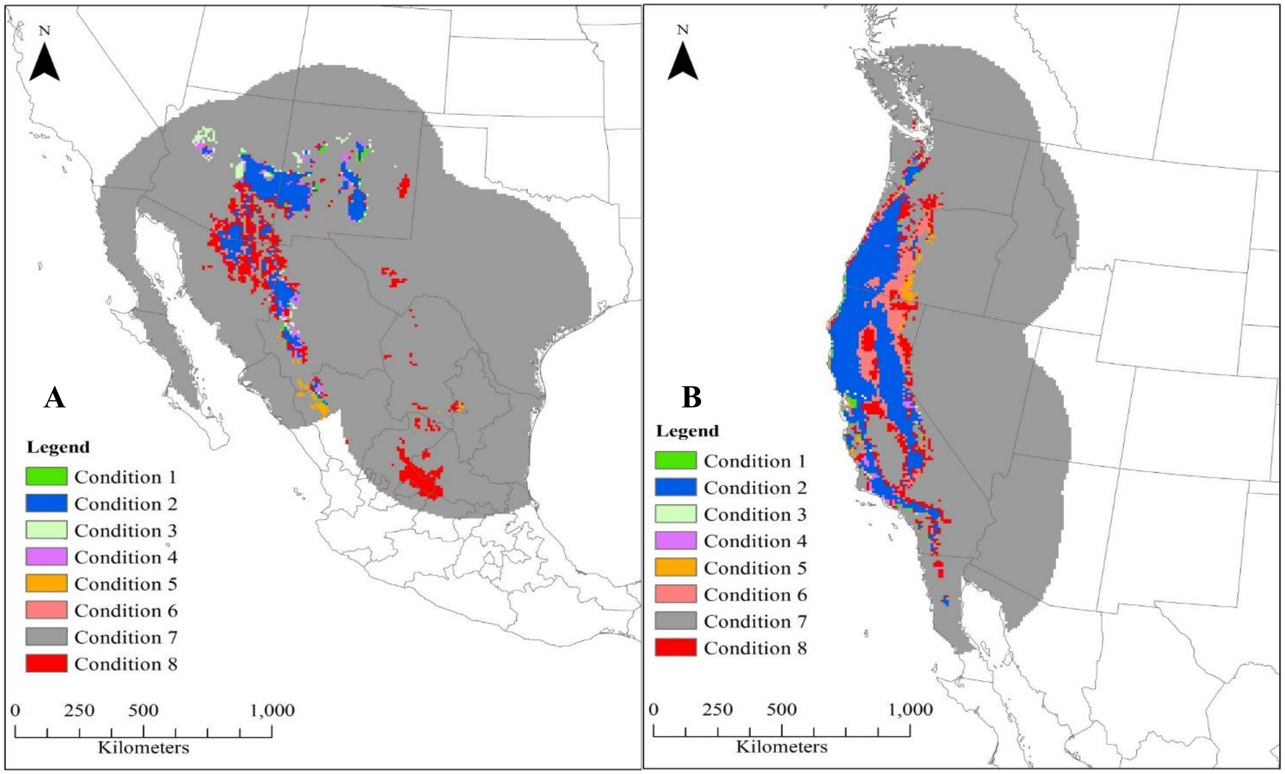
[1] Descriptions for possible distribution conditions are given in Table 2.

Figure S12. Future predicted changes[1] in distributions of scaled quail (*Callipepla squamata*; **A**) and northern bobwhite (*Colinus virginianus*; **B**) projected to 2070 and based on ensemble ecological niche models at 100% model agreement as estimated through Maxent.



[1] Descriptions for possible distribution conditions are given in Table 2.

Figure S13. Future predicted changes[1] in distributions of Montezuma quail (*Cyrtonyx montezumae*; **A**) and mountain quail (*Oreortyx pictus*; **B**) projected to 2070 and based on ensemble ecological niche models at 100% model agreement as estimated through Maxent.



[1] Descriptions for possible distribution conditions are given in Table 2.

VITA

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WITH FUTURE IMPLICATIONS

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