SPACE USE AND SURVIVAL OF SCALED QUAIL IN THE NONBREEDING SEASON

By

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SPACE USE AND SURVIVAL OF SCALED QUAIL
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Abstract: Scaled quail (*Callipepla squamata*) occur throughout the Chihuahuan Desert and the southwestern United States. Scaled quail populations have been declining over recent decades and factors influencing this decline are not fully understood. Research pertaining to factors influencing nonbreeding season scaled quail survival and space use is limited. To address research gaps about scaled quail habitat use, we investigated scaled quail survival and resource selection during the nonbreeding season. We used radio-telemetry to monitor scaled quail movements and survival. We measured vegetation at points used by quail and available points and analyzed the effect of land cover and distance to landscape features that may influence scaled quail space use and survival. Nonbreeding season scaled quail home ranges during the nonbreeding season were strongly linked to anthropogenic areas with a variety of man-made cover. They also selected for higher densities of tall shrubs (>1.5 m) that were mostly comprised of tree cholla. Survival of scaled quail was lower with closer proximity to tree cholla and in areas with higher percent cover of low-level shrubs (<1.5 m). As nocturnal ecology of scaled is poorly understood, we also recorded roost site locations and conducted a covey flushing experiment to examine the effects of late-evening flush events on roosting dynamics. We randomly assigned coveys into control and treatment groups, and treatment groups were flushed <1 hour from official sunset twice per week. We recorded vegetation measurements at roost points and within 15 m at the roost array. Scaled quail coveys selected roost points with less grass cover and more low-level vertical obstruction at the roost array scale (within 15 m). We found that microclimates at roost points were cooler than what was randomly available. Even so, we found a negative effect of lower average minimum daily temperatures on survival of nonbreeding scaled quail. From our covey flushing experiment, we found that coveys disturbed <1 hour from sunset frequently regrouped to roost together and did not have lower survival than control groups. Our results emphasize the importance of cover availability and structure heterogeneity required by scaled quail coveys throughout the nonbreeding seasoning.

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CHAPTER I

DIURNAL SURVIVAL AND SPACE USE OF SCALED QUAIL

Abstract

Scaled quail (*Callipepla squamata*) is a species of New World Quail that inhabits desert grasslands and shrublands throughout the southwestern United States and central Mexico. They are a popular gamebird and populations have been declining since the 1960s. Management of scaled quail populations requires an understanding of how habitat requirements change seasonally. Previous scaled quail research has primarily investigated the breeding season and there is a significant lack of information concerning the nonbreeding season. To address research needs, we investigated scaled quail survival and space use during the nonbreeding season in southwestern Kansas. We used radio-telemetry to monitor scaled quail survival and movements. We collected weather vegetation data at both used and randomly available points. We additionally collected weather data throughout the study period. We assembled location data for structures that we believed could influence covey space use, including tree cholla, water developments, artificial cover structures, oil and gas infrastructure, and other anthropogenic areas. Scaled quail coveys strongly selected for locations with greater densities of tall shrubs (> 1.5m) that mainly consisted of tree cholla. They also selected for locations with higher amounts of tall vertical obstruction and less percent grass cover. Nonbreeding season home ranges were strongly connected to anthropogenic areas that harbored an assortment of cover structures such as brush piles, old buildings, and farm machinery. Scaled quail diurnal survival was most influenced by cover of low-level shrubs (< 1.5m) and distance to tree cholla. Coveys that used locations with higher percent cover of low growing shrubs had decreased survival. Similarly, survival was reduced by closer proximity to tree cholla despite the strong selection for this vegetation. Scaled quail survival and space use during the nonbreeding season is linked to the heterogeneity and availability of cover within their home range. Our results not only provide insight into the nonbreeding season habits of scaled quail, but also offer management implications for supplemental cover provided by land managers in landscapes lacking the appropriate cover.

Introduction

Scaled quail (*Callipepla squamata*) are an economically and culturally important gamebird that inhabits semi-arid grasslands and shrublands throughout the Southwest United States (Carroll 1994). Scaled quail populations have declined throughout their distribution since 1960 but reasons behind their decline are largely unknown (Brennan 1994, Church et al. 1993). Other North American quail species have also experienced population decreases, which are believed to be linked to the widespread conversion of quail habitat to other land cover (Brennan 1993, Church et al. 1993). Similarly, changing habitat conditions may be a limiting factor for scaled quail populations (Bridges et al. 2002).

Shrubland is an important vegetation type for scaled quail that is often characterized by low shrubs with sparse herbaceous cover underneath (Silvy et al. 2007, Reid et al. 1993). Scaled quail use areas with high amounts of bare ground, woody cover, and short grass heights (Wilson and Crawford 1987, Rollins 1980). Grasses and shrubs offer loafing and escape cover, as well as provide forage in the form of seeds (Silvy et al. 2007). It has been suggested that vegetation with an open structure at the ground level is beneficial for scaled quail (Schemnitz, 1961), which is likely linked to their tendency to run from potential predators rather than flush (Schemntiz 1964). Landscapes that provide a diversity of shrub, grass, and forb cover with variable structure and appropriate amounts of bare ground can support high populations of scaled quail (Saiwana et al. 1998, Campbell et al. 1973). While scaled quail appear to have distinct habitat needs in terms of vegetation composition and arrangement, it is largely unknown how those needs change seasonally.

While most of the research on scaled quail has taken place during the breeding season, there have been a few studies during the nonbreeding season. In southeastern Arizona, nonbreeding scaled quail coveys select for areas with >75% grass canopy cover, avoid areas with tree cover >10%, and use areas with higher visual obstruction (Wilson and Crawford 1987, Bristow and Ockenfels 2006). While grass and forb cover are important components of nonbreeding scaled quail habitat in Arizona, herbaceous cover may not provide suitable protection from predation and temperature extremes across all portions of the scaled quail's distribution (Fulbright et al. 2019). For example, in the northern periphery of their distribution, scaled quail coveys were documented using shrubs and man-made structures for cover during the fall and winter (Schemnitz 1961). Further, the survival of nonbreeding scaled quail is thought to be influenced by the quality and availability of cover options, due to their role in moderating the effects of extreme temperatures and providing cover from predation (Snyder 1967, Stormer 1981).

Due to the overall importance of cover for scaled quail, the use of man-made cover structures has been proposed as a means of promoting scaled quail populations in some portions of their distribution. Schemnitz's (1961) study of scaled quail habitat selection throughout the Oklahoma Panhandle showed that man-made structures (i.e., buildings, machinery, post piles, board piles, junk piles, and brush piles) were a significant component of habitat used by quail year-round, especially during the nonbreeding season. Scaled quail remained closely associated with cover provided by both shrubs and man-made structures during winter and artificial structures were important winter forage and loafing sites (Schemnitz 1961). Schemnitz recommended that future management for scaled quail implement artificial cover structures. Biologists in southeastern Colorado investigated the effects of habitat manipulations such as grazing exclosures, guzzlers, and artificial cover structures on scaled quail populations and documented significant increases in winter use when compared to control areas that lacked any developments (Snyder 1967). The addition of artificial cover increased use by scaled quail during the fall and winter for areas that had not been used during previous nonbreeding seasons (Snyder 1967). On the Cimarron National Grassland, artificial cover structures (i.e., wooden teepees, quail barns) have been added to the landscape to increase useable space for quail, as shrub cover is thought to be a limiting factor.

While anthropogenic changes, such as the creation of supplemental cover, can benefit scaled quail, other anthropogenic activities can have negative effects on wildlife management. Other gallinaceous birds, such as tetraonids (grouse spp.), have generally shown displacement behavior and/or decreased survival in relation to oil and gas developments (Hovick et al. 2014). Data on quail in relation to energy development has been mixed, but generally neutral. In the nonbreeding season, northern bobwhite coveys exhibited minor avoidance of high densities of oil well pads (Duquette et al. 2019). Yet, oil and gas structures did not increase mortality risks on bobwhites in relation to hunting pressure (Tanner et al. 2016). Limited investigations into the effects of energy development on scaled quail indicate that oil and gas disturbance and vehicle traffic did not influence survival during the breeding season (Davis et al. 2022). The effects of energy development on scaled quail habitat use and resource selection could vary seasonally and have not been evaluated during the nonbreeding season.

Understanding how scaled quail respond to vegetation cover, structure, and arrangement, as well as to anthropogenic structures, is crucial to providing more effective management suggestions for this species. The information currently available about scaled quail ecology primarily pertains to the breeding season. Therefore, our study aimed to supplement knowledge gaps about habitat use and survival of scaled quail during the nonbreeding season. Our objectives were to 1) investigate how space use of nonbreeding scaled quail is influenced by vegetation cover, shrubs, anthropogenic activities, and supplemental cover and 2) determine if vegetation structure, anthropogenic developments, and artificial cover structures affect survival. We hypothesized that scaled quail would select for higher amounts of woody cover provided by shrubs and use artificial cover where shrub cover was limited.

Methods

Study site

The 43,477-ha Cimarron National Grassland (hereafter, CNG) is managed by the U.S Forest Service (USFS) and is the largest area of public land in Kansas (Finch 1996). It is in the southwestern corner of Kansas in Morton and Stevens County near the city of Elkhart (Figure 1). The grassland was created from land acquired during the Roosevelt Administration in the 1930s as part of the National Soil Conservation Program (Hurt 1985). Early efforts focused on restoring drought-stricken, heavily eroded rangeland and former cropland to mixed-grass and shortgrass prairie. During the Dust Bowl era, Morton County was the most wind-eroded and degraded county within the Great Plains region, as 78.4% of its land was considered seriously damaged (Joel 1937). Restoration efforts by the Soil Conservation Service (now known as the Natural Resources Conservation Service) emphasized grazing over cultivation to restore topsoil, vegetation, and decrease water runoff (Guest 1968, Lewis 1989). Administration of the land was transferred to the USFS in 1954 whose management goals prioritize “multiple use” objectives such as grazing, mineral production, recreation, and wildlife habitat. The Kansas Department of Wildlife and Parks (KDWP) helps manage wildlife and recreation on the grassland.

The climate of the CNG is characterized as semi-arid with a mean annual temperature of 13 °C and an average annual precipitation of 381 mm (Guest 1968). Much of the precipitation occurs from April to September (Cable et al. 1996) and growing season length averages about 178 days (McLaughlin 1942). Topography of Morton County is predominately flat and elevation ranges from 1,128 meters in the west to 960 meters in the east (McLaughlin 1942). The Cimarron River flows northeast through Morton and Stevens counties and is often dry. In deep, sandy soils along the river’s flood plains occur gallery forests consisting of plains cottonwood (*Populus deltoides*). Lands north of the river are mainly shortgrass prairie with some hills and sandy fine loam soils (Guest 1968). Vegetation consists largely of warm-season grasses such as purple three-awn (*Aristida pupurea*), blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), western wheatgrass (*Elymus smithii*), ring muhly (*Muhlenbergia torreyi*) and sand dropseed (*Sporobolus cryptandrus*) (Kuhn et al. 2011). The south side of the river is characterized by both stabilized and active sand dunes that are dominated by sandsage prairie (Kuhn et al. 2011). Soils are mostly sands and loamy fine sands (Guest 1968). Plant cover in this community consists of dense stands of sand sagebrush (*Artemsia filifolia*), rubber rabbitbrush (*Ericameria nauseosa*), and soapweed yucca (*Yucca glauca*) (Kuhn et al. 2011). There are also scattered occurrences of sand plum (*Prunus angustifolia*) and tree cholla (*Cylindropuntia imbricate*). A majority of the tree cholla were transplanted by biologists to provide wildlife habitat (Cable et al. 1996). Some common forbs include western ragweed (*Ambrosia psilostachya*), pigweed (*Amaranthus spp.*), sand lily (*Mentzelia nuda*), and lavenderlead sundrops (*Oenothera lavandulifolia*) (Cable et al. 1996). Russian thistle (*Salsola pestifer.*) and Kochia (*Bassia scoparia*) are non-native, annual forbs that commonly occur across the grassland (Long 1941).

The USFS works to provide grazing opportunities on the grassland for local ranchers. The Morton County Grazing Association is allowed to graze approximately 5,000 cattle for six months (usually May through October) (Hartman and MacDonald 1988). Livestock are grazed on 30 grazing allotments across the grassland, and stocking rates are based on annual precipitation (Lyle et al. 2009). Cattle are usually introduced when the summer rains arrive but not before May 1 (Van Buskirk 2015).

Cover and water are resources thought to be limiting quail populations on the grassland. Managers began adding artificial cover structures and guzzlers around the 1960s and continue to install them today. Cover structures consist of man-made wooden teepees and quail shelters that provide overhead cover. Grazing exclosures were used to fence off small portions of the grassland for wildlife and protect historic homestead sites. Guzzlers were placed on the grassland

and inside grazing exclosures as supplemental water sources. Cover structures and guzzlers are commonly found within grazing exclosures to minimize damage from cattle (J. Prendergast, KDWP, pers. comm.).

Capture and radio-telemetry

We trapped scaled quail in the fall 2020 and 2021 (September through October) using baited walk-in funnel traps (Stoddard 1931). As scaled quail begin grouping together into winter coveys in August (Schemnitz 1961), we also located previously collared birds to aid in capturing additional birds within coveys. We used spotlighting and night-netting as described by Labisky (1968). We focused trapping efforts primarily south of the river due to higher scaled quail abundance but included a small sample of traps north of the river where scaled quail had been observed previously (K. Schultz, KDWP, pers. comm.). We weighed (g), aged (adult vs. subadult), and sexed (male vs. female) all captured quail based on plumage characteristics (Wallmo 1956, Cain and Beasom 1983). However, due to difficulty in determining sex by appearance, we also collected feather samples from the flank of the birds for genetic confirmation of sex. We fit quail weighing > 120 grams with a whip antennae radio transmitter necklace ranging from 5.0 to 6.5 g (American Wildlife Enterprises, Monticello, Florida , USA). All bycatch bobwhites and any scaled quail weighing less than 120 grams were aged, sexed, banded, and released. All trapping and handling was done with approval from the Institutional Animal Care and Use Committee (IACUC) at Oklahoma State University under IACUC-20-18 and conducted under permits number SC-086-2020 and number SC-116-2021 from the Kansas Department of Wildlife and Parks.

As trapping efforts largely focused on known covey locations as observed by biologists, technicians, and cooperating landowners, there was concern that our monitored birds may have been biased to locations near human development. To control for this potential bias, we ran an additional 60 stratified random traps in attempts to locate unknown coveys. We generated random trap locations within a polygon that encompassed around 9,300 hectares of public land. This polygon mainly consisted of sandsage-grassland south of the Cimarron River. We limited the extent of the polygon to areas surrounding known covey locations and areas containing artificial cover structures purposefully built for quail management. While we believed scaled quail would avoid the dense tree canopy associated with the Cimarron River, we included traps that also sampled roads along the river. All random traps were generated within 15 m of roads to enable easy access so we acknowledge there could be a road bias with our data.

We located all radio-marked birds a minimum of three times per week via homing until February each year. To ensure that scaled quail locations were not biased by the time of day, coveys were tracked during different hours of the day (morning, mid-day, and afternoon). Due to the propensity of scaled quail to run when approached, we used a combination of homing and triangulation techniques (White and Garrot 1990) to obtain approximate locations for coveys while attempting to minimize disturbance to the birds. If quail locations were thought to have been influenced by disturbance, they were censored from our datasets.

Weather and vegetation sampling

We collected weather data including days with precipitation events (0/1), daily average temperature (C°), daily minimum temperature (C°), and daily average wind speed (m per s) throughout the field seasons from the weather station in Richfield, Kansas (37.259, -101.792) (Kansas Mesonet). This station was approximately 24.14 kilometers from the grassland and 38.62 kilometers from Elkhart, KS.

We conducted vegetation sampling at locations used by scaled quail and at random (available) points. For each used point, we generated one available location that had a random bearing between 0 to 359° and was within 40 to 500 meters of the used point. Available points were at least 40 meters from the used points to avoid overlap of vegetation sampling as our sampling transects were 15 m from each sample point (see below). We used a maximum possible distance of 500 meters based on the average daily distances traveled by scaled quail in northwest Oklahoma from a previous study during the nonbreeding season (October 1st – March 31st; E. P. Tanner, unpublished data).

We used the line-point intercept method (Canfield 1941, Herrick et al. 2005) to assess percent cover of plant functional groups (grasses, forbs, and shrubs ≥ 1.5 meters) and ground cover (bare ground, rock, and litter) at both used and random locations (Figure 2). The centerpoint for our transects were coordinates from covey locations or randomly generated available points. From the centerpoint, we generated a random bearing between 0 to 359° to establish the direction of a 15 m transect. We then sampled an additional 3 transects at 90° intervals from the first so that a total of 4 transects were sampled at each point. We dropped a sampling pin from a height of 76 cm every 1.5 m along the transect tape (Caratti 2006) for a total of 40 pin drops at each location. We recorded every layer that touched the pin on the way to the ground as a "hit" for vegetation groups, therefore multiple vegetation layers were possible for each transect pin. We categorized the ground surface as bare ground, rock, litter, snow, or a vegetation functional group if covered by a plant. We identified shrubs to the species, with other plants grouped as either a forb or grass. We calculated percent cover for each cover category at each transect. We then averaged percent cover for all functional groups and ground cover classes across the four transects. Further, we also recorded the slope at used and available points. From the centerpoint, we used a clinometer to determine the degree of slope if the array had topography that could influence quail use.

We used a Nudds profile board (Nudds 1977) modified for sand shinnery oak communities (Guthery 1981) to assess vertical vegetation cover and structure. The profile board was 2.5 m tall and 30.48 cm wide with 12 alternating 21 cm intervals marked with black and white colors. We placed the board at the center of scaled quail locations or available points. We recorded readings from 15 m away at a height of 1 m, with the board facing four different bearings that were 90° apart. We estimated the amount of vertical obstruction from surrounding vegetation as a density score with the following categories for each interval: 1=0 to 20%, 2=21 to 40%, 3=41 to 60%, 4=61 to 80%, and 5=81 to 100% (Nudds 1977). We converted each density score into a midpoint percent value, with 1=10%, 2=30.5% 3=50.5%, 4=70.5%, and 5=90.5%. We grouped the profile board strata into three different vertical obstruction classes: low (1-3), medium (4-6), tall (7-9), and tallest (10-12). Once grouped, we averaged all midpoint percent values for the height classes across all four transects to calculate percent vertical obstruction for low, medium, tall, and tallest cover classes. The tallest and medium percent vertical obstruction categories were not used in any of the analyses, as they were highly correlated ($r \geq 0.7$) to low and tall categories. Low and tall vertical obstruction were moderately correlated ($r = 0.43$), so we used WAIC values from the univariate models to decide which variable to include in our final models. If both variables were considered significant enough to include in the next modeling stage, only the one with the lowest WAIC value was included.

We recorded the occurrence of trees and shrubs taller than 1.5 m within 100 m of either used or random points using the point-centered quarter method (Cottam and Curtis 1956). We used either the use or random locations as the centerpoint for our sampling unit. The sampling unit around each point was divided into four equal quarters (90°) to determine the distance to the nearest tree or tall shrub (> 1.5 m). The bearings used for the quarters corresponded with the bearings used for the vegetation sampling transects. For each quarter, a laser range finder was used to record the distance (m) from the centerpoint to the closest tall tree or shrub. If there were no tall shrubs or trees within the quarter, we did not collect data for that quarter's tall shrub and tree density. If there were multiple trees or tall shrubs in the quarter, we only recorded the one closest to the centerpoint. All tall shrubs were identified to species. The occurrence of trees on or near the grassland was mostly isolated plantings near homes and remnants of plantings from homesteads and we did not identify to species.

Geospatial data

We created data layers with points for tree cholla, stock tanks (water), artificial cover structures, and oil and gas developments to create 30-m resolution Euclidean distance rasters in ArcMap Version 10.8 (ESRI 2020). All these features were mapped as discrete points. The U.S Forest Service provided data layers with locations of stock tanks and oil and gas wells. We created data layers for tree cholla and artificial cover structures by ground-truthing previously known locations and searching for additional unknown tree cholla and structures. To create the artificial cover structures data layer, we recorded all wooden teepees, quail shelters, and guzzlers we encountered within the grassland. We did not consider wildlife guzzlers as water resources in this analysis because 40% of them did not retain water. They were included in artificial cover due to most of them providing supplemental overhead cover. We analyzed stock tanks as water sources and included them separately from other artificial structures. Finally, there were other random anthropogenic features that occurred across the landscape including homes, old buildings, and a landfill. As these features occurred over a larger spatial area and were more complex in structure, we mapped these as polygons and included them as a unique structure type called anthropogenic areas.

We used 30-m resolution land classifications from the U.S Department of Agriculture's National Agricultural Statistics Service's Cropland Data Layer (USDA-NASS CDL 2020) to create land cover rasters which included: crops (any cultivated crop), grassland (herbaceous cover), and shrub (areas dominated by shrubs). The CDL used satellite imagery from the 2020 growing season for cropland classification and National Land Cover Database (NLCD 2019) for ground training and validation of non-agricultural categories. We extrapolated values from all three layers for all used and available points, with a 1 or 0 indicating presence or absence of that cover class.

Data analysis

We extrapolated tall shrubs and tree density from the sample unit to a per hectare value by multiplying by 10,000. We recorded all occurrences of tall shrubs by species. We averaged vegetation measurements across the four transects at each sampled location to calculate an overall percentage for that variable. We evaluated differences in vegetation composition and structure using an independent two-sample t-test and considered differences as significant for p-values < 0.05.

Movements and space use of scaled quail during the nonbreeding season are not independent, as birds move together as coveys. Therefore, we grouped variables such as vegetation measurements and distance to structures by covey. We calculated average vegetation measurements for each covey across multiple vegetation transects. We determined the average distance for coveys to structures including tree cholla, stock tanks, artificial cover, anthropogenic areas, and oil and gas developments. All values for the covariates were scaled by subtracting the mean and dividing by the standard deviation. Once scaled, these covariates were treated like covey-specific covariates and used to examine differences in survival of individuals between coveys. Telemetry locations and vegetation sampling (for both used and random) were censored to only include data collected after November 1st of each year, as this was when coveys had generally stopped long-range movements associated with the "fall shuffle" (Agee 1957). Additionally, frost and the end of the warm growing season typically coincided with this date. Removing locations from September through October minimized the possibility of including data that was not representative of nonbreeding season survival and home ranges.

Survival analysis

We used radio-telemetry data to estimate daily survival of scaled quail. We determined individual fates from the time of capture until death, collar loss, transmitter failure, or end of the monitoring period (mid-February for both years). Quail that did not survive >7 days post-capture (Guthery and Lusk 2004) were removed from the data to avoid a potential negative bias from capture stress/myopathy. For each observation of our individual i on occasion j, we created encounter histories where S_{ij} =1 if the bird was alive or S_{ij} = 0 if it died. If a bird was not located, we logged the occasion as missing data. Our model integrated over all possibilities when survival state was unknown.

We used a known-fate logistic exposure model with a Bayesian framework (Royle and Dorazio 2008) to estimate daily survival rates. We centered and scaled all continuous variables around the mean so coefficient estimates would directly reflect effect sizes. Our linear predictor function took the general form of:

$$\text{logit}(S_{ij}) = \beta_0 + \beta_1 X_{it} + \ldots + \beta_x X_{it}$$

We fit models using the JAGS 4.3 (Plummer 2017) and the R2jags package version 0.7-1 (Su and Yajima 2015) in Program R version 4.2.1 (R Core Team 2021). We had no data to inform priors, so all parameters were assigned uninformative priors for normally distributed parameters with a mean of 0 and a standard deviation of 1.7. We sampled posterior distributions using 3 Markov chain Monte Carlo (MCMC) chains with 10,000 iterations each and the first 1,000 discarded as burn-in samples (Plummer 2017). We confirmed model convergence by visually inspecting MCMC plots and checking that Gelman-Rubin convergence diagnostics were < 1.1 (Gelman and Rubin 1992). We ranked models by sampling deviance from model outputs and calculating Watanabe-Akaike Information Criterion (WAIC) values (Watanabe and Opper 2010). We calculated what percent of the 27,000 posterior draws matched the sign of the median (f)

estimates to quantify confidence in whether covariates had positive or negative effects (Arnold 2010, Jones et al. 2017). For covariates that were moderately correlated (r = 0.3 to 0.5), we used WAIC rankings to determine which variable had a lower WAIC value. We excluded the variable with the higher WAIC in further model building steps.

Prior to testing the univariate models, we assessed whether year or covey size should be included in our models. We treated field seasons as different years and categorized covey sizes based on the number of radio-marked individuals on that occasion. Categories included small (≤ 7 birds), medium (8-14 birds) and large (≥15 birds) coveys. These categories fit our monitored population as coveys averaged ~11 individuals ($\bar{x}$ = 10.3 ± 5.46) and only one covey surpassed a high of 20 individuals. Using these size parameters offered some flexibility to account for birds that were potentially not radio-marked within coveys. Based on direct and frequent visual observation of coveys, as well as recapture rates, we are confident that at least 60% of all individuals within each covey were radio-marked.

To determine which variables influenced daily survival of scaled quail, we tested 13 univariate models in four different covariate groups that included individual-varying characteristics, weather variables, vegetation cover, and distance to landscape features (Table 1). Individual-varying covariates consisted of sex (male, female, or undetermined) and age (adult or subadult). The weather covariates we examined were days with measurable precipitation, mean daily temperature (°C), and mean daily wind speed (m per s). To examine potential effects of vegetation cover on survival, we tested models including covariates for percent cover of shrubs, grass, bare ground, low vertical obstruction, and tall vertical obstruction. We also included distances to landscape features such as tree cholla, stock tanks, artificial cover designed for quail (e.g. wooden teepees, guzzlers, and quail barns), anthropogenic areas, and oil and gas developments. Tree cholla was analyzed separately from other vegetation measurements due to their complex structure and discrete locations. Anthropogenic areas included a variety of structures associated with homes, farms, and a landfill.

From our univariate models, we determined that variables had strong support of an effect if the model outperformed the null by ≥ 2 WAIC and had a credible effect. If more than one variable was supported in the same covariate group, we modeled the variables together to determine which combination was the top model for that group. We created all permutations of supported variables and ranked them WAIC to determine which combination best fit the data. We considered the addition of a variable to be beneficial if it lowered the WAIC value by ≥ 2. If only one univariate model from a group was considered supported, we used that as the top model. We focused our results on variables in the top model with 95% credible intervals (CRI) that did not overlap zero.

Resource selection analysis

We analyzed location data for the nonbreeding season (November - 19 February) from scaled quail coveys. We used coveys as the experimental unit for this analysis because covey affiliation was strong among birds. We defined a covey as a group with > 2 birds that were located together for ≥ 7 days. We calculated separate home ranges for all coveys with ≥ 30 locations using the fixed kernel density method (Worton 1989) with the adehabitatHR package version 0.4.19 (Calenge 2006) in Program R (version 4.2.1, R Core Team 2021), and defined our home range extent as the 95% isopleth for each covey. Our 95% utilization distributions encompassed points used by coveys across the day and at night. All coveys had ≥ 18 roost locations included in their home range estimation. We defined availability as within home range utilization distributions to assess potential non-random habitat use. For every point used by a covey, we generated 5 random available points within each covey’s home range.

We investigated resource selection by scaled quail coveys at two different scales. The first scale included fine-scale vegetation measurements at the array level (within 15m) for percent cover of plant functional groups such as shrubs, forbs, and grasses, as well as ground cover estimates for bare ground, litter, and rock. We also included measurements for vertical obstruction across two height classes: low and tall. The second scale examined broader vegetation metrics by using land cover classes that included herbaceous, cropland, and shrubland. We classified land cover within all home ranges using these three cover categories. This second scale also incorporated the arrangement of landscape features, such as artificial cover structures, stock tanks, tree cholla, anthropogenic areas, and oil and gas developments.

We used the INLA package (version 22.05.07, Rue et al. 2009) in Program R to fit all binomial selection models using integrated nested Laplace approximation (INLA). We used the created univariate mixed-effects models for a logistic regression in a Bayesian framework. We fit mixed-effects models with use as the response variable and explanatory variables included covariates accounting for vegetation measurements, land cover, and distance to landscape features (Table 2). We assigned used points a weight of 1 and available points a weight of 1000 (Muff et al. 2020). To account for variability in selection among coveys, all models included a random intercept for covey and a random slope for all explanatory variables (Muff et al. 2020, Gillies et al. 2006). We assigned the random intercept for covey a large, fixed variance of 10^6 so that covey intercepts were not shrunk towards an overall mean (Muff et al. 2020). We used a penalized complexity prior for the precision of the random slopes (Muff et al. 2020, Simpson et al. 2017).

In the first step of our model selection, we ranked 16 univariate models using Watanabe-Akaike Information Criterion (WAIC) values (Watanabe and Opper 2010). The array scale of the analysis included 7 models and the landscape scale had 8 models. We used WAIC and credible intervals to select variables included in the next modeling stage. Models with WAIC ≥ 2 from the null were considered competitive (Burnham and Anderson 2002). The credible intervals of the posterior distributions that did not overlap 0 were considered strong support of either a positive or negative effect of a variable (Hespanhol et al. 2019, Hooten and Hobbs 2015).

If a model was considered competitive and had a variable with a credible effect (credible interval did not include 0), we considered that variable to be supported as influencing selection. We included all supported variables in a series of final models to further assess their importance and effect sizes. At both the array and landscape level, we created as many permutations as possible for our model variables. We calculated WAIC scores for all models and ordered them by ascending WAIC. We considered the model with the lowest WAIC value to be the best of that group. Once a top model was determined by WAIC, we interpreted results for all fixed effects, but focused our interpretation on variables with credible intervals that did not include 0.

Results

We monitored survival of 154 radio-marked scaled quail from 11 coveys during September – February of 2020-2022 (Figure 1). Each monitoring period consisted of 172 days, for a total of 344 exposure days. Seven quail from the 2020-2021 season were recaptured and given new radio-collars in 2021-2022. After removing quail that did not survive >7 days post-capture (*n* = 21), single quail not in a covey (*n* = 2), and coveys that went missing (*n* = 1), the diurnal survival analysis included 126 quail from 10 different coveys. Of these quail, 56 were adults and 70 were juvenile. There were 71 known mortalities, 51 birds were still alive at the end of the monitoring period (late February each year), and 4 birds that had unknown fates (individual lost, collar failure, etc.). We lost 14% of radio-collared birds less than 7 days after capture, which was largely attributed to avian predation (*n* = 8) and collar slips of juvenile birds that were not recollared (*n* = 4). Our trapping efforts occurred during the fall raptor migration (Goodrich and Smith 2008) and may have contributed to the high mortality rates documented during trapping.

Only one death documented < 7 days post-capture was presumed to be related from trapping stress, where the carcass was found within 15 m of the trap site with no obvious signs of predation. Death of radio-collared individuals was most attributed to predation by mammals or raptors, but some were linked to anthropogenic activity. We documented 4 birds harvested by hunters, 2 drowned in water tanks, and 1 hit by a vehicle. Another notable cause of mortality was Winter Storm Uri from February 13th-17th, 2021. This period had an average maximum daily temperature of -11°C and 3.30 mm of precipitation. Of the 25 radio-collared quail still being monitored, 16% (n = 4) died during the storm.

Survival analysis

We estimated the nonbreeding season (November-February) survival of scaled quail to be 0.50 (95% CRI: 0.41 to 0.57). Survival estimates across the 2020-2021 and 2021-2022 seasons did not differ significantly, but survival was lower during 2020-2021 (0.42, 95% CRI: 0.26 to 0.58) than in 2021-2022 (0.55, 95% CRI: 0.45 to 0.66). We did not include covey size or season within our survival models as WAIC values and credible intervals did not support a strong effect of these variables.

There was no evidence of an effect of age or sex on diurnal survival of scaled quail, as no models containing individual characteristics, including age and sex, outcompeted the null model (Table 3). Similarly, our models that included weather variables did not have clear support of an effect on survival. Specifically, the models containing mean daily temperature (°C) and mean wind speed (m per s) did not outcompete the null model. The model including days with precipitation did outcompete the null by > 2 WAIC, but the credible interval contained 0, indicating a weak effect on survival.

The only model in the vegetation cover group that outcompeted the null model was the one that included percent shrub cover (Table 3). Higher amounts of low-level shrub cover

(<1.5m) had a strongly negative relationship with survival of scaled quail. Individuals within coveys that used areas with high percent shrub cover had lower survival. The models including tall vertical obstruction, low vertical obstruction, percent grass cover, percent forb cover, and percent bare ground did not perform better than the null model.

Of the landscape features models, distance to tree cholla, distance to stock tanks, distance to artificial cover structures, and distance to anthropogenic areas all performed better than the null model (Table 3). Distance to anthropogenic areas did not have a credible effect (CRI included 0) so there was not a strong effect on survival, and it was not included in further model stages. Distance to tree cholla, distance to stock tanks, and distance to artificial cover all had credible effects. No model combinations of these three variables produced a model with a WAIC score lower than tree cholla alone (Table 4).

The model only including tree cholla was the best fit for the data and the top model explaining the survival of scaled quail to landscape features. There was strong support of a negative relationship between proximity to tree cholla and survival. Birds within coveys that used locations closer to tree cholla had lower survival.

Vegetation structure and composition

We recorded 4,841 diurnal locations and measured vegetation characteristics at 264 used and 354 available points. We found that scaled quail coveys used locations with greater amounts of forbs, less grass cover, and greater percent vertical obstruction than what was recorded at available points (Table 5). There were no significant differences between shrub cover (<1.5m tall), cactus cover (not including tree cholla), bare ground, rock, or litter. Coveys did not use areas with significantly different slope from what was randomly available on the landscape. Points used by coveys had greater tall shrub and tree density. Of the tall shrubs (> 1.5m) that occurred at used points, 85% were tree cholla and 15% were sand plum (Figure 3). No sand plum taller than 1.5m was recorded at available locations. Of the 145 used points that had tall shrubs or trees within 100m, 67% of them had trees.

Resource selection analysis

The model that included tall shrub density, tall vertical obstruction, and percent grass cover was the top model explaining diurnal resource selection at the array scale (Table 6, Table 7). The density of shrubs taller than 1.5m had the largest effect on scaled quail use. Coveys strongly selected for points with high amounts of tall shrubs within 100m of a point. They also selected points with increased amounts of tall vertical obstruction and avoided areas with higher amounts of grass cover than what was available.

At the landscape scale, the top model included cropland cover, herbaceous cover, and distance to anthropogenic areas (Table 7). Scaled quail coveys strongly selected for locations closer to anthropogenic areas and avoided using cropland during the day. Including herbaceous land cover improved model fit but this variable lacked strong support for either a negative or positive influence on selection.

Discussion

Our results indicated that vegetation structure and landscape features were important for scaled quail during the nonbreeding season. Space use and survival was largely driven by the availability of loafing cover. Coveys strongly selected for locations with higher density of tall shrubs and anthropogenic areas. Tall shrubs, such as tree cholla, and anthropogenic areas with an assortment of man-made cover were used heavily for cover. Coveys also avoided locations with high percent grass cover and areas with cropland cover. Scaled quail survival was lower in areas with high amounts of low-level shrub cover and for birds closer to cholla cactus. While scaled quail coveys selected for locations closer to anthropogenic areas, there was not a significant effect of distance to anthropogenic areas on survival.

Scaled quail use areas with open ground that facilitates easy movement between patches of grass, shrub, and cactus cover (Bristow and Ockenfels 2006, Goodwin and Hungerford 1977). Vertical cover should be balanced with an open understory that allows birds to move efficiently. As scaled quail feed primarily on seeds provided by forbs during the winter (Schemnitz 1961), forb cover can provide both food and tall screening cover with an open understory. Similarly, we found that scaled quail avoided areas with higher amounts of grass cover, which further supports their use of early seral stage shrublands (Saiwana et al. 1998). Areas with greater percent cover of grasses can reduce bare ground availability, which is important for survival of scaled quail, as they are believed to prefer running rather than flying (Silvy et al. 2007, Schemnitz 1961). Without areas of exposed bare ground or cover that is open at the ground-level, scaled quail may be increasingly limited in their ability to outmaneuver predators. However, not all landscapes that provide tall vertical obstruction and an open understory are suitable for scaled quail, as supported by their avoidance of cropland cover in our study. Scaled quail population abundance has been shown to be negatively correlated with cropland, particularly when cropland patches become larger and more homogeneous (Rho et al. 2015, Bridges et al. 2002). While cropland can provide winter food near loafing/escape cover supplied by man-made structures that are associated with agricultural practices (e.g., old machinery, brush piles), large patches of cropland cover may not provide resources needed to sustain scaled quail coveys throughout the year (Schemnitz 1993, Schemnitz 1961). The avoidance of cropland by scaled quail coveys may indicate that this land cover class does not meet all resource requirements, such as food and cover, throughout the nonbreeding season.

In the sandsage-grassland community, sandsage and soapweed yucca are widely distributed and used heavily by scaled quail during the spring and summer (Schemnitz 1961). While sandsage and soapweed yucca provide sufficient cover for scaled quail during the breeding and brooding periods, they are apparently inadequate during the winter months, as they do not offer suitable loafing cover (Snyder 1967, Schemnitz 1961). For example, sand sagebrush is considered deciduous in winter (Schultz 2012), which may limit the overhead cover afforded by this shrub during the nonbreeding season. We found scaled quail coveys that used areas with higher amounts of low-level shrub cover (i.e., sand sagebrush and soapweed yucca) had lower survival. During the winter, scaled quail require cover that provides protection from wind, temperature, and avian predators. Soapweed yucca and sand sagebrush may provide sufficient cover when birds move in pairs or with broods but generally lack the structure and size needed to provide cover for larger groups (Schemnitz 1961). The size of cover may need to be larger to accommodate more birds as scaled quail move in coveys during the nonbreeding season. From previous research, the suggested size of loafing cover for scaled quail ranges from 1 to 1.3m^2 of cover, with larger cover needed for more birds (Stormer 1981). Sand sagebrush and soapweed yucca may not provide large enough areas of overhead and lateral cover to be used as loafing cover in winter. Further, as raptor populations peak in the fall and winter, predation pressure from avian predators may be the driving factor for the seasonal change in loafing cover requirements (Atuo and O’Connell 2017). Coveys need dense, sturdy overhead cover to provide both concealment and protection from raptors.

The presence of cover, such as sand plum thickets, tree cholla, and man-made structures, is an important component of covey home ranges during the nonbreeding season (Stormer 1981, Schemnitz 1961). We found that diurnal space use of scaled quail in the nonbreeding season was largely influenced by the arrangement of cover within their home range. Coveys selected for locations that had high densities of tall shrubs (mainly tree cholla) with tall vertical obstruction and increased proximity to anthropogenic areas. As shrub thicket availability was limited in and around the Cimarron National Grassland, coveys heavily used tree cholla and man-made structures within anthropogenic areas for cover. Anthropogenic areas that provided high densities of a variety of man-made cover in the form of buildings, old farm machinery, and brush were consistently used by coveys during the day. In northern portions of their distribution, scaled quail are known to make nonbreeding season movements from public lands to private properties with assorted man-made structures (Snyder 1967, Schemnitz 1961). While our covey sample size was limited, our results indicated that the availability of cover structures found in anthropogenic areas attracted and concentrated quail. Deficient cover within the sandsage-grassland community may limit its ability to retain scaled quail coveys during the fall and winter. The supplementation of cover through the addition of artificial cover and transplanting of shrubs, such as tree cholla and sand plum, has potential to increase space use of scaled quail. Other research pertaining to bobwhites have also supported that the availability of cover appears to be a limiting factor for fall and winter home ranges (Robinson 1957, Lehmann 1946).

While scaled quail readily use man-made structures, shrubs, and cactus for cover (Snyder 1967), little is known about how their arrangement can influence survival. Our results indicated a negative relationship between locations closer to tree cholla and daily survival of birds. The availability of cover that provide protective cover from predators and weather are important for scaled quail survival (Stormer 1981, Steele 1957). A majority of the tree cholla on the grassland were transplanted by managers as supplemental quail cover (Cable et al.1996). These transplants are often in areas deficient of cover, where low densities and inadequate interspersion of woody cover options may result in higher predation risk for scaled quail. While tree cholla is attractive cover for scaled quail coveys, it has the potential to draw coveys into areas otherwise deficient of other cover options, creating a potential ecological trap (Gates and Gysel 1978). Ecological traps occur when animals incorrectly assess habitat as good quality based on cues they use to select habitats (Battin 2004). For example, bobwhites in Missouri selected for woody cover associated with closer distances to trees in the winter, but increased proximity to trees was related to lower survival rates (Mosloff et al. 2021). While woody cover is a strong cue for habitat selection by quail, it may influence them to select for areas with higher predation risk. The limited availability of diverse escape cover within areas where isolated tree cholla have been planted may concentrate and focus predators, putting quail at risk if additional cover is not present. Similar results have been noted in nesting studies regarding Northern cardinals (*Cardinalis cardinalis*), where strong selection for nest sites in exotic shrubs significantly lowered survival during the beginning of the nesting season (Rodewald et al. 2009). Decreased survival rates of Northern cardinal nests may have been linked to an increased density of early nests within a limited diversity of shrubs, as a reduction in nest diversity can increase predation risk (Remes 2003). Similarly, scaled quail may also have increased predation risk where shrub diversity and availability are limited. Based on previous literature, the ideal distribution and density of loafing/escape cover for scaled quail has been suggested to be at least 1 cover option per 20-28 ha but up to 3 cover options per ha (Rollins 2000, Schemnitz 1961). As low densities of tree cholla may negatively influence survival during the nonbreeding season, it is important that managers consider the concentration, arrangement, and interspersion of cover across the landscape. Further, supplemental cover provided by transplanted tree cholla and man-made structures should only be provided in areas where other habitat needs of quail are met (Snyder 1970, Snyder 1967).

Conclusion

Our study provides more insight into the general ecology and management of scaled quail during the nonbreeding season. Specifically, we examined both survival and space use of scaled quail at the northern periphery of their distribution. From our findings, vertical obstruction provided by vegetation is important for cover but should be balanced with an open understory. Vegetation composition, particularly in the form of low-growing shrub cover and grasses, can be detrimental for survival if it becomes too thick for scaled quail to move through. Similarly, low-growing shrubs such as soapweed yucca and sand sagebrush may not provide sufficient loafing or escape cover throughout the year.

The arrangement of cover within covey home ranges can have important implications for both survival and space use. Without naturally occurring tall shrubs such as sand plum, scaled quail strongly selected for transplanted tall shrubs, including tree cholla, and readily used man-made structures as cover. Yet, the density and arrangement of these structures may influence survival, as seen through our findings that there was a negative relationship between survival and coveys that regularly used isolated tree cholla. While cover can be supplemented through transplanting shrubs and creating artificial cover structures, the arrangement of these tall shrubs and structures should be carefully considered, as there is likely a minimum threshold necessary to avoid negatively influencing survival.

Table 1. The variables included in the survival analysis to create univariate models investigating potential effects of individual characteristics, weather, vegetation cover, and landscape features on survival of scaled quail (*Callipepla squamata*) during the day. All data was collected in Morton County, Kansas, USA during the nonbreeding seasons (November – February) of 2020-2022.

Group	Parameters	Description
Individual		
	Age	Adult or subadult (1/0)
	Sex	Male or female (1/0)
Weather		
	Precip	Day with or without precipitation (1/0)
	Tavg	Average daily temperature (°C)
	Wind	Average wind speed (m per s)
Vegetation cover		
	Bare	Bare ground (%)
	Grass	Grass cover (%)
	Forb	Forb cover (%)
	Shrub	Low-level shrub (<1.5m) cover (%)
	Low vob	Low vertical obstruction (%)
	Tall vob	Tall vertical obstruction (%)
Landscape features		
	DistAnthro	Distance to anthropogenic areas (m)
	DistOilGas	Distance to oil and gas pumps (m)
	DistCholla	Distance to tree cholla (m)
	DistStock	Distance to stock tanks (m)
	DistArtCov	Distance to artificial cover structures (m)

Table 2. Candidate variables included in the diurnal resource selection analysis are listed below with descriptions and the scale at which they were included in the analysis. Data was collected from radio-marked scaled quail (*Callipepla squamata*) during the nonbreeding seasons (November–February) of 2020-2022 in Morton County, Kansas, USA.

Group	Parameters	Description
Array scale		
	Bare	Bare ground (%)
	Litter	Litter (%)
	Grass	Grass cover (%)
	Forb	Forb cover (%)
	Shrub	Low-level shrub (<1.5m) cover (%)
	Low vob	Low vertical obstruction (%)
	Tall vob	Tall vertical obstruction (%)
	Tall shrub	Density of tall shrubs (> 1.5m) within 100m
Landscape scale		
	DistAnthro	Distance to anthropogenic areas (m)
	DistOilGas	Distance to oil and gas pumps (m)
	DistCholla	Distance to tree cholla (m)
	DistStock	Distance to stock tanks (m)
	DistArtCov	Distance to artificial cover structures (m)
	Crop	Cropland land cover class (1/0)
	Shrubland	Shrubland land cover class (1/0)
	Herb	Herbaceous land cover class (1/0)

Table 3. Univariate models investigating the effects of individual characteristics, weather, vegetation cover, and landscape features on daily survival of radio-marked scaled quail (*Callipepla squamata*) in Morton County, Kansas, USA during the nonbreeding seasons (November–February) of 2020-2022. We used Watanabe-Akaike Information Criterion (WAIC) to evaluate and rank models. We considered models competitive if the ΔWAIC was ≥ 2 lower from the null. Bold indicates competitive models with credible effects (CRI does not contain 0). Mean estimates, upper and lower bounds of the 95% credible intervals, and the proportion of the posterior distribution with the same sign as the mean (*f*) are shown below.

Group	Model	Mean	2.5%	97.5%	*f*	ΔWAIC	WAIC
Individual							
	Null	-	-	-	-	0	758.2
	Age (adult)	0.031	-0.421	0.489	0.55	2.9	761.1
	Sex (male)	0.409	-0.068	0.874	0.95	166.9	925.1
Weather							
	Precip	-0.421	-1.214	0.531	0.83	0	754.8
	Null	-	-	-	-	3.4	758.2
	Tavg	0.345	0.058	0.627	0.99	3.9	758.7
	Wind	-0.038	-0.274	0.217	0.63	6.1	760.9
Vegetation cover							
	Shrub	**-0.330**	**-0.609**	**-0.062**	**0.99**	**0**	**752.9**
	Null	-	-	-	-	5.3	758.2
	Grass	-0.164	-0.416	0.081	0.90	6.9	759.8
	Tall vob	-0.055	-0.322	0.222	0.66	7.2	760.1
	Low vob	-0.270	-0.560	-0.003	0.98	7.2	760.1
	Forb	-0.089	-0.316	0.147	0.78	8.3	761.2
	Bare	0.012	-0.217	0.242	0.54	10.0	762.9
Landscape features							
	DistCholla	**0.523**	**0.212**	**0.872**	**1.0**	**0**	**743.0**
	DistStock	**0.425**	**0.136**	**0.717**	**1.0**	**7.1**	**750.1**
	DistArtCov	**0.405**	**0.134**	**0.683**	**1.0**	**7.2**	**750.2**
	DistAnthro	-0.217	-0.441	0.021	0.96	13.3	756.3
	Null	-	-	-	-	15.2	758.2
	DistOilGas	0.011	-0.292	0.329	0.52	17.8	760.8

Table 4. Top multivariate models containing significant variables affecting survival of scaled quail (*Callipepla squamata*) in Morton County, Kansas, USA from 2020-2022. Watanabe-Akaike Information Criterion (WAIC) was used to evaluate and rank models. The models with the lowest WAIC were considered the best for each group. Bold indicates fixed effects in top models that had credible effects (CRI did not include 0). Mean estimates, 95% credible intervals, and the proportion of the posterior distribution with the same sign as the mean (*f*) are shown below.

Group	Models	ΔWAIC	WAIC	Fixed Effects	Mean	2.5%	97.5%	*f*
Landscape features								
	DistCholla	0	743.0	**DistCholla**	**0.523**	**0.212**	**0.872**	**1.0**
	DistCholla + DistArtCov	2.3	745.3	DistCholla	0.426	-0.025	0.540	0.97
				DistArtCov	0.130	-0.302	0.540	0.73
	DistCholla + DistStock	2.8	745.8	DistCholla	0.503	-0.048	1.072	0.96
				DistStock	0.022	-0.526	0.553	0.54
	DistsCholla + DistStock + DistArtCov	4.9	747.9	DistCholla	0.445	-0.150	1.060	0.93
				DistStock	-0.046	-0.630	0.525	0.56
				DistArtCov	0.149	-0.287	0.549	0.75
	DistStock	7.1	750.1	DistStock	0.425	0.136	0.717	1.0
	DistArtCov	7.2	750.2	DistArtCov	0.405	0.134	0.683	1.0
	DistStock + DistArtCov	7.9	750.9	DistStock	0.230	-0.211	0.657	0.85
				DistArtCov	0.251	-0.144	0.666	0.89

Table 5. Summary statistics for vegetation variables measured at points used by scaled quail (*Callipepla squamata*) coveys during the day and randomly generated available points within 40-500 m of used points. All sampling was done during the nonbreeding seasons (November–February) of 2020-2022 in Morton County, Kansas, USA. Mean differences with a $p < 0.05$ were considered statistically significant and are in bold.

	Used				Available				
Variable	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	p-value
Shrub cover (%)	0.0	72.5	17.57	1.11	0.0	67.5	15.10	0.84	0.066
Grass cover (%)	0.0	97.5	42.34	1.75	0.0	112.5	50.65	1.68	**<0.001**
Forb cover (%)	0.0	105.0	19.60	1.31	0.0	90.5	15.81	0.99	**0.019**
Cactus cover (%)	0.0	15.0	0.32	0.09	0.0	15.0	0.32	0.07	0.970
Bare ground (%)	0.0	100.0	66.24	1.36	0.0	100.0	63.91	1.30	0.224
Rock (%)	0.0	22.5	0.11	0.09	0.0	22.5	0.07	0.06	0.688
Litter (%)	0.0	100.0	26.26	1.34	0.0	100.0	27.71	1.28	0.440
Tallest vertical obstruction (%)	0.0	67.9	3.57	0.59	0.0	41.9	0.83	0.17	**<0.001**
Tall vertical obstruction (%)	0.0	80.5	7.97	0.83	0.0	45.3	3.67	0.35	**<0.001**
Medium vertical obstruction (%)	0.0	90.5	24.28	1.23	0.0	87.2	17.64	1.00	**<0.001**
Low vertical obstruction (%)	0.0	90.5	55.63	1.48	0.0	90.5	48.97	1.39	**0.001**
Slope (degrees)	0.0	22.0	5.51	0.54	0.0	12.0	4.71	0.43	0.262
Tall shrub density (per ha)	0.0	383.8	4.72	2.20	0.0	10.7	0.08	0.03	**0.015**
Tree density (per ha)	0.0	946.7	8.73	4.22	0.0	10.66	0.5	0.29	**0.025**

Table 6. Univariate models created to investigate diurnal resource selection of scaled quail (*Callipepla squamata*) coveys in Morton County, Kansas, USA from 2020-2022. We included variables measured at both the array scale and landscape scale. We used Watanabe-Akaike Information Criterion (WAIC) to evaluate and rank models. We considered models to be competitive if ΔWAIC was ≥ 2 lower than the null model. Models that outcompeted the null and had credible effects (CRI did not overlap 0) are in bold. Mean estimates, 95% credible intervals, and the proportion of the posterior distribution with the same sign as the mean (*f*) are shown below.

Group	Models	Mean	2.5%	97.5%	*f*	ΔWAIC	WAIC
Array scale							
	Tall shrub	**5.779**	**3.150**	**9.753**	**1.0**	**0**	**4135.5**
	Tall vob	**0.805**	**0.150**	**1.505**	**1.0**	**19.6**	**4155.1**
	Forb	0.456	-0.063	1.004	0.96	44.1	4179.6
	Grass	**-0.364**	**-0.543**	**-0.198**	**1.0**	**54.8**	**4190.3**
	Shrub	-0.079	-0.587	0.359	0.63	57.1	4192.6
	Low vob	**0.266**	**0.105**	**0.425**	**1.0**	**64.1**	**4199.6**
	Null	-	-	-	-	72.8	4208.3
	Litter	0.159	-0.274	0.570	**0.80**	74.6	4210.1
	Bare	-0.021	-0.298	0.264	0.57	79.9	4215.4
Landscape scale							
	DistAnthro	**-3.132**	**-5.193**	**-1.322**	**1.0**	**0**	16517.3
	DistOilGas	0.481	-0.242	1.213	0.91	167.4	16684.7
	DistCholla	-1.703	-3.616	0.113	0.97	339.3	16856.6
	DistStock	0.412	-0.461	1.287	0.83	350.0	16867.3
	Herb	**0.466**	**0.024**	**0.907**	**1.0**	389.2	16906.5
	Shrubland	-0.019	-0.743	0.672	0.52	400.0	16917.3
	DistArtCov	0.648	-0.095	1.398	0.96	412.4	16929.7
	Crop	**-1.065**	**-1.500**	**-0.668**	**0.98**	**421.9**	**16939.2**
	Null	-	-	-	-	504.7	17022.0

Table 7. Top multivariate models containing significant variables affecting diurnal resource selection of scaled quail (*Callipepla squamata*) coveys in Morton County, Kansas, USA from 2020-2022. Watanabe-Akaike Information Criterion (WAIC) was used to evaluate and rank models. The models with the lowest WAIC were considered the best for each group. Bold indicates fixed effects in top models that had credible effects (CRI did not include 0). Mean estimates, 95% credible intervals, and the proportion of the posterior distribution with the same sign as the mean (*f*) are shown below.

Group	Models	ΔWAIC	WAIC	Fixed Effects	Mean	2.5%	97.5%	*f*
Array scale								
	Tall shrub + Tall vob + Grass	0	4051.0	**Tall shrub**	**8.038**	**5.222**	**11.149**	**1.0**
				Tall vob	**0.855**	**0.196**	**1.547**	**1.0**
				Grass	**-0.433**	**-0.694**	**-0.216**	**1.0**
	Tall shrub + Tall vob	16.3	4067.3	Tall shrub	6.788	4.361	10.323	1.0
				Tall vob	0.848	0.159	1.580	1.0
	Tall shrub + Grass	50.0	4101.0	Tall shrub	7.255	4.536	11.204	1.0
				Grass	-0.452	-0.683	-0.206	1.0
	Tall vob + Grass	97.4	4148.4	Tall vob	0.822	0.155	1.543	1.0
				Grass	-0.340	-0.588	-0.128	1.0
Landscape scale								
	DistAnthro + Crop + Herb	0	16329.4	**DistAnthro**	**-3.083**	**-5.236**	**-1.301**	**1.0**
				Crop	**-1.084**	**-1.813**	**-0.371**	**1.0**
				Herb	0.114	-0.457	0.700	0.66
	DistAnthro + Crop	86.5	16415.9	DistAnthro	-3.403	-5.771	-1.352	1.0
				Crop	-1.120	-1.590	-0.680	1.0
	DistAnthro + Herb	86.8	16416.2	DistAnthro	-3.132	-5.237	-1.320	1.0
				Herb	0.387	-0.051	0.823	0.96
	Crop + Herb	460.3	16789.7	Crop	-1.042	-1.936	-0.162	1.0
				Herb	0.155	-0.555	0.882	0.67

Figure 1. Locations of scaled quail (*Callipepla squamata*) coveys in Morton County, Kansas, USA during the 2020-2022 nonbreeding seasons (November–February). Coveys with birds monitored across both years are indicated by a half circle. The Cimarron National Grassland is denoted by the green polygons.

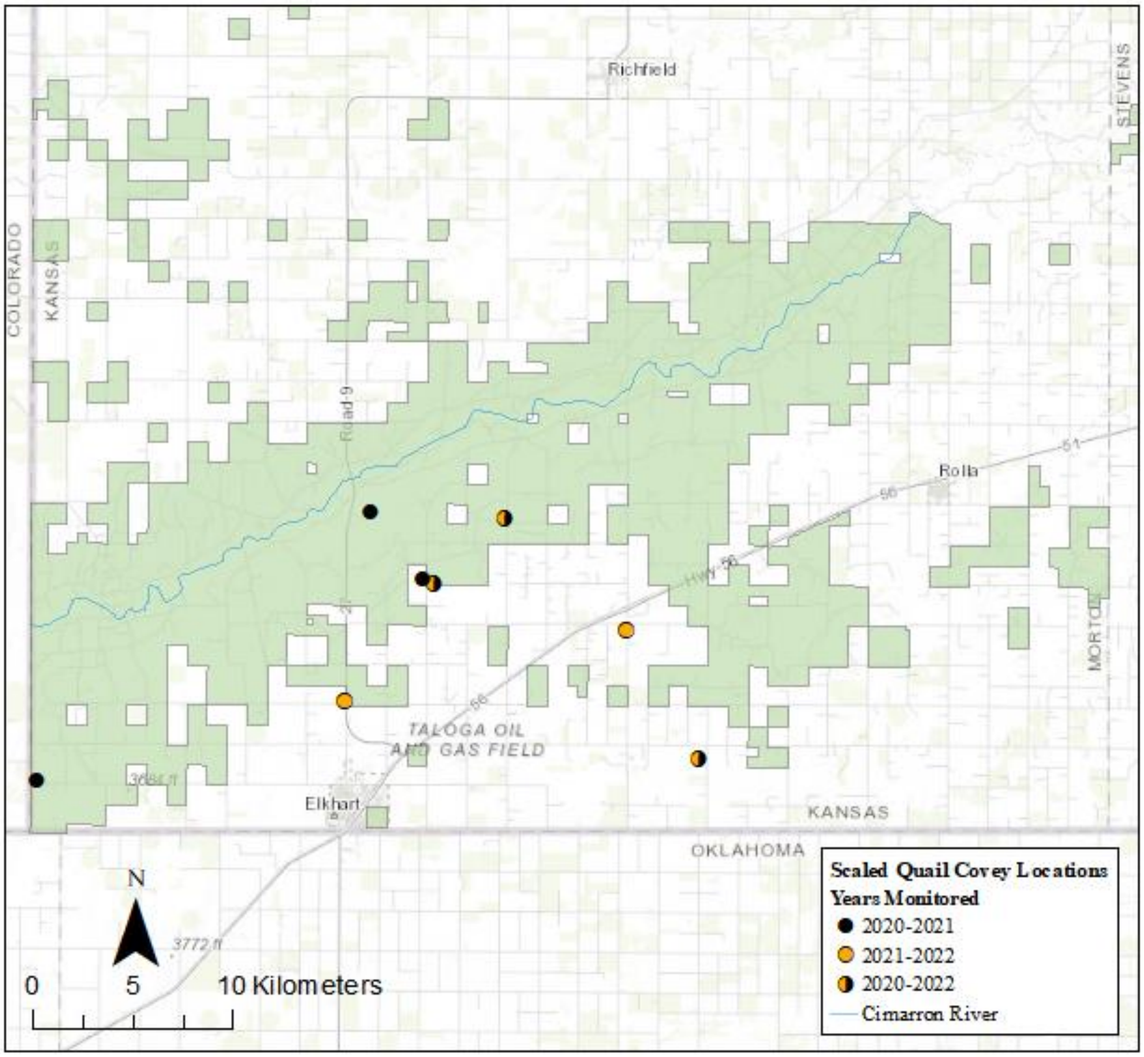


Figure 2. Diagram of 15 m vegetation sampling transects (array) used to measure vegetation composition and structure at used and available points. We used pin drops at 10 locations every 1.5 m along each of the four transects to assess percent cover of plant functional groups and ground cover categories. We measured average vertical obstruction using a Nudd's board at the centerpoint. Sampling points were either used by scaled quail (*Callipepla squamata*) or available points within 40-500 m from used points. Vegetation sampling was conducted in Morton County, Kansas, USA during the nonbreeding seasons (November–February) of 2020-2022.

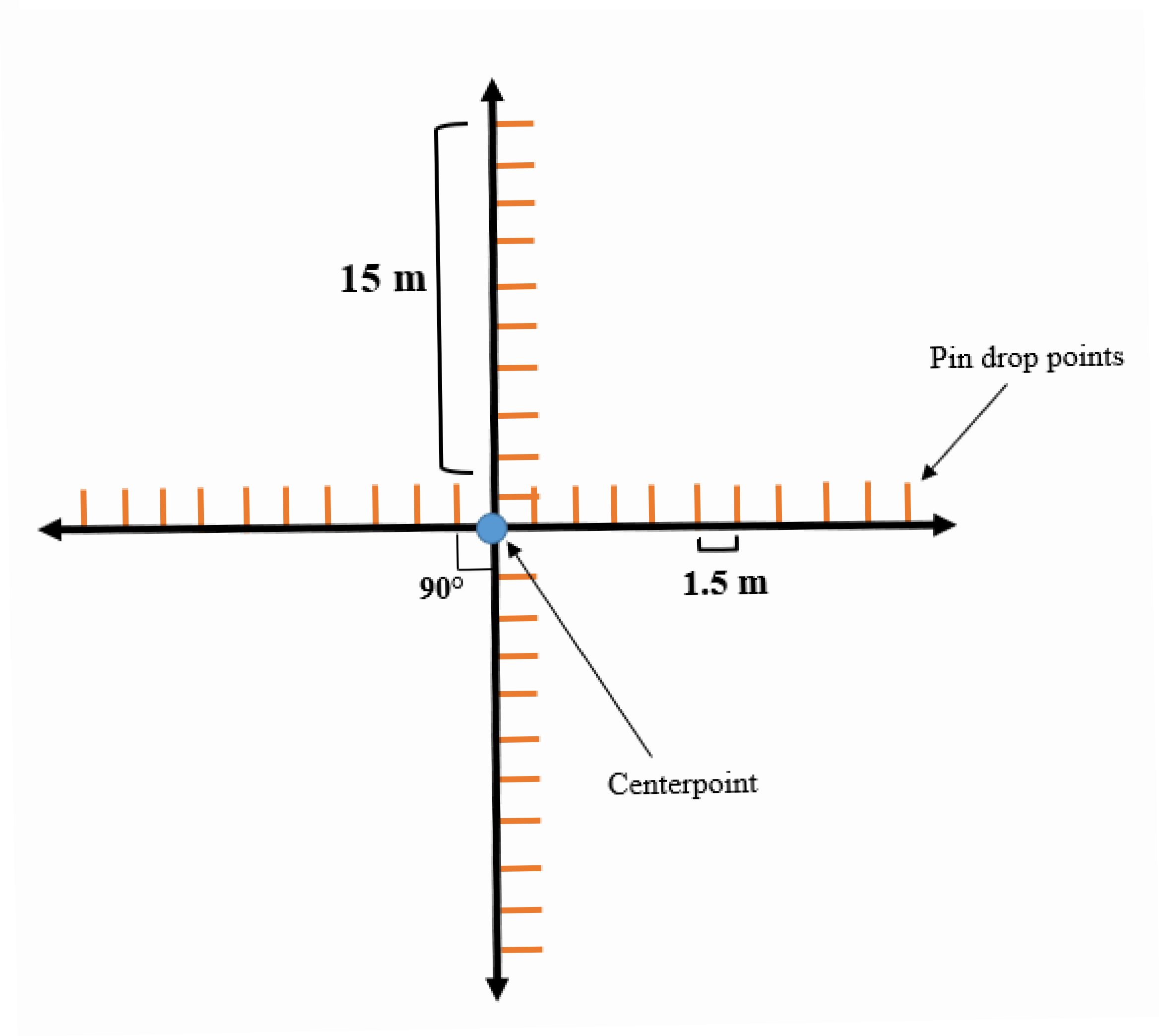
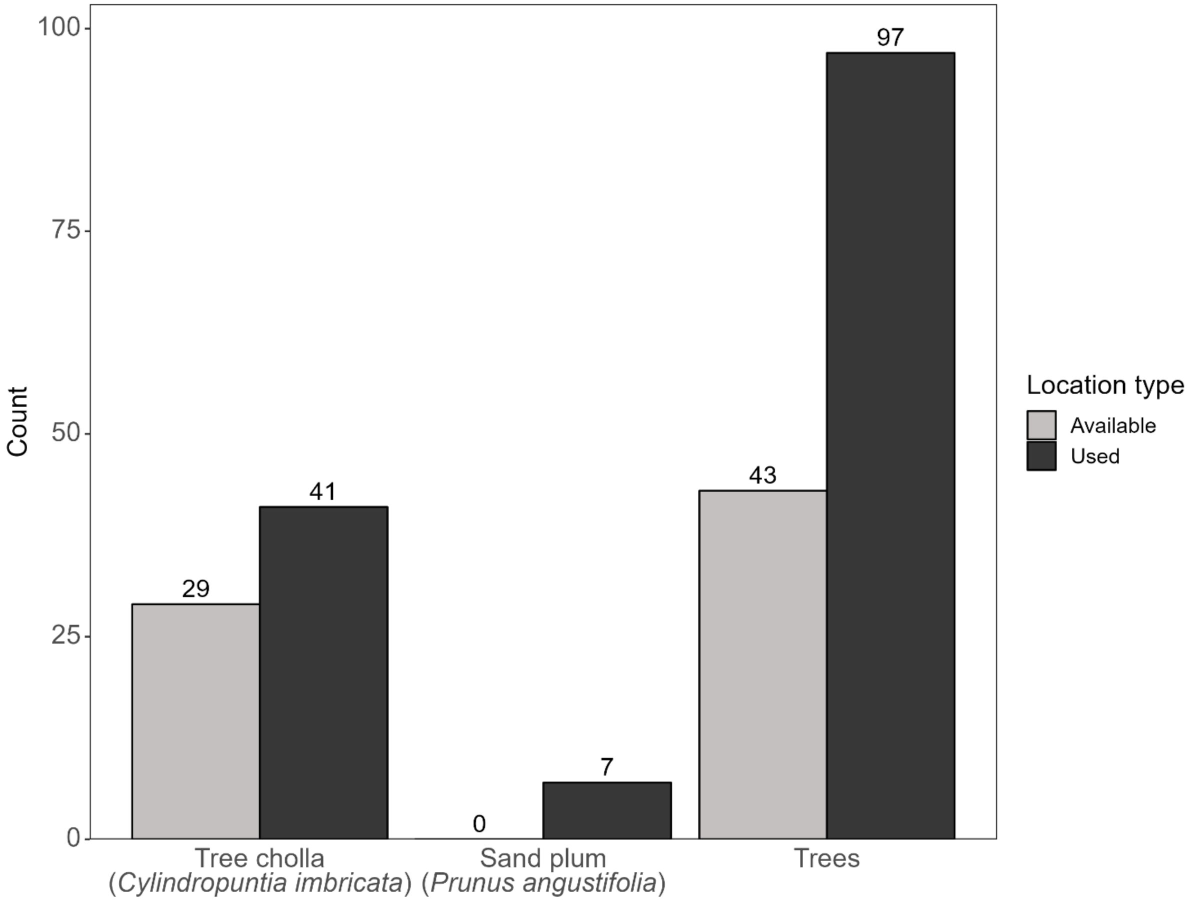


Figure 3. Point-centered quarter observations of tall shrubs (>1.5 m) and trees within 100 m of points used by scaled quail (*Callipepla squamata*) and available points within 40-500 m of the used point. Of the points that recorded either a tall shrub or tree within 100 m, 91 were used by scaled quail and 56 were available points. Tree cholla occurred most frequently of the two tall shrub species observed. Sand plum taller than 1.5 m was recorded at points used by scaled quail. Data was collected from Morton County, Kansas, USA during the nonbreeding seasons (November – February) from 2020-2022.



CHAPTER II

SCALED QUAIL ROOST SITE SELECTION AND SURVIVAL

Abstract

Scaled quail (*Callipepla squamata*) are a culturally and economically important gamebird that has experienced populations declines since the 1960s. Factors influencing their decline are not fully understood and limited research on this species has focused primarily on diurnal space use and survival. Without information that includes all aspects of scaled quail habitat requirements, managers are unable to make fully informed decisions. Our study provides insight into the effects of temperature, vegetation structure, and land cover on survival and nocturnal resource selection of scaled quail. We used radio-telemetry to monitor survival and roost site locations of scaled quail coveys in the nonbreeding season. Additionally, we collected vegetation measurements and thermal samples from roost points and available locations. Our study also included an experiment to determine the effects of late-evening flush events on communal roosting and survival of scaled quail. We found that coveys selected for roost sites with less grass cover and more low-level vertical obstruction 15 m around the roost. Coveys used roosts with colder temperatures than what was randomly available. Despite this, we found that lower average minimum daily temperatures were associated with lower nonbreeding season survival. Further, lower amounts of bare ground at roost points negatively influenced survival of scaled quail. Finally, we found that coveys flushed prior to nightfall frequently regrouped to roost together and did not have lower survival than groups that were not flushed. In summary, our results indicated that roost site selection was influenced by vegetation structure at the roost point. Further, the strong affinity for communal roosting suggests this behavior is important for overnight survival.

Introduction

Scaled quail (*Callipepla squamata*) occupy desert shrublands and grasslands of northern Mexico and the southwestern United States (Zornes and Bishop 2009). While listed as a species of Least Concern by the International Union for Conservation of Nature (IUCN 2020), scaled quail populations have declined over recent decades and reasons why are still not well understood (Brennan 1994, Church et al. 1993). Declines of up to 50% have been observed in populations in the northern periphery of their distribution and may be attributed to land use and land cover changes (Schemnitz 1993). Investigations into similar declines in other portions of this species' distribution support a negative correlation between scaled quail abundance and shifts in agricultural practices and/or changes in shrub cover (Bridges et al. 2002).

Research investigating factors that influence scaled quail populations is limited. Most studies that pertain to habitat use and survival of scaled quail focus largely on diurnal observations (Kauffman et al. 2021, Tanner et al. 2019, Pleasant et al. 2006), even though this only accounts for half of their annual time budget. As factors that affect space use and survival can change across temporal scales (Fisher et al. 2004, Boeker and Scott 1969), studies investigating nocturnal ecology are needed to ensure management recommendations account for all aspects of a species' habitat needs. Temperature variations, differences in predator activity, and anthropogenic activity can all cause shifts in nighttime resource selection that may differ from that observed during the day (Tanner et al. 2021, Lendrum et al. 2017, Moreno et al. 1996, Kufeld et al. 1988). Even species that are primarily diurnal can exhibit strong selection for nocturnal resting sites where vegetation characteristics are conducive to thermoregulation and provide concealment without obstructing escape from predators (Perkins et al. 2014, Tillman 2009, Tirpak et al. 2005).

While scaled quail roost site selection is understudied, limited research suggests that it differs from diurnal habitat selection. Scaled quail use tall mesquite (>2 m; *Prosopis glandulosa*), yucca (*Yucca angustifolia*), and tree cholla (*Opuntia imbricata*) as important components for diurnal loafing cover (Stormer 1981), but not for roost sites (Stormer 1984). Unlike other *Callipepla* species, scaled quail roost on the ground. Roost sites have previously been reported to occur in short herbaceous cover (<0.5 m) or on bare ground with no overhead canopy (Wallmo 1957, Stormer 1981, Stormer 1984). Further, roost sites were largely located in valley slopes and rolling breaks, indicating that topography may be a key characteristic of nocturnal habitat selection (Stormer 1984). This may be related to sunrise exposure and/or avoiding cold, dense air pockets that sink into low lying areas. Additionally, areas with roost locations had short, dispersed yucca but it is unclear whether selection was driven by the vegetation, topographic position, or both (Stormer 1984).

Another key factor influencing scaled quail roosting ecology is covey dynamics. During the nonbreeding season, scaled quail form large coveys but average covey size fluctuates throughout the species' distribution. Schemnitz (1961) observed 9 coveys over two years averaging approximately 37.4 birds per covey in northeastern Oklahoma, while other observations in New Mexico and southeastern Arizona averaged 13 birds per covey (Bristow and Ockenfels 2006). Coveys of up to 150 birds have been observed during the nonbreeding season in Texas (Wallmo 1957). During the nonbreeding season, scaled quail coveys sometimes break into smaller subgroups at night, as scaled quail roost in groups of 2-5 birds, forming a circle tail-to-tail with their heads outward (Wallmo 1957). The number of birds available for roost circle formation may be increasingly important during the colder nonbreeding season, particularly in low density populations. Understanding how covey dynamics can influence populations is important, particularly when it comes to their nocturnal behavior.

The presence of conspecifics can decrease thermoregulatory costs for birds that form communal roosts (Beauchamp 1999) and might have greater benefits for species with a higher surface-to-body mass ratio (Merola-Zwartjes 1998). The reduction in thermoregulatory costs can be particularly important during the nonbreeding season when extreme low temperatures may occur. At the northern periphery of their distribution, bobwhites experience high levels of winter mortality (Leopold 1937, Errington 1936) that may correspond to increased snow accumulation over prolonged periods of time (Janke 2017). A study conducted on wild bobwhite indicated that communal roosting could be energetically beneficial at temperatures <16.2° C and roosting behavior may be especially advantageous during winter (Hiller and Guthery 2005). Further studies conducted in laboratory settings have also supported that thermal stress caused by lower temperatures influences energy needs of quail. The metabolic rates of winter-acclimated bobwhites were strongly related to operative temperature at temperatures < 24.1°C and increased linearly with wind speeds at both -15° C and 0° C (Burger et al. 2017). Another investigation concluded that lone quail had higher energy demands than those in roost circles when temperatures were <5° C (Case 1973). Further, the composition and arrangement of individuals within a roost circle fluctuated depending on temperature. Captive bobwhites formed compact circles more frequently in lower temperatures (Case 1973). The number of quail within a roosting formation may be essential to efficient thermoregulation, as too few or too many individuals influence how compact the formation will be. The ability of the covey to regulate heat loss is directly proportional to the size of the covey, with notable decreases in individual survival for smaller coveys (Gerstell 1939).

Communal roosting in scaled quail may also be an adaptation for predator avoidance. The increased number of birds may benefit the covey as more individuals are aware of predators and can cause decreased individual risk (Beauchamp 1999). Additionally, the formation of roost circles may reduce predation as the group flushes collectively, startling or confusing the predator (Case 1973). However, scaled quail flushed before going to roost may not regroup and it is unknown how this affects overnight survival if birds are unable to rejoin into a group for the night. As observed by Wallmo (1957), a covey disturbed while roosting (i.e. after sunset) did not reassemble until the following morning. This can have detrimental effects on individual fitness because there will be increased energy demands without the thermoregulatory benefits provided by the covey and birds could be more vulnerable to predation or environmental exposure after expending energy to flee.

Activities that cause birds to flush can alter covey composition which may have indirect effects on individual quail survival. An investigation into the effects of hunting on bobwhite covey behavior in South Carolina showed that 86% of the hunted birds regrouped by dusk after being flushed and that 94% of coveys that were accidentally flushed regrouped within 24 hours (Dixon et al. 1996). Further, the regrouping of experimentally hunted coveys did not appear related to the time of day (mid-morning vs mid-afternoon) when they were flushed (Dixon et. al 1996). However, this is one of the only studies that provides insight into the effects of flushing on covey behavior during the nonbreeding season. Despite this, some state wildlife agencies restrict late afternoon hunting as a cautionary rule to limit potential roost disruption. For example, hunters in Oklahoma must stop hunting quail at 4:30 PM on some wildlife management areas due to the belief that disturbing coveys prior to them roosting may be detrimental to their survival (Oklahoma Department of Wildlife Conservation, pers. comm.). Further research on the effects of late evening flush events may provide more insight into the ramifications of late afternoon disturbance/hunting on roost site selection and survival during the nonbreeding season.

Given the potential importance of roost site selection and covey dynamics in scaled quail thermoregulation and predator avoidance, it would benefit managers to have a more comprehensive understanding of scaled quail roosting ecology. Roost site availability and dispersion across the landscape may be a limiting factor for some populations of scaled quail, especially for those on the periphery of their distribution where temperatures may be more extreme. Covey dynamics are another important aspect of roosting ecology, but research related to the role it plays in survival of scaled quail is limited. Our research objectives were to 1) examine roost site selection and survival of nonbreeding scaled quail and 2) investigate the effects of late evening disturbance on roost circle formation and survival. We hypothesized that scaled quail would select roost sites based on thermoregulatory benefits provided by the microclimate at the roost point. We also hypothesized that late-evening disturbance would not negatively influence survival and covey roost circle formation of roosting scaled quail.

Methods

Study site

The Cimarron National Grassland (hereafter, CNG) is 43,477ha of public land that is managed by the U.S Forest Service. The grassland is primarily within Morton County in southwestern, Kansas, near the city of Elkhart. Most of the land was acquired from farmers devastated by the Dust Bowl during 1930s (Hurt 1985). Morton County was one of the most wind-eroded and soil degraded counties in the nation, with as much as 78% of the land considered seriously damaged (Joel 1937). The Soil Conservation Service (now known as the Natural Resources Conservation Service) restoration initiatives prioritized topsoil regeneration, reestablishment of vegetation, and decreasing water runoff (Guest 1968, Lewis 1989). Administration of the land was transferred to the U.S Forest Service in 1954 and management now emphasizes “multiple use” objectives that include grazing, mineral production, recreation, and wildlife habitat.

The CNG is characterized as semi-arid, with a mean annual temperature of 13 °C and an average annual precipitation of 381 mm (Guest 1968). Much of the precipitation occurs from April to September (Cable et al. 1996). The growing season averages about 178 days (McLaughlin 1942). Morton County has predominately flat topography with elevation that ranges from 1,128 meters in the west to 960 meters in the east (McLaughlin 1942). The Cimarron River flows through the middle of the CNG. Plains cottonwoods (*Populus deltoides*) grow along the river's flood plains. Lands north of the river are mainly shortgrass prairie with sandy loam soils (Guest 1968). The shortgrass prairie consists of warm-season grasses such as purple three-awn (*Aristida pupurea*), blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), western wheatgrass (*Elymus smithii*), ring muhly (*Muhlenbergia torreyi*), and sand dropseed (*Sporobolus cryptandrus*) (Kuhn et al. 2011 The south side of the river is primarily sandsage prairie with mostly sandy soils (Kuhn et al. 2011, Guest 1968). The sandsage prairie is dominated by dense stands of sand sagebrush (*Artemsia filifolia*), rubber rabbitbrush (*Ericameria nauseosa*), and yucca (*Yucca glauca*) (Kuhn et al. 2011). There are also scattered occurrences of sand plum (*Prunus angustifolia*) and tree cholla (*Cylindropuntia imbricate*). A majority of the tree cholla was transplanted by biologists to provide wildlife habitat (Cable et al. 1996). Some commonly occurring forbs are western ragweed (*Ambrosia psilostachya*), pigweed (*Amaranthus spp.*), sand lily (*Mentzelia nuda*), and lavenderlead sundrops (*Oenothera lavandulifolia*) (Cable et al. 1996). Russian thistle (*Salsola pestifer*.) is an introduced forb that has spread throughout the grassland (Long 1941).

Quail populations on the grassland are thought to be limited by cover and water. Around the 1960s, managers began adding artificial cover structures and guzzlers. Cover structures consist of man-made wooden teepees and quail shelters that provide overhead cover. Grazing exclosures were also used to fence off portions of the grassland to create patches with dense cover. Guzzlers and cover structures are sometimes included in grazing exclosures to minimize damage from cattle (J. Prendergast, KDWP, pers. comm.).

Capture and radio-telemetry

We used baited walk-in funnel traps (Stoddard 1931) to trap scaled quail in the fall (September through October) of 2020 and 2021. We also located previously collared birds to aid in capturing additional birds within coveys using spotlighting and night-netting as described by

Labisky (1968). We focused trapping efforts primarily south of the river, due to higher scaled quail abundance in the sandsage prairie (K. Schultz, KDWP, pers. comm.). We weighed (g), aged (adult vs. subadult), and sexed (male vs. female) all trapped scaled quail based on plumage characteristics (Cain and Beasom 1983, Wallmo 1957). Due to difficulty in determining sex by appearance alone, we also collected feather samples for genetic confirmation of sex. We fit individuals weighing > 120 grams with a whip antennae radio transmitter necklace ranging from 5.0 to 6.5 g (American Wildlife Enterprises, Monticello, Florida , USA). Bobwhites or scaled quail weighing < 120 g were aged, sexed, banded, and released. We conducted trapping and handling with approval from Oklahoma State University under IACUC-20-18 and under permits number SC-086-2020 and number SC-116-2021 from the Kansas Department of Wildlife and Parks.

Due to low densities of scaled quail, our trapping efforts largely focused on known covey locations as observed by biologists, technicians, and cooperating landowners. We were concerned that our monitored birds may have been biased to locations near human development, so we ran an additional 60 stratified random traps in attempts to locate unknown coveys. We constrained trap locations within a polygon that encompassed around 9,300 hectares of public land mainly consisting of sandsage-grassland south of the Cimarron River. We also included traps that sampled roads along the Cimarron River, even though we believed scaled quail would avoid the dense tree canopy associated with riparian areas. We generated traps within 15 m of roads to enable easy access so we acknowledge there could be a road bias with our data.

We located all radio-marked birds a minimum of three times per week via homing until February each year. Coveys were tracked during different hours of the day (morning, mid-day, and afternoon) to ensure that scaled quail locations were not biased by the time of day. We used a combination of homing and triangulation techniques (White and Garrot 1990) to obtain approximate locations for coveys and attempted to minimize disturbance to the birds.

Vegetation and thermal sampling

We collected weather data including days with precipitation events (0/1), daily average temperature (C°), daily minimum temperature (C°), and daily average wind speed (m/s) throughout the field seasons from the weather station in Richfield, Kansas (37.259, -101.792) (Kansas Mesonet). This station was approximately 15 miles from the grassland and 24 miles from Elkhart, KS. We also included percent moon illumination data from the U.S Naval Observatory (https://aa.usno.navy.mil/data/MoonFraction). Wind chill was calculated using the following formula provided by the National Oceanic and Atmospheric Administration:

$$Wind\ Chill\ (°\mathrm{F}) = 35.74 + 0.6125T - 35.75(V^{0.16}) + 0.4275T(V^{0.16})$$

T = Air Temperature (°F)

V = Wind speed (mph)

Wind chill was calculated by converting temperatures from Celsius to Fahrenheit and wind speeds from kilometers per hour to miles per hour. We only calculated wind chill for temperatures below 50 °F and wind speeds > 3 miles per hour. We then converted wind chill back to Celsius to be consistent with other temperature measurements included in the analysis.

We conducted vegetation sampling at locations used by scaled quail and at random (available) points. We generated one available location that had a random bearing between 0 to 359° and was within 40 to 500 meters of used points. We limited available points to at least 40 meters from used points to avoid overlap of vegetation sampling. We used a maximum possible distance of 500 meters based on the average daily distance traveled by scaled quail in northwest Oklahoma from a previous study during the nonbreeding season (October 1st – March 31st; E. P. Tanner, unpublished data).

We used the line-point intercept method (Canfield 1941, Herrick et al. 2005) to assess percent cover of plant functional groups (grasses, forbs, and shrubs ≥ 1.5 meters) and ground cover (bare ground, rock, and litter) at both used and random locations. The centerpoint for our transects were coordinates from covey locations or randomly generated available points. From the centerpoint, we generated a random bearing between 0 to 359° to establish the direction of a 15 m transect. We then sampled an additional 3 transects at 90° intervals from the first so that a total of 4 transects were sampled at each point. We dropped a sampling pin from a height of 76 cm every 1.5 m along the transect tape (Caratti 2006) for a total of 40 pin drops at each location. We recorded every layer that touched the pin on the way to the ground as a "hit" for vegetation groups, therefore multiple vegetation layers were possible for each transect pin. We categorized the ground surface as bare ground, rock, litter, snow, or a vegetation functional group if covered by a plant. We identified shrubs to the species, with other plants grouped as either a forb or grass. We calculated percent cover for each cover category at each transect. We then averaged percent cover for all functional groups and ground cover classes across the four transects.

We used a Nudds profile board (Nudds 1977) modified for sand shinnery oak communities (Guthery 1981) to assess vertical vegetation cover and structure. The profile board was 2.5 m tall and 30.48 cm wide with 12 alternating 21 cm intervals marked with black and white colors. We placed the board at the center of scaled quail locations or available points. We recorded readings from 15 m away at a height of 1 m, with the board facing four different bearings that were 90° apart. We estimated the amount of vertical obstruction from surrounding vegetation as a density score with the following categories: 1=0 to 20%, 2=21 to 40%, 3=41 to 60%, 4=61 to 80%, and 5=81 to 100% (Nudds 1977). We converted each density score into a midpoint percent value, with 1=10%, 2=30.5% 3=50.5%, 4=70.5%, and 5=90.5%. We grouped the profile board strata into three different vertical obstruction classes: low (1-3), medium (4-6), tall (7-9), and tallest (10-12). Once grouped, we averaged all midpoint percent values for the height classes across all four transects to calculate percent vertical obstruction for low, medium, tall, and tallest cover classes. The tallest and medium percent vertical obstruction categories were not used in any of the analyses, as they were highly correlated ($r \geq 0.7$) to low and tall categories. Low and tall vertical obstruction were moderately correlated ($r = 0.43$), so we used WAIC values from the univariate models to decide which variable to include in our final models. If both variables were considered significant enough to include in the next modeling stage, only the one with the lowest WAIC value was included.

We assessed the density of trees and shrubs taller than 1.5 m using the point-centered quarter method (Cottam and Curtis 1956). We used the use and random locations as the centerpoint for our sampling unit. The sampling unit around each point was divided into four equal quarters (90°) to determine the distance to the nearest tree or tall shrub (> 1.5 m). The bearings used for the quarters corresponded with the bearings used for the vegetation sampling transects. If there were multiple trees or tall shrubs in the quarter, we only recorded the one closest to the centerpoint. All tall shrubs were identified to species. We were unable to identify tree species due to lack of foliage during the fall and winter. For each quarter, a laser range finder was used to record the distance (m) from the centerpoint to the closest tall tree or shrub. If there were no tall shrubs or trees within the quarter, we did not collect data for that quarter’s tall shrub and tree density.

We added additional vegetation sampling methods to provide a more precise assessment of vegetation cover and composition directly at roost sites. We returned to roost locations the following morning to search the area for fresh roost piles. We searched the area by scanning the ground for the fecal pile while circling the midpoint of the coordinates recorded for the roost site. If found, roost piles were flagged for future vegetation sampling. If no fecal pile was located, we used the midpoint of the roost coordinates to conduct vegetation sampling. If multiple roost piles were found, we conducted vegetation sampling at the roost pile that was closest to the roost point coordinates from the nighttime telemetry. At each roost point, we used a 0.5 m x 0.5 m cover frame centered over the fecal pile or the approximate roosting location to estimate ground cover composition for roost site locations. We estimated percent cover for functional groups such as bare ground, rock, litter, grass, forb, and short shrubs less than 1.5 m tall. All functional groups were recorded as a cover class of percent cover using the following categories: 0=0%, 1=<5%, 2=5-25%, 3=25-50%, 4=50-75%, 5=75-95%, and 6=95-100% (Daubenmire 1959). Each cover class was then assigned to a percent value based on the midpoint of the cover class range with 1=2.5%, 2=15.0%, 3=37.5%, 4=62.5%, 5=85.0%, and 6=97.5%. We also recorded the height (cm) of the tallest vegetation above the cover frame.

We attached a digital level to the Nudd's board to measure 8 angles (evenly spaced and pivoting around the point) of overhead visual obstruction from the roost point to calculate an average angle of obstruction (Kopp et al. 1998). We lowered the board until it hit the tallest nearby vegetation and repeated this at even intervals until we obtained 8 angles over the roost site. We recorded angles in degrees between 0-90°.

We used temperature data-loggers (Thermochron ibuttons; hereafter, ibuttons) to collect temperature samples at roost sites for 24 hours. The ibutton logged temperature (°C) every 15 minutes. We censored temperature data to only include records from 18:00-6:00 to assess temperature experienced by birds when roosting. We attempted to sample during weather periods that were similar (±5°C) to those that the roosting quail experienced while using that site but as close to the day of roosting as possible. If forecasts indicated extreme precipitation events (e.g., blizzards), we did not conduct roost site thermal sampling, unless conditions matched a previous roost location. We attached ibuttons to metal stakes and inserted them into the ground so that they were approximately 10 cm above the surface to simulate temperatures experienced by the body core of an adult scaled quail. Metal stakes were used to hold ibuttons because a previous study found there was no statistical difference between temperatures collected from loggers placed on metal, wood, or plastic stakes (Kauffman et al. 2021).

Flushing experiment

We randomly assigned each covey as either a control or treatment covey. For control coveys, we located the covey >1 hour past official sunset by approaching roosting birds until we were approximately 10-30 m from the roost location. We circled the roosting covey and obtained two azimuths with 90° differences around the roost site to triangulate the roost and reduce error in location estimation (Hiller and Guthery 2005, Nams and Boutin 1991). Once confident of roost site location, we projected a point to the estimated roost site (within 10-30m). A hand-held Global Positioning System (GPS) unit (GARMIN International Inc., Olathe, Kansas, USA) was used to mark the coordinates of the roost point. We visually confirmed roosting bird locations if possible but prioritized not flushing or disturbing the birds.

For the treatment coveys, we located the radio-marked birds <1 hr before official sunset (i.e. before they were on the roost) using homing and triangulation and marked the location with a GPS. We scanned through all known radio frequencies to check for other radio-marked birds within the covey. Once all radio-marked birds were accounted for, we quickly moved towards the group to purposefully flush the covey. We attempted to count all birds upon flushing and checked radio signals to ensure all radio-marked individuals had been disturbed and flushed. Following flushing, we marked the flush point with a GPS and left the area. We returned to the flush site >1 hour after official sunset following the flush event and located the experimental groups via telemetry. We recorded any missing individuals and noted whether the covey had fully regrouped for roosting. We recorded GPS coordinates for roost sites once birds were located using the same methods described above. If birds were separated, we recorded all roost locations.

For both the control and experimental group, we revisited roost site locations the following morning >1 hour after official sunrise to find roost sites and check for any mortality within the covey. We searched the surrounding area (within 15 m) of the recorded roost location for a fresh fecal pile indicative of quail roosting locations (Wallmo 1957). If found, we took photographs of the pile and recorded the approximate number of droppings to determine an index of roost group size. We checked all radio signals for each bird to determine if any mortality events had occurred during the preceding night. If a transmitter signaled mortality, we located the bird/transmitter and collected the carcass and the GPS location.

Data analysis

As scaled quail move in coveys during the nonbreeding season, vegetation measurements and distance to structures were grouped by covey. Each vegetation transect was linked to a covey location, so we calculated averaged vegetation measurements for each covey across multiple vegetation transects. All values for the covariates were scaled by subtracting the mean and dividing by the standard deviation. Once scaled, these covariates were treated like covey-specific covariates and used to examine differences in survival of individuals between coveys. Telemetry locations and vegetation sampling (for both used and random) were censored to only include data collected after November 1st of each year, as this was when coveys had generally stopped long-range movements associated with the “fall shuffle”. Additionally, frost and the end of the warm growing season typically coincided with this date. Removing locations from September through October minimized the possibility of including data that was not representative of nonbreeding season survival and home ranges.

We used 30-m resolution land classifications from the U.S Department of Agriculture’s National Agricultural Statistics Service’s Cropland Data Layer (USDA-NASS 2020) to create land cover rasters which included: crops, grassland (herbaceous cover), and shrub (areas dominated by shrubs). All cultivated crop categories were combined to create an overall cropland layer. We extrapolated values from all three layers for all used and available points, with a 1 or 0 indicating presence or absence of that cover class.

Survival analysis

We used radio-telemetry data to estimate daily survival of scaled quail. We determined individual fates from the time of capture until death, collar loss, transmitter failure, or end of the monitoring period (mid-February for both years). Quail that did not survive >7 days post-capture (Guthery and Lusk 2004) were removed from the data to avoid a potential negative bias from capture stress/myopathy. For each observation of our individual i on occasion j, we created encounter histories where $S_{ij} = 1$ if the bird was alive or $S_{ij} = 0$ if it died. If a bird was not located, we logged the occasion as missing data. Our model integrated over all possibilities when survival state was unknown.

We used a known-fate logistic exposure model with a Bayesian framework (Royle and Dorazio 2008) to estimate daily survival rates. We centered and scaled all continuous variables around the mean so coefficient estimates would directly reflect effect sizes. Our linear predictor function took the general form of:

$$\text{logit}(S_{ij}) = \beta_0 + \beta_1 X_{it} + \ldots + \beta_x X_{it}$$

We fit models using the JAGS 4.3 (Plummer 2017) and the R2jags package version 0.7-1 (Su and Yajima 2015) in Program R version 4.2.1 (R Core Team 2021). We had no data to inform priors, so all parameters were assigned uninformative priors for normally distributed parameters with a mean of 0 and a standard deviation of 1.7. We sampled posterior distributions using 3 Markov chain Monte Carlo (MCMC) chains with 10,000 iterations each and the first 1,000 discarded as burn-in samples (Plummer 2017). We confirmed model convergence by visually inspecting MCMC plots and checking that Gelman-Rubin convergence diagnostics were < 1.1 (Gelman and Rubin 1992). We ranked models by sampling deviance from model outputs and calculating Watanabe-Akaike Information Criterion (WAIC) values (Watanabe and Opper 2010). We calculated what percent of the 27,000 posterior draws matched the sign of the median (*f*) estimates to quantify confidence in whether covariates had positive or negative effects (Arnold 2010). For covariates that were moderately correlated (r = 0.3 to 0.5), we used WAIC rankings to determine which variable had a lower WAIC value. We did not include the variable with the higher WAIC in further steps of our model building.

Prior to testing the univariate models, we assessed whether year or covey size should be included in our models. We treated field seasons as different years and categorized covey sizes based on the number of radio-marked individuals on that occasion. Categories included small (≤ 7 birds), medium (8-14 birds) and large (≥15 birds) coveys. These categories fit our monitored population as coveys averaged ~11 individuals ($\bar{x}$ = 10.3 ± 5.46) and only one covey surpassed a high of 20 individuals. Using these size parameters offered some flexibility to account for birds that were potentially not radio-marked within coveys. Based on direct and frequent visual observation of coveys, as well as recapture rates, we are confident that at least 60% of all individuals within each covey was radio-marked.

We tested univariate models in four different covariate groups to determine which best described daily survival of scaled quail. The four groups were individual-varying characteristics, weather variables, vegetation cover, and landscape features. We included 18 covariates in univariate models that we believed may influence survival of scaled quail (Table 1). Individual-varying covariates consisted of sex (male, female, or undetermined), age (adult or juvenile), and treatment (control or experiment covey). The weather covariates we examined were days with measurable precipitation, average minimum daily temperature (°C), wind chill factor (°C), moon illumination (%), average temperature at the roost point (°C), and difference from temperature at the roost point and ambient temperature (°C). To examine potential effects of vegetation cover on survival, we tested models including covariates measured at both the roost point and roost array scale. At the roost point scale, we included measurements for percent cover of bare ground, percent cover of litter, percent grass cover, and angle of overhead obstruction. We included percent bare ground, percent grass cover, percent cover of low-level shrubs (<1.5 m), low vertical obstruction, and tall vertical obstruction from measurements collected at the roost array scale.

We ran an additional set of models if more than one variable was supported in the same covariate group. From our univariate models, we considered variables as having strong support of an effect if the model outperformed the null by >2 WAIC and had a credible effect. We created all permutations of supported variables and ranked them by WAIC to determine which combination best fit the data. We considered the addition of a variable to be beneficial if it lowered the WAIC value by > 2. If only one univariate model from a group was considered supported, we used that as the top model.

Resource selection analysis

We analyzed location data for the nonbreeding season (November –19 February) from scaled quail coveys. We used coveys as the experimental unit for this analysis because covey affiliation was strong among birds. We defined a covey as a group with > 2 birds that were located together for ≥ 7 days. We calculated separate home ranges for all coveys with ≥ 30 locations using the fixed kernel density method (Worton 1989) with the adehabitatHR package version 0.4.19 (Calenge 2006) in Program R (version 4.2.1, R Core Team 2021), and defined our home range extent as the 95% isopleth for each covey. Our 95% utilization distributions encompassed points used by coveys across the day and at night. All coveys had ≥ 18 roost locations included in their home range estimation. To assess availability, we generated 5 randomly generated available points for every point used by a covey within each covey's home range.

We investigated nocturnal resource selection by scaled quail coveys at three different spatial scales. The first scale included fine-scale vegetation measurements at the roost point scale for percent cover of plant functional groups such as shrubs, forbs, and grasses, as well as ground cover estimates for bare ground and litter. We also recorded litter depth, angle of overhead obstruction, and height of the tallest piece of vegetation at the roost point. The second scale included vegetation measurements at the roost array scale (within 15 m of the roost point). We measured vegetation for percent cover of low-level shrubs (<1.5 m), percent grass cover, and recorded percent ground cover of bare ground and litter. We also used a Nudd's board to measure the amount of low and tall vertical obstruction at the roost array. The third scale examined broader vegetation metrics by using land cover classes that included herbaceous, cropland, and shrubland. We classified land cover within all home ranges using these three cover categories.

We used the INLA package (version 22.05.07, Rue et al. 2009) in Program R to fit all binomial selection models using integrated nested Laplace approximation (INLA). We used the created univariate mixed-effects models for a logistic regression in a Bayesian framework. We fit mixed-effects models with use as the response variable and explanatory variables included covariates accounting for vegetation measurements at the roost point and roost array, and land cover classes (Table 2). We assigned used points a weight of 1 and available points a weight of 1000. To account for variability in selection among coveys, all models included a random intercept for covey and a random slope for all explanatory variables (Muff et al. 2020, Gillies et al. 2006). We assigned the random intercept for covey a large, fixed variance of 10^6 so that covey intercepts were not shrunk towards an overall mean (Muff et al. 2020). We used a penalized complexity prior for the precision of the random slopes (Muff et al. 2020, Simpson et al. 2017) with an alpha of 0.05.

In the first step of our model selection, we ranked 18 univariate models using Watanabe-Akaike Information Criterion (WAIC) values (Watanabe 2010). The roost point scale included 6 models and 7 at the roost array scale. We used WAIC and credible intervals to select supported variables. Models that outcompeted the null model by ≥ 2 ΔWAIC were considered competitive (Burnham and Anderson 2002). The credible intervals of the posterior distributions that did not overlap 0 were considered strong support of either a positive or negative effect of a variable (Hespanhol et al. 2019, Hooten and Hobbs 2015).

If a model group had more than one model that was considered competitive and had a variable with a credible effect (credible interval did not include 0), we included all supported variables in a series of final models to further assess their importance and effect sizes. In the final models, we created as many permutations as possible for our supported model variables. We calculated WAIC scores and ordered models by ascending WAIC. We considered the model with the lowest WAIC value to be the best of that group. Once a top model was determined by WAIC, we interpreted results for all fixed effects, but focused our interpretation on variables with credible intervals that did not include 0.

Results

Summary statistics

We monitored survival of 154 radio-marked scaled quail from 11 coveys during September – February 2020-2022. We recaptured 7 quail from the 2020-2021 season and attached new radio-collars in 2021-2022. We censored quail from our analysis that that did not survive >7 days post-capture (n = 21), single quail not in coveys (n = 2), coveys that went missing (n = 1), and birds that did not survive until November 1st (n = 24). After censoring, the nocturnal analysis included 102 birds from 10 different coveys. Of these birds, 56 were adults and 46 were juveniles. There were 48 known mortalities, 51 birds were still alive at their last check, and 3 had unknown fates (individual lost, collar failure, etc.). We lost 14% of radio-collared birds less than 7 days after capture, which was largely attributed to avian predation (n = 8) and collar slips of juvenile birds that were not recollared (n = 4). The fall raptor migration (Goodrich and Smith 2008) may have contributed to the high mortality rates documented during trapping. Death of radio-collared individuals was mostly attributed to predation by mammals or raptors, but some were linked to anthropogenic activity. We documented 4 birds harvested by hunters, 2 drowned in water tanks, and 1 hit by a vehicle. Another notable cause of mortality was Winter Storm Uri from February 13th-17th, 2021. This period had an average maximum daily temperature of -11°C and 3.30 mm of precipitation. Of the 25 radio-collared quail still being monitored, 16% ($n = 4$) died during the storm.

Vegetation structure and composition

We recorded 307 roost (used) locations and measured vegetation characteristics at 146 of them, along with 350 (random) available points. We found that scaled quail roosted at points with significantly lower percent cover of grass and litter depth than what was recorded at available points (Table 3). Roost points also had significantly more bare ground than what was observed at available points. Angle of overhead obstruction, cactus cover, rock, litter, forb cover, and height of tallest vegetation were not statistically different between used and available locations.

At the array level (15 m) around roost points, the amount of vertical obstruction across tall, medium, and low cover categories was significantly greater than at available points (Table 4). Additionally, vegetation within 15 m of roost points had higher percent vertical obstruction than what was found randomly on the landscape. There were no statistically significant differences of shrub cover, grass cover, forb cover, cactus cover, bare ground, rock, litter, or slope between used roost arrays and available arrays. The tallest cover category for percent vertical obstruction was also not significantly different and vegetation on the grassland rarely reached these strata.

We were able to locate roost piles for 64% of the roost locations that we collected vegetation data from. The number of roost piles at or around the approximated roost point ranged from 1-4 distinct piles with an average (± SE) of 1.36 ± 0.70, indicating that coveys sometimes created multiple roost circles. The approximate count of droppings varied greatly, with a range from 4-250 droppings from a single roost pile.

Thermal sampling

We recorded 3,525 temperature readings measured at roost points used by scaled quail, 10,522 readings from random (available) points within 2-10 m from the roost, and 4,774 temperatures at random (available) points between 40-500 m from the roost. The average temperature (± SE) was 4.30 °C ± 0.5 at roost points, 4.30 °C ± 0.4 at 2-10 m, and 6.76 °C ± 0.4 at 40-500 m (Figure 1 and 2). Roost points were not significantly different (p-value=0.771) from 2-10 m available points but were statistically colder (p-value <0.0001) than temperatures at 40-500 m available points.

Resource selection analysis

The model containing grass cover (%) was the best for describing selection directly at the roost point (Table 5). Scaled quail showed strong selection for roost points with less grass cover. All other models that included variables for litter (%), litter depth (cm), bare ground (%), and average angle of overhead obstruction (°) were not supported as having a strong effect on roost point selection.

The models including variables for low vertical obstruction (%) and bare ground (%) measured at the roost array scale (15 m around the roost points) had supported variables (Table 6). While the model containing tall vertical obstruction (%) was supported by the WAIC and credible interval criteria, it had a higher WAIC score than low vertical obstruction and was not included in the secondary modeling stage due to moderate correlation with low vertical obstruction. The top model was the one that only contained low vertical obstruction, as it had a lower WAIC value than the model combining both low vertical obstruction and bare ground

(Table 6). Our results indicated that scaled quail strongly selected roost points that had higher amounts of low vertical obstruction within 15 m.

At the landscape scale, no models had strong support of an effect on nocturnal resource selection. Roosting scaled quail neither strongly avoided nor selected any of the land cover classes we included in our models.

Survival analysis

We estimated nonbreeding season survival of scaled quail to be 0.60 (95% CRI: 0.52 to 0.69). Of the univariate models for individual characteristics, only age and treatment outperformed the null by > 2 WAIC. However, neither age nor treatment had a credible effect, as both credible intervals included zero. There was no strong support for an effect of age, sex, or treatment group on survival (Table 7).

The weather models including average minimum temperature (C°), wind chill (C°), and moon illumination (%) were considered supported based on our criteria for WAIC values and credible effects (Table 8). While the model containing both average minimum daily temperature and wind chill had the lowest WAIC value, the model containing only average minimum daily temperature was still considered competitive with a ΔWAIC ≤ 2. The addition of the wind chill variable did not substantially improve model fit, so the simpler model with only average minimum daily temperature was considered our top model. There was strong support that higher average minimum daily temperatures were associated with higher survival.

The model including bare ground (%) performed the best of the models with vegetation variables measured at the roost point (Table 7). Both WAIC values and credible intervals indicated a strong effect on survival related to the percent cover of bare ground at the roost point. Higher amounts of bare ground were associated with higher survival. No other models including litter (%), average angle of overhead obstruction (°), and grass cover (%) were supported as influencing survival.

The null model outperformed all models that included variables for vegetation cover at the roost array (Table 7). Shrub cover (%), tall vertical obstruction (%), low vertical obstruction (%), bare ground (%), and grass cover (%) all had credible intervals that included zero. The null model was the simplest model chosen by WAIC and no vegetation variables measured at the roost array level were strongly supported as strongly influencing survival.

Flushing experiment

We included 102 birds across 10 different coveys in our flushing experiment (Table 9) across both years of the study. Forty-nine quail were included in treatment groups and 53 were included in control groups. There was a total of 19 mortalities in the treatment groups and 29 within control groups. No mortalities were observed within treatment groups directly following intentional disturbance. Of the 140 covey flushes, coveys regrouped to roost 84% of the time. Nonbreeding seasonal survival of birds within the control groups was 0.57 (95% CRI:0.43 to 0.66) and 0.66 (95% CRI: 0.51 to 0.80) in the treatment groups (Figure 3). While not considered credible (Table 7), our results indicated slightly higher survival in treatment groups than in the control groups.

Discussion

We found that roost locations with more bare ground were associated with higher seasonal survival of scaled quail. Roosting coveys strongly selected for roost points with less grass cover and greater amounts of low vertical obstruction. Scaled quail survival was also influenced by average minimum daily temperatures, which can be more extreme at night, particularly during the nonbreeding season. However, roost locations selected by scaled quail were colder than the landscape despite our finding that average minimum daily temperatures negatively affected survival. Additionally, scaled quail coveys showed a strong propensity for roosting communally in roost circles. Coveys disturbed prior to nightfall typically regrouped to roost, suggesting that communal roosting is an important driver of survival and roost site selection.

The survival of quail is partially influenced by thermoregulatory needs, which are elevated during periods of extreme temperatures (Tanner et al. 2017, Smith et al. 2015, Weathers 1981). Our results showed that nonbreeding survival of scaled quail was affected by the average minimum daily temperature. Specifically, scaled quail survival was lower during periods with low minimum temperatures. When temperatures reach extremes, quail can mitigate thermal stress through behavioral choices such as roosting communally and selecting for microclimates that reduce energetic needs (Kline et al. 2019, Guthery et al. 2005, Chamberlain 2005). Interestingly, our results indicated that scaled quail selected roost points that were cooler than available at broader scales (Figure 2). Our random sampling indicated that warmer potential roost sites are available, but scaled quail chose cooler roost points characterized by more bare ground with greater amounts of low vertical obstruction within 15 m. While increased cover around the roost location could reduce heat lost from wind (Burger et al. 2017, Klimstra and Ziccardi 1963), our findings suggest that roost point selection may be driven by other factors besides thermal considerations. Previous research has shown that microclimate temperatures at bobwhite roosts did not provide energetic benefits that differed from those at available points within 60 m (Guthery et al. 2005). Further, varying vegetation heights at roost points did not change thermoregulatory requirements of roosting bobwhite and may not substantially alter the microclimate temperatures (Chamberlain et al. 2002). Predator avoidance may be more important than the microclimate experienced at the roost point (Perkins et al. 2014, Hiller and Guthery 2005).

During the day, quail resource selection is largely driven by canopy cover that provides protection from predators (Mosloff et al. 2021, Brooke et al. 2015, DeMaso et al. 2014) as well as extreme weather (Kline et al. 2019, Janke et al. 2015, Hiller and Guthery 2005). Our results suggest that scaled quail shift from selecting overhead cover during the day to using sparsely vegetated areas with limited canopy at night (Stormer 1984, Klimstra and Ziccardi 1963). This may be a response to changing predator pressures, as most raptors responsible for quail mortalities are diurnal hunters (Atuo and O'Connell 2017). While our results did not show roost points had smaller angles of overhead obstruction (less overhead cover), coveys selected for locations with less grass cover directly at the roost point. Grass cover at roost points was strongly avoided, potentially because grass canopy can obstruct flight of escaping birds (Perkins et al. 2014, Tillman 2009, Robinson 1957, Stoddard 1931). Further, the selection of increased low vertical obstruction around roost points may suggest mammalian predation was a driver of nocturnal resource selection. Increased cover around roost points could provide concealment and hinder movements of approaching predators (Stormer 1984, Wallmo 1957). The mechanism of roost site selection is yet unknown and should be further investigated.

Communal roosting among quail coveys is an important, yet poorly understood, characteristic of quail behavior. Disturbance of coveys prior to roosting (i.e., through hunting) is believed to negatively affect overnight survival of birds (Wallmo 1957, Errington 1945) and some state wildlife regulations reflect this by limiting late afternoon hunting. Yet, our results showed no negative effect of late-evening flush events on overnight survival of scaled quail within treatment coveys. In fact, we detected no mortality events directly following disturbance and treatment coveys typically regrouped to roost together. The strong tendency of coveys to reassemble highlighted the importance of communal roosting at night. While it is still largely unknown how frequent disturbance influences energetic demands of birds, it did not alter the behavior of communal roosting nor increase seasonal mortality. In summary, our findings did not substantiate the belief that disturbance of coveys prior to roosting is detrimental to survival. However, such disturbance is often associated with harvest of individual quail, which can alter covey size and reduce roost circle thermoregulatory efficiency (Williams et al. 2003, Case 1973). While our study did not alter covey size, this may be a factor associated with disturbance that has important implications for survival. Further, hunting may also include other stressors such as guns, dogs, and longer pursuits, which could influence survival of disturbed birds differently than what we saw with our experiment.

Conclusion

As habitat requirements differ between night and day, diverse landscapes are likely to provide resources necessary to support scaled quail. Further, communal roosting behavior was a powerful driver of scaled quail covey dynamics at night. If the covey was disturbed before nightfall, they often regrouped prior to roosting. While our results showed disturbance of coveys prior to nightfall did not significantly affect survival of roosting birds, there was clear indication that communal roosting was important during the nonbreeding season. However, regulations that prevent activities (e.g. hunting) that disturb coveys prior to roosting, with the justification that such disturbance is detrimental for survival, may not influence scaled quail survival. Even so, our experiment did not lower covey size through harvest, which may be a more substantial factor influencing survival of remaining birds. More research is needed to understand how other aspects of these activities may alter roost circle arrangement and overnight survival.

Table 1. We examined 18 variables associated with roost site selection that could potentially affect survival of scaled quail (*Callipepla squamata*). These variables included individual characteristics, weather variables, vegetation cover at the roost array, and vegetation cover at the roost point. All data was collected from Morton County, Kansas, USA during the nonbreeding seasons (November – February) from 2020-2022.

Group	Parameters	Description
Individual		
	Age	Adult or subadult (1/0)
	Sex	Male or female (1/0)
	Treatment	Experiment or control group (1/0)
Weather		
	MinTemp	Average minimum daily temperature (°C)
	WindChill	Wind chill factor (°C)
	Moon	Moon illumination (%)
	Precip	Days with or without precipitation (1/0)
	RoostTemp	Mean temperature at roost site (°C)
	DiffTemp	Difference from temperature at roost point and ambient temperature (°C)
Vegetation: Roost Point		
	Bare	Bare ground (%)
	Litter	Litter cover (%)
	Grass	Grass cover (%)
	Angle	Angle of overhead obstruction above roost point (°)
Vegetation: Roost Array		
	Bare	Bare ground (%)
	Grass	Grass cover (%)
	Shrub	Low-level shrub (<1.5m) cover (%)
	Low vob	Low vertical obstruction (%)
	Tall vob	Tall vertical obstruction (%)

Table 2. We included 16 variables in the nocturnal analysis that addressed three different scales of resource selection for roosting scaled quail (*Callipepla squamata*). These variables included vegetation measurements at the roost array scale, vegetation measurements at the roost point scale, and land cover classes. All data was collected from Morton County, Kansas, USA during the nonbreeding seasons (November – February) from 2020-2022.

Group	Parameters	Description
Roost point scale		
	Bare	Bare ground (%)
	Litter	Litter cover (%)
	Grass	Grass cover (%)
	Ldepth	Litter depth at roost center (cm)
	Angle	Angle of overhead obstruction above roost point (°)
	Height	Height of tallest piece of vegetation (cm)
Roost array scale		
	Bare	Bare ground (%)
	Litter	Litter cover (%)
	Grass	Grass cover (%)
	Shrub	Shrub cover (%)
	Low vob	Low vertical obstruction (%)
	Tall vob	Tall vertical obstruction (%)
	Slope	Flat or slope (0/1)
Landscape scale		
	Crop	Cropland land cover class (0/1)
	Shrubland	Shrubland land cover class (0/1)
	Herb	Herbaceous land cover class (0/1)

Table 3. Summary statistics for vegetation variables measured at scaled quail (*Callipepla squamata*) roost points and random (available) points within 40-500 m. Vegetation sampling was conducted in Morton County, Kansas, USA during the nonbreeding seasons (November – February) of 2020-2022. P-values < 0.05 indicate significant differences between group means and are in bold.

	Used				Available				
Variable	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	p-value
Angle of overhead obstruction (°)	1.54	86.2	48.03	1.34	0.0	86.8	44.86	1.65	0.136
Bare ground (%)	0.0	97.5	45.76	2.37	0.0	97.5	37.35	2.44	**0.014**
Grass (%)	0.0	85.0	21.03	1.96	0.0	97.5	31.84	2.55	**<0.001**
Cactus (%)	0.0	37.5	0.68	0.30	0.0	37.5	0.99	0.40	0.530
Rock (%)	0.0	2.5	0.07	0.03	0.0	2.5	0.05	0.03	0.703
Litter (%)	0.0	97.5	23.43	1.73	0.0	97.5	19.57	1.78	0.121
Forbs (%)	0.0	62.5	4.65	0.67	0.0	62.5	6.54	1.00	0.119
Vegetation height (cm)	0.0	120.0	39.06	1.84	0.0	85.5	35.76	1.70	0.187
Litter depth (cm)	0.0	60.0	4.95	0.71	0.0	120.0	7.96	1.28	**0.040**

Table 4. Summary statistics for vegetation variables measured at arrays around roost points used by scaled quail (*Callipepla squamata*) coveys and arrays (within 15 m) around random (available) points. Vegetation sampling was conducted in Morton County, Kansas, USA during the nonbreeding seasons (November – February) of 2020-2022. P-values < 0.05 indicate significant differences between group means and are in bold.

	Used				Available				
Variable	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	p-value
Shrub cover (%)	0.0	70.0	17.65	1.41	0.0	67.5	15.05	0.84	0.101
Grass cover (%)	0.0	125.0	49.68	2.79	0.0	112.5	50.65	1.68	0.758
Forb cover (%)	0.0	70.0	15.39	1.37	0.0	90.0	15.81	0.99	0.814
Cactus cover (%)	0.0	7.5	0.55	0.12	0.0	15.0	0.32	0.07	0.089
Bare ground (%)	0.0	100.0	60.17	2.02	0.0	100.0	63.91	1.30	0.122
Rock (%)	0.0	0.0	0.00	0.00	0.0	22.5	0.07	0.06	0.479
Litter (%)	0.0	87.5	29.78	1.91	0.0	100.0	27.71	1.28	0.376
Tallest vertical obstruction (%)	0.0	32.3	1.37	0.35	0.0	14.9	0.83	0.17	0.119
Tall vertical obstruction (%)	0.0	47.0	6.29	0.75	0.0	45.3	3.67	0.35	**<0.001**
Medium vertical obstruction (%)	0.0	85.5	26.56	1.80	0.0	87.2	17.64	1.00	**<0.001**
Low vertical obstruction (%)	2.5	90.5	60.34	2.07	0.0	90.5	48.97	1.39	**<0.001**
Slope (degrees)	0.0	12.0	4.71	0.65	0.0	12.0	4.50	0.43	0.788

Table 5. Univariate models including variables that potentially explain roost site selection of scaled quail (*Callipepla squamata*) at three different scales. All models were ranked by Watanabe-Akaike Information Criterion (WAIC) values. We considered models to be competitive that outcompeted the null model by ≥ 2 ΔWAIC and had variables with credible intervals that did not include zero. Competitive models with supported variables are in bold. Shown below are all model mean estimates, upper and lower bounds of the 95% credible intervals, and the proportion of the posterior distribution with the same sign as the mean (*f*). Data collection was conducted in Morton County, Kansas, USA during the nonbreeding seasons (November – February) from 2020-2022.

Group	Models	Mean	2.5%	97.5%	*f*	ΔWAIC	WAIC
Roost point scale							
	Grass	**-0.412**	**-0.674**	**-0.180**	**1.0**	**0**	**2382.2**
	Litter	0.417	-0.489	1.375	0.83	5.7	2388.0
	Null	-	-	-	-	15.2	2397.4
	Ldepth	-0.238	-0.514	0.007	0.97	18.0	2400.2
	Bare	0.283	0.035	0.529	0.98	18.8	2401.0
	Angle	0.173	-0.039	0.385	0.94	21.0	2403.2
	Height	0.178	-0.201	0.557	0.85	32.4	2414.6
Roost array scale							
	Low vob	**0.563**	**0.324**	**0.813**	**1.0**	**0**	**2551.5**
	Shrub	0.141	-0.341	0.527	0.77	17.1	2568.6
	Tall vob	**0.357**	**0.145**	**0.580**	**1.0**	**21.0**	**2572.5**
	Slope	0.027	-0.668	0.957	0.48	27.0	2578.5
	Bare	**-0.211**	**-0.402**	**-0.011**	**0.98**	**28.2**	**2579.7**
	Grass	0.014	-0.377	0.393	0.54	28.3	2579.8
	Litter	0.233	-0.030	0.501	0.96	29.1	2580.6
	Null	-	-	-	-	558.6	3110.1
Landscape scale							
	Crop	-0.950	-2.201	0.084	0.97	0	5729.0
	Shrubland	0.221	-0.234	0.703	0.85	18.1	5747.1
	Herb	0.249	-0.345	0.748	0.84	18.3	5747.4
	Null	-	-	-	-	24.5	5753.6

Table 6. Supported variables measured at the roost array level are listed with possible combinations. Measurements were recorded within 15 m of roost sites used by scaled quail (*Callipepla squamata*) in Morton County, Kansas, USA. Data was collected during the nonbreeding seasons (November – February) from 2020-2022. Fixed effects within the top model that have credible effects (95% CRI does not include 0) are in bold.

Group	Models	ΔWAIC	WAIC	Fixed Effects	Mean	2.5%	97.5%	*f*
Roost array scale								
	Low vob	0	2551.5	**Low vob**	**0.563**	**0.324**	**0.813**	**1.0**
	Low vob + Bare	0.2	2551.7	Low vob	0.580	0.320	0.853	1.0
				Bare	-0.272	-0.489	-0.048	0.99
	Bare	28.2	2579.7	Bare	-0.211	-0.402	-0.011	0.98

Table 7. We created 18 univariate models to investigate individual characteristics, weather, and vegetation cover at both the roost point and the area within 15 m (array) of the roost point on survival of radio-marked scaled quail (*Callipepla squamata*) in Morton County, Kansas, USA. All models were evaluated and ranked by Watanabe-Akaike Information Criterion (WAIC) values. We considered models to be competitive with ΔWAIC ≥ 2 from the null model and had variables with credible intervals that did not include zero. Competitive models with supported variables are in bold. Shown below are all model mean estimates, upper and lower bounds of the 95% credible intervals, and the proportion of the posterior distribution with the same sign as the mean (*f*).

Group	Models	Mean	2.5%	97.5%	*f*	ΔWAIC	WAIC
Individual							
	Age (adult)	-0.462	-1.021	0.096	0.95	0	532.4
	Treatment (experiment)	0.445	-0.117	1.014	0.94	0.3	532.7
	Null	-	-	-	-	2.5	534.9
	Sex (male)	0.388	-0.184	0.956	0.91	136.3	668.7
Weather Covariates							
	MinTemp	**0.674**	**0.330**	**1.000**	**1.0**	**0**	**519.0**
	WindChill	**0.440**	**0.147**	**0.541**	**0.71**	**7.4**	**526.4**
	Moon	**0.327**	**0.036**	**0.624**	**0.58**	**12.0**	**531.0**
	Precip	-0.002	-1.204	1.728	0.55	14.5	533.5
	DiffTemp	0.203	-0.124	0.550	0.88	14.9	533.9
	Null	-	-	-	-	15.9	534.9
	Roost	0.088	-0.158	0.330	0.76	16.3	535.3
Vegetation Cover: Roost Point							
	Bare	**0.394**	**0.065**	**0.741**	**0.99**	**0**	**529.6**
	Litter	-0.235	-0.550	0.060	0.94	2.2	531.8
	Angle	-0.285	-0.628	0.025	0.96	3.8	533.4
	Grass	-0.298	-0.596	0.007	0.97	3.5	533.1
	Null	-	-	-	-	4.9	534.9
Vegetation Cover: Roost Array							
	Null	**-**	**-**	**-**	**-**	**0**	**534.9**
	Shrub	-0.129	-0.447	0.168	0.79	0.4	535.3
	Tall vob	-0.040	-0.352	0.263	0.60	0.9	535.8
	Low vob	-0.145	-0.469	0.147	0.82	0.7	535.6
	Bare	-0.095	-0.374	0.179	0.75	1.0	535.9
	Grass	-0.213	-0.556	0.111	0.90	1.3	536.2

Table 8. Supported roost array variables and possible combinations describing survival of nonbreeding scaled quail (*Callipepla squamata*) in Morton County, Kansas, USA from 2020-2022. Models are ranked by WAIC values and models ≤ 2 from the top model are considered competitive. Variables in the top model with credible effects (95% CRI does not overlap 0) are in bold.

Group	Models	ΔWAIC	WAIC	Fixed Effects	Mean	2.5%	97.5%	*f*
<u>Roost array scale</u>								
	MinTemp + WindChill	0	518.2	MinTemp	0.495	0.084	0.889	0.99
				WindChill	0.192	-0.006	0.508	0.97
	MinTemp	0.8	519.0	**MinTemp**	**0.674**	**0.330**	**1.000**	**1.0**
	MinTemp + Moon	2.6	520.8	MinTemp	0.587	0.239	0.920	1.0
				Moon	0.770	-0.042	1.603	0.97
	MinTemp + WindChill + Moon	3.6	521.8	MinTemp	0.443	0.045	0.824	0.99
				WindChill	0.164	-0.016	0.470	0.94
				Moon	0.689	-0.141	1.525	0.95
	WindChill + Moon	7.6	525.8	WindChill	0.368	0.093	0.648	1.0
				Moon	0.774	-0.030	1.608	0.97
	WindChill	8.2	526.4	WindChill	0.440	0.147	0.541	0.71
	Moon	12.8	531.0	Moon	0.327	0.036	0.624	0.58

Table 9. Summary of scaled quail (*Callipepla squamata*) coveys included in pre-roosting flushing experiment during the nonbreeding seasons (November – February) from 2020-2022 in Morton County, Kansas, USA. Treatment coveys were flushed twice per week <1 hour before sunset. All quail were checked for mortality the morning following intentional disturbance.

		N^1	# of Mortalities
Treatment			
	Covey A	14	9
	Covey D	6	0
	Covey E	7	5
	Covey G	11	2
	Covey I	5	3
	Covey J	6	0
	Total	49	19
Control			
	Covey B	6	3
	Covey C	12	7
	Covey F	25	13
	Covey H	10	6
	Total	53	29

[1] initial number of birds at the beginning of the experiment period

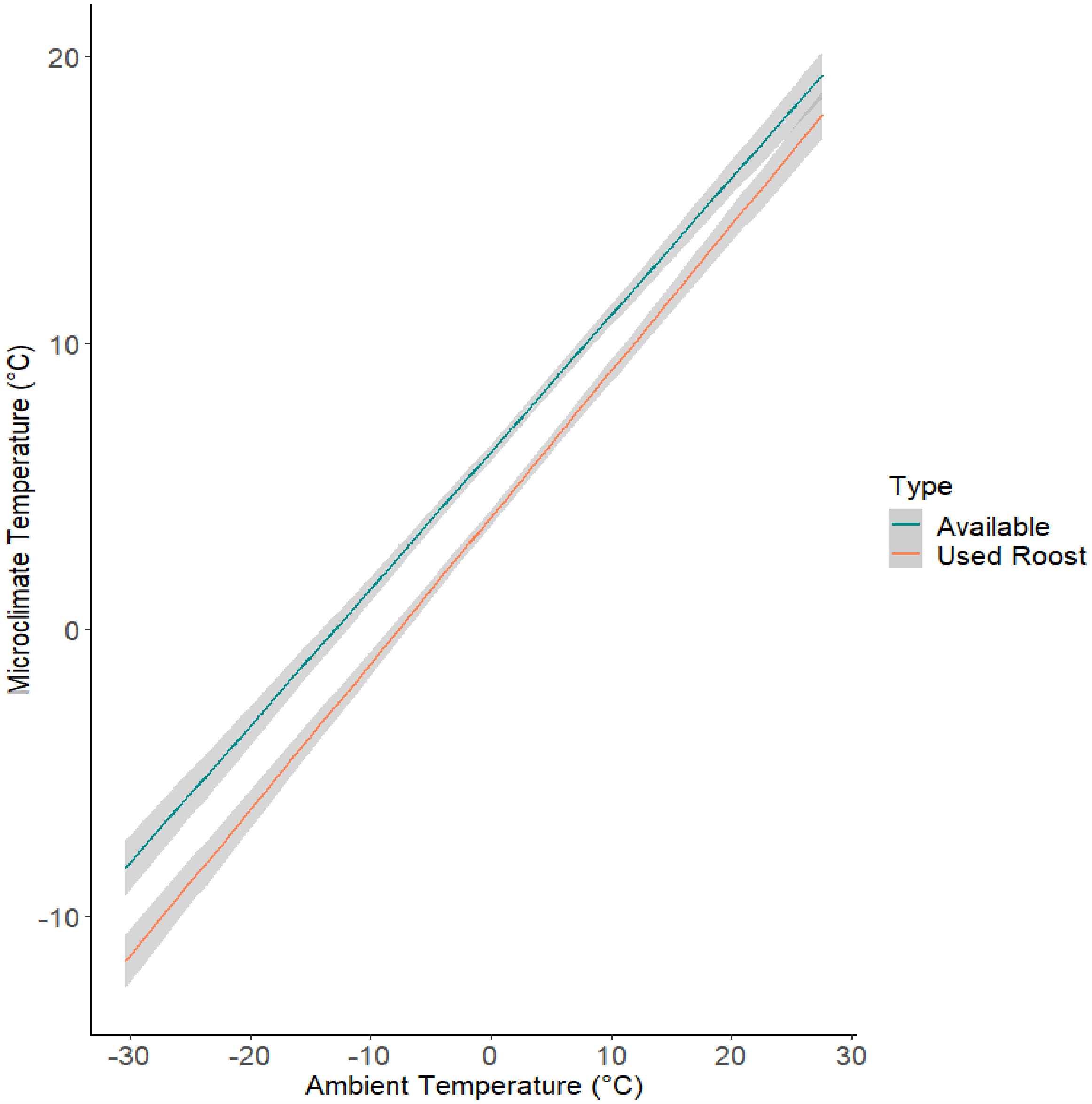


Figure 1. Linear regression between ambient and microclimate temperatures (°C) at roost points used by scaled quail (*Callipepla squamata*) and random (available) points 40-500 m from the roost point. We only included temperatures logged during the hours of 18:00 – 6:00. All thermal sampling was conducted during the nonbreeding seasons (November – February) of 2020-2022 in Morton County, Kansas, USA.

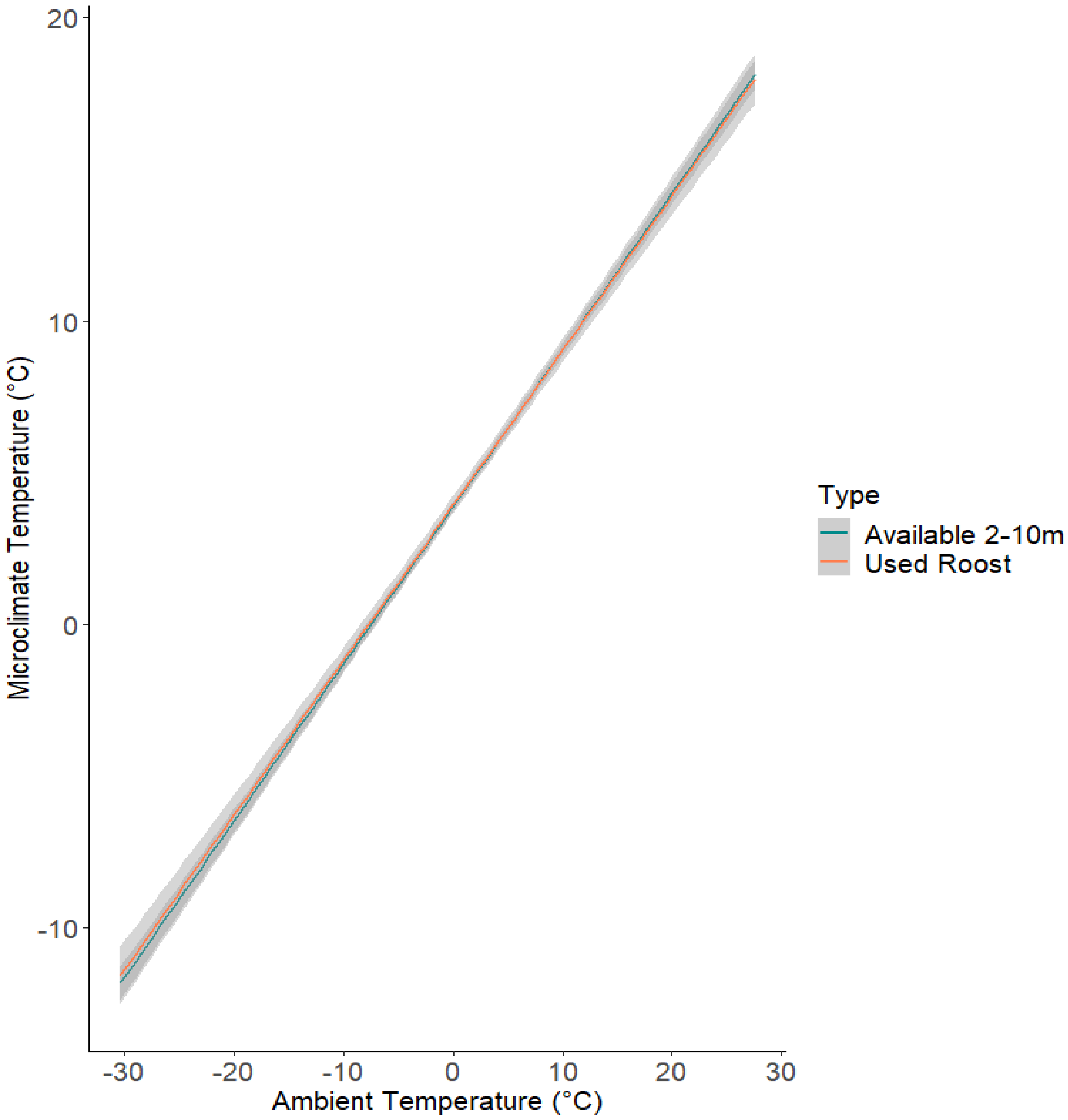
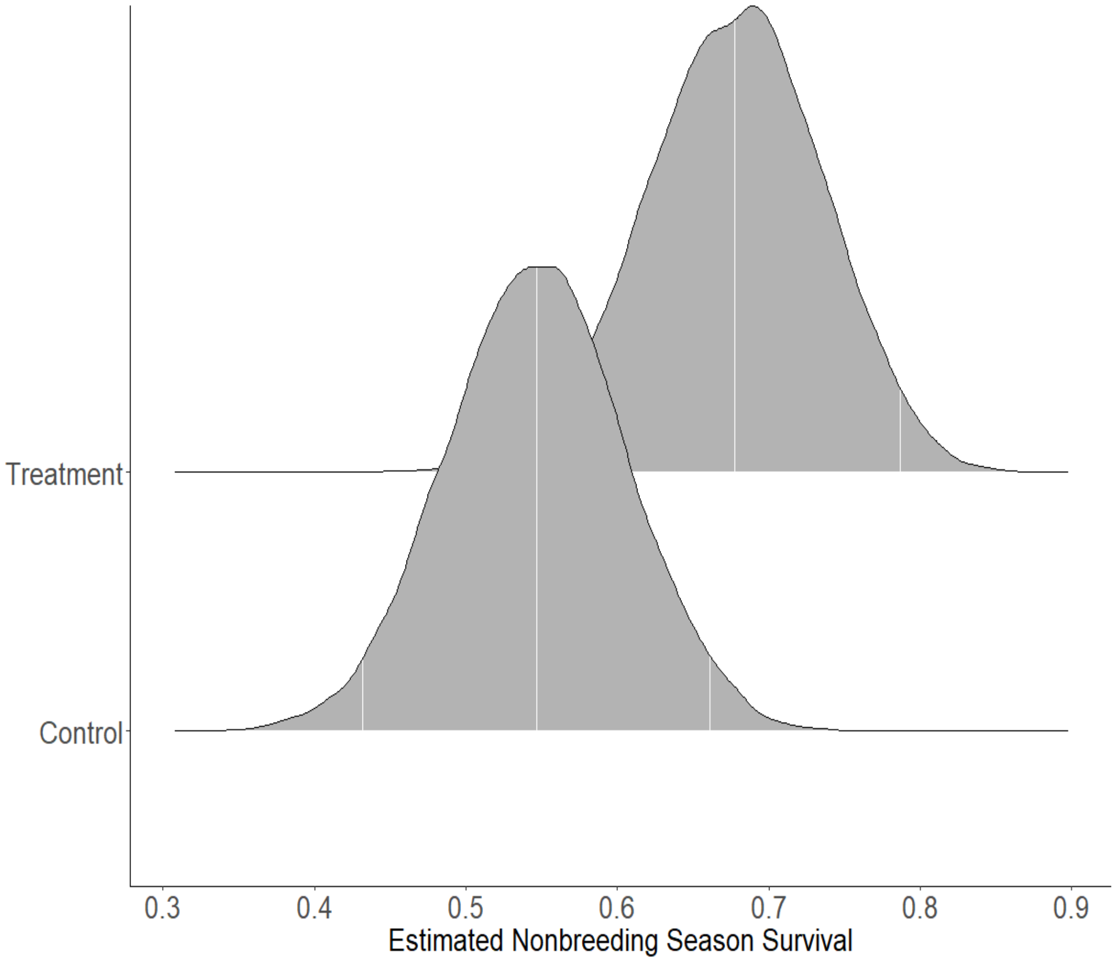


Figure 2. Linear regression between ambient and microclimate temperatures at roost points used by scaled quail (*Callipepla squamata*) and random (available) points within 2-10 m of the roost point. We only included temperatures sampled during the hours of 18:00 – 6:00. All thermal sampling was conducted during the nonbreeding seasons (November – February) of 2020-2022 in Morton County, Kansas, USA.

Figure 3. Posterior distributions transformed (logit) to portray real nonbreeding season (November – February) survival rates of scaled quail (*Callipepla squamata*) in treatment and control groups. The experiment was conducted in Morton County, Kansas, USA from 2020-2022. Probability estimates for seasonal survival are shown as the shaded region with 95% credible intervals. Individuals within the treatment groups (upper distribution) had considerably higher predictions for seasonal survival than those in the control groups (lower distribution).



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