BREEDING SEASON HABITAT USE AND SURVIVAL OF SCALED QUAIL

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BREEDING SEASON HABITAT USE AND SURVIVAL OF SCALED QUAIL

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Abstract: Over the last few decades, scaled quail (*Callipepla squamata*) populations have been declining throughout the southwestern United States. Despite interest in managing for this species, scaled quail habitat use has been poorly studied, particularly in terms of nest site selection. Appropriate management strategies require a comprehensive understanding of what constitutes habitat, and how choices about habitat use influence survival. We investigated breeding season habitat use and survival of scaled quail in response to vegetation, temperature, time since fire, and anthropogenic structures. We used radio telemetry to identify and monitor nests of marked quail. After nest fate, we investigated nest site characteristics both at the nest bowl and in the area surrounding the nest. We found that scaled quail nested in areas with taller vegetation, greater cover of grass and litter, and warmer microsite temperatures during the day. Relative to the area surrounding the nest, nest bowls had even greater cover of grass, litter, and shrubs, and were significantly cooler during daylight hours. Despite apparent selection for particular nest site characteristics, these were not found to influence nest fate or daily nest survival. From May through July, we collected similar data at locations of non-brooding adults, brooding adults, and stratified random locations. Both brooding and non-brooding adults used locations with greater vertical obstruction and a higher density of tall (≥1.5 m) shrubs. In particular, density of tall honey mesquite (*Prosopis glandulosa*) was almost 20 times greater at locations of non-brooding adults than at random locations. Both brooding and non-brooding adults showed selection for total mesquite cover, although this selection appeared to be stronger for non-brooding adults. Weather explained more variation in survival than vegetation, time since fire, or anthropogenic structures. Specifically, survival of non-brooding adults, brooding adults, and broods decreased with increasing daily temperature, precipitation, and solar radiation, respectively. These results highlight the importance of vegetation structure and microsite temperature in providing breeding season habitat for scaled quail, and suggest that management resources should be directed towards establishing and maintaining structural and compositional diversity of vegetation.

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CHAPTER I

NEST SITE SELECTION AND SURVIVAL OF SCALED QUAIL

Abstract

Scaled quail (*Callipepla squamata*) is a ground-nesting species that has exhibited long-term declines throughout its distribution. Managing quail populations requires an understanding of the factors that influence nest site selection and survival. However, little is known about scaled quail nest site selection and the relationship with nest fate. To better understand how scaled quail select nest sites, and to evaluate whether these decisions influence nest fate, we investigated nest site characteristics of scaled quail at three spatial scales: nest bowl, nest array, and landscape. We used radio telemetry to identify the nests of marked scaled quail and monitored nests until fate. We recorded temperature, vegetation, and topographical characteristics at scaled quail nests, in the area around the nest, and at random landscape locations. At the array scale, we found that scaled quail nested in areas with taller vegetation, greater horizontal cover of grass and litter, and warmer daytime temperatures. Similarly, at the nest bowl scale, scaled quail selected for similar vegetation characteristics but shrub cover was higher. The nest bowls had high grass and shrub cover and were significantly cooler than the immediate area during daylight hours. However, despite apparent selection for various vegetation characteristics and cooler temperatures, none of the factors we tested were found to influence nest fate or daily nest survival. Although the consequences of selection are inconclusive, scaled quail exhibited a hierarchical pattern of nest site selection. Our results provide a more comprehensive understanding of what constitutes nesting habitat for scaled quail, and will assist managers in choosing appropriate management strategies for this species.

Introduction

Scaled quail (*Callipepla squamata*) are a species of ground-dwelling bird that inhabits arid and semiarid grasslands and shrublands. Their distribution is centered on the Chihuahuan desert, and despite being well-adapted to the climate of this region, scaled quail populations have been declining since the 1960s (Brennan et al. 1994, Rollins 2000, Pardieck et al. 2019). The causes of decline have not been confirmed, although it is often attributed to changes in land cover associated with livestock grazing, fire suppression, and shrub encroachment (Brennan 1994, Rollins 2000, Pleasant et al. 2006). Given the popularity of scaled quail as a game species, there is considerable interest in identifying those factors that influence quail population dynamics and managing habitat accordingly to increase quail production.

Rates of nest initiation and nest survival are key processes influencing quail population dynamics (DeMaso et al. 2011, Guthery and Kuvlesky 1998). However, the nesting ecology of scaled quail is poorly understood. While nest substrates have been described (Carroll et al. 2018, Buntyn et al. 2012, Goodwin and Hungerford 1977, Schemnitz 1961), little information exists relative to factors influencing nest site selection and its implications for nest success. To our knowledge, only two published studies have investigated nest site selection and nest success of scaled quail (Carroll et al. 2018, Pleasant et al. 2006), and both of these studies occurred along the eastern periphery of scaled quail distribution. The limited published data suggests that scaled quail select nest sites that provide greater visual obstruction, less bare ground, and greater shrub diversity than the surrounding landscape (Pleasant et al. 2006). Additionally, nest fate was found to be positively related to vertical obstruction at the nest bowl and the number of forb species in the area surrounding the nest. The authors speculated that these characteristics provided visual concealment and increased the area within which predators must search to find the nest. Similar characteristics were observed at nests in western Oklahoma (Carroll et al. 2018). However, despite apparent selection for particular vegetation characteristics, nest fate was best explained by nest bowl temperature, with hatched nests being significantly warmer than failed nests (Carroll et al. 2018). Overall, selected nest sites were distinctly cooler than the surrounding landscape, moderating temperature by 6°C on average compared to adjacent microsites <2 m away (Carroll et al. 2018). These studies suggest that both the vegetation community and the thermal environment play an important role in determining nest survival rates in scaled quail, and consequently, variation in these characteristics may ultimately influence population dynamics.

Recent studies have increasingly recognized temperature as a critical component of habitat (Elmore et al. 2017). Like other landscape features such as vegetation, soil, topography, and moisture (Petrone et al. 2004, Riera et al. 1998), temperature has both spatial and temporal heterogeneity (Geiger 1965, Suggitt et al. 2011). Factors influencing temperature include vegetation (Hovick et al. 2014, Carroll et al. 2015*b*, Rakowski et al. 2018, Attum et al. 2013, Allred et al. 2013, van Beest et al. 2012), topography (Hall et al. 2016, Olson et al. 2014), and their interactions. Even relatively small changes in these features have the potential to alter near-ground temperatures and create distinct microclimates (Limb et al. 2009, Hovick et al. 2014), which may differ markedly from the climate of the overall landscape. These microclimates, such as the cooler temperatures provided by a shrub canopy (Tracol et al. 2011) or warmer temperatures experienced on south-facing slopes (Bennie et al. 2008), can be highly relevant to habitat selection choices of organisms (Suggitt et al. 2011).

Thermal selection for nest locations has been demonstrated to affect nest fate in several species of ground-nesting birds (Carroll et al. 2015*a*, Carroll et al. 2018, Hovick et al. 2014, Raynor et al. 2018). Both acute and chronic exposure to extreme temperatures can reduce hatchability or slow embryonic development (French 2000, Reyna 2019), increasing the duration of incubation and therefore the amount of time in which the nest may be discovered and depredated. The incubating adult can mediate the thermal environment through incubation behaviors (Brown and Downs 2003, Carroll et al. 2018, Coe et al. 2015, White and Kinney 1974), but increased activity of the adult due to thermal stress (Conway and Martin 2000, Londoño et al. 2008) may simultaneously increase its visibility to predators (Lyon and Montgomerie 1987, Martin et al. 2000, Martin and Ghalambor 1999). In this way, the temperature of the nest can influence nest fate not only through direct mortality, but also by indirectly increasing the risk of depredation.

Given the paucity of information relative to scaled quail nest ecology, we examined nest site selection of scaled quail in the geographical core of their distribution. Our objectives were to 1) characterize multi-scale nest site selection by scaled quail in terms of vegetation, topography, and temperature at three spatial scales: nest bowl, nest area, and landscape; and 2) determine characteristics that influence nest fate and daily nest survival.

Methods

Study site

We examined nest site selection of scaled quail at the Sand Ranch Area of Critical Environmental Concern (ACEC) in Chaves County, New Mexico. The property is over 23,000 ha in size and is managed cooperatively by the Bureau of Land Management and the New Mexico Department of Game and Fish. Management practices at the site include dormant season prescribed burns. Burns were conducted in 2016, 2017, and 2019 on specific pastures within the ACEC, but burns were not conducted in 2018 due to dry conditions. Two unplanned wildfires also occurred on the property during this study: East Cato wildfire (2017, 153.0 ha) and Cato wildfire (2018, 33.6 ha).

Vegetation composition and structure at the site is heterogeneous. The primary plant communities consist of sand shinnery oak (*Quercus havardii*) and honey mesquite (*Prosopis glandulosa*) shrublands. Other prominent woody species include sand sagebrush (*Artemisia filifolia*), four-wing saltbush (*Atriplex canescens*), soapweed yucca (*Yucca glauca*), broom snakeweed (*Gutierrezia sarothrae*), and prickly pear (*Opuntia* spp.). Prevalent forbs include western ragweed (*Ambrosia psilostachya*), croton (*Croton* spp.), evening primrose (*Oenothera* sp.), catclaw sensitive briar (*Acacia greggi*), daisy fleabane (*Erigeron* sp.), phlox (*Phlox* sp.), wild buckwheat (*Eriogonum annum*), ratany (*Krameria* spp.), and broom groundsel (*Senecio spartioides*) (Davis et al. 1979). Dominant grasses include sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), three-awn (*Aristida* spp.), sand dropseed (*Sporobolus cryptandrus*), red lovegrass (*Eragrostis secundiflora*), and hairy grama (*Bouteloua hirsuta*). The general topography consists of undulating sand dunes interspersed with flat expanses of tighter soils (Davis et al. 1979), and major soil types include Roswell, Roswell-Jalmar, and Faskin fine sands (NRCS 2017). The climate is semiarid with an average annual precipitation of 39.2 cm and mean annual maximum and minimum temperatures of 6.6°C and 23.6°C (PRISM Climate Group 2019). During our study the site received 36.2 cm of precipitation in 2018 and 55.6 cm in 2019, most of which occurred from July through October. Ambient temperatures during the study period (February –August) ranged from -7.8 to 41.7°C in 2018 and -9.4 to 39.4°C in 2019 (Horel et al. 2002).

Quail capture and monitoring

We captured adult scaled quail using walk-in funnel traps (Stoddard 1931). Trapping began in mid-February and continued through late April of both years. We fitted captured quail with necklace-style radio transmitters weighing approximately 6-7 grams with an expected battery life of 11 months (American Wildlife Enterprises, Monticello, FL and Advanced Telemetry Systems, Isanti, MN). Capture and handling protocols were approved by the Oklahoma State University Institutional Animal Care and Use Committee (Protocol No. AG-17-23).

Each radio-marked quail was located 2-3 times per week using a homing method that encompassed circling at a distance of 15-20 m from the quail (White and Garrot 1990).). Quail locations were estimated by measuring the azimuth and distance to the bird from the observer. We determined a quail to be on nest when it had been located at the same point for three consecutive checks. Once a nest was confirmed, we calculated the forecasted hatch date by projecting 23 days (Johnsgard 2017) forward from the estimated start of incubation. Nesting quail were checked 3 times per week until the nest either hatched or failed. We considered a nest successful if at least 1 egg hatched.

Thermal and weather sampling

We collected thermal data at scaled quail nest locations and stratified random locations to evaluate multi-scale thermal selection of nesting quail. To standardize sampling, we began collecting thermal data at hatched nests on the day after the hatch was discovered and on the forecasted hatch date for failed nests.

At nest and random locations, we established 20 m arrays centered on the sample point (the actual nest or the random point) and extending away from the sample point in the directions of a random azimuth and 180° from the random azimuth. We characterized the thermal environment using self-contained temperature data-loggers (Thermochron ibuttons, Mouser Electronics, Inc., Mansfield, Texas, USA; hereafter, ibuttons) programmed with a 15-minute sampling rate. We deployed ibuttons by attaching them to metal stakes using double-sided mounting tape. We pushed the stakes into the soil so that each ibutton was locatedlocated at a height of 10 cm above the ground surface to approximate temperatures experienced at the height of a quail's body core. We placed one ibutton at the sample point and then every 2 m along the array for a total of 11 ibuttons per array. Each ibutton location constituted a "microsite." At nest locations, the ibutton at the center of the array was placed inside the nest bowl. We collected temperature data for 48 hours at each array. We compared these temperatures with weather data recorded hourly by an on-site weather station (33°29’59 N, -103°55’5.40 W) (Horel et al. 2002). The weather station recorded temperature, solar radiation, relative humidity, and precipitation.

Vegetation sampling

After 48 hours of thermal data collection, we returned to each array to retrieve the ibuttons and collect data on vegetation cover and structure. We estimated vertical obstruction at the center of each array using a Nudds profile board (Nudds 1977) modified for use in a sand shinnery oak community (Guthery 1981). We attached a digital level to the Nudds profile board to measure the angle of overhead obstruction. This measurement provides an index of the three-dimensional structure surrounding a given location (Kopp et al. 1998, Harrell and Fuhlendorf 2002). We collected angle measurements in 8 evenly-spaced cardinal directions by placing one end of the profile board at the sample point and tilting the board until it hit the top of the nearest obstructing vegetation. These 8 angles were averaged to calculate the average angle of obstruction for each sample point. To quantify the density of tall woody vegetation in the area surrounding the nest, we used a point-centered quarter method (Cottam and Curtis 1956) at the center point of each nest array and random array. In each quarter, we measured the distance to the nearest tall mesquite shrub (>1.5 m) and the nearest tall non-mesquite shrub (>1.5 m) using a laser rangefinder, truncated to 100 m. We selected 1.5 m as our threshold based on previous work that suggests scaled quail prefer to loaf under shrubs ranging from 0.5 to 1.5 m tall (Goodwin and Hungerford 1977, Stormer 1981). However, anecdotal evidence suggests that scaled quail frequently use tall shrubs for cover and perching. Therefore, we used a height of 1.5 m as a threshold to test whether tall shrub cover is an important component of scaled quail nesting cover. Overhead obstruction, vertical obstruction, and density of tall shrubs were measured at the center point of each array, therefore, comparisons between them were at the array level only.

At each individual microsite (11 per array) we measured horizontal vegetation cover and structure. We estimated horizontal ground cover composition using a 0.5 m x 0.5 m cover frame centered over each ibutton location. Within the frame we visually estimated percent cover of 7 functional groups (bare ground, rock, litter, grass, forbs, shrubs, and dead woody vegetation) using the cover classes described by Daubenmire (1959). We defined dead woody vegetation as any defoliated, dead woody stems that stood at least 10 cm tall. If a dead woody stem was less than 10 cm tall, we considered it litter because it did not provide any overhead structure. We defined litter as any dead plant material on the soil surface which was not rooted in the ground. We also measured the height of the tallest living vegetation and the tallest dead woody vegetation within the frame, and litter depth at the center of the frame.

We characterized the topography at each microsite by determining a slope index. To determine the slope index for each microsite, we used a digital level affixed to a 1 m square board. We centered the level at each microsite along the length of the array and lowered the level until it was flush with the ground surface. We recorded the absolute value of the angle reading from the digital level as the local slope for that microsite. Additionally, we classified each array as either “rough” or “flat” based on the overall topography observed at the array level. Rough arrays were those characterized by sand dunes, mesquite hummocks, or choppy terrain; flat arrays were those that lay on relatively level ground (<5°) with no hills, hummocks, or mounds. If an array was surrounded by dunes but lay on level ground between them, then the array was classified as flat. Therefore, we had 2 levels of topography for further analysis.

Data analysis

To evaluate nest site selection, we used one-way ANOVA to compare mean differences in vegetation and topography. Separate analyses were conducted to compare 1) nest and random arrays, 2) nest bowls and adjacent nest array microsites, 3) hatched and failed nests arrays, and 4) hatched and failed nest bowls. To analyze vertical obstruction, we combined the Nudds strata into three groups that approximated the height of the line of sight for potential nest predators: low (<4.0 dm; American badger (*Taxidea taxus*), striped skunk (*Mephitis mephitis*), and swift fox (*Vulpes velox*)), medium (4.0-8.0 dm; coyote (*Canis latrans*) and javelina (*Tayassu tajacu*)), and high (>8.0 dm, above the line of sight for most terrestrial nest predators). For comparisons between nest bowls and other microsites within the nest array, we analyzed microsites near the nest bowl (2 m away) separately from microsites far from the nest bowl (4-10 m away). This allowed us to evaluate whether nest site characteristics changed with increasing distance from the nest. We used post-hoc Tukey tests to conduct pairwise comparisons for all analyses.

For all thermal analyses, we only included those microsite temperatures that were recorded closest to the hour. This allowed us to compare microsite temperatures with hourly ambient temperatures at the same temporal scale. We used these data to create linear models of thermal environments for selected and non-selected locations at both the array scale and the nest bowl scale. We used a one-way repeated measures mixed-model ANOVA with microsite included as a random effect to assess differences in temperature between 1) nest and random arrays, 2) nest bowls and adjacent nest array microsites, 3) hatched and failed nest arrays, and 4) hatched and failed nest bowls. Because thermal relationships changed throughout the diel cycle, we ran separate tests for the full thermal dataset and for subsets by time periods relevant to the on- and off-bout patterns of incubating scaled quail (Carroll et al. 2018): morning (06:00-08:00), midday (10:00-14:00), evening (17:00-19:00), and night (22:00-02:00). We conducted all statistical analyses in Program R (version 3.6.1, R Core Team 2019).

Possible factors influencing daily nest survival were examined using the nest survival model in Program MARK (version 6.2, Cooch and White 2019). We created 38 univariate candidate models divided into eight model groups: vegetation, quadratic vegetation, obstruction, topography, time since fire, microclimate (mean, minimum, and maximum nest bowl temperatures), weather (daily mean ambient temperature, daily mean relative humidity, daily precipitation, and daily maximum solar radiation), and temporal variables. Quadratic vegetation variables were included to test whether the relationship between vegetation and nest survival followed a quadratic relationship, with probability of survival being highest at threshold values. We hypothesized each of the variables included in these models to influence daily nest survival probability either based on previous research (Fogarty et al. 2017, Hovick et al. 2014, Pleasant et al. 2006) or based on the results of our nest site selection analysis. We evaluated each model group separately using Akaike Information Criterion adjusted for small sample sizes (AIC_C). We considered models for which $\Delta AIC_C < 2$ competitive (Burnham and Anderson 2002).

Results

During the 2018 and 2019 breeding seasons, we monitored 150 adult scaled quail and detected 48 nests. Nests were initiated from May 11—July 7 in 2018 (*n* = 18) and May 3—June 29 in 2019 (*n* = 30). Of those nests, 25 (53%) failed and 22 (47%) survived to hatch. We measured thermal and vegetation characteristics at 39 nest locations (22 failed and 17 hatched) and 65 stratified random locations.

In 2018, there were four different times since fire present on the ACEC: less than 1% in 0-11 months since fire, 25% in 12-23 months since fire, 6% in 24-35 months since fire, and 69% unburned. Nests in 2018 were detected only in pastures 12-23 months since fire (35% of nests) and unburned pastures (65% of nests) (*n* = 17). In 2019, 2% of the ACEC was in 0-11 months since fire, less than 1% in 12-23 months since fire, 25% in 24-35 months since fire, and 73% unburned. Nests were detected in pastures 0-11 months since fire (7% of nests), 24-35 months since fire (34% of nests), and unburned pastures (59% of nests) (*n* = 29).

At the array scale, nest and random arrays were distinct in both vegetation and temperature. Vertical obstruction at nest arrays was significantly greater than at random arrays for all three height categories (Figure 1 and Table 1). Nests also had significantly greater overhead obstruction than random locations, with an average overhead obstruction of 81.74° ± 2.43 and 30.99° ± 1.88 observed at nest and random arrays, respectively (Figure 1 and Table 1). Nest arrays were characterized by greater cover of litter and grass, less bare ground, and taller live vegetation and dead woody vegetation than random arrays (Figure 2 and Table 1). No significant differences were detected for rock, forbs, shrubs, dead woody vegetation, or litter depth (Figure 2 and Table 1). Although not statistically significant, nest arrays had greater densities of tall mesquite shrubs than random arrays (Table 1). They also had significantly greater density of non-mesquite shrubs (1.49 shrubs/ha ± 0.38) than random arrays (0.10 shrubs/ha ± 0.30) (Figure 3 and Table 1). Fifty-four percent of nest arrays were in rough topography, while only 40% of random arrays were in rough topography, but average microsite slope did not vary between the two location types (Table 1).

In terms of temperature, nest arrays were significantly different from random arrays (Figure 4). In particular, nests arrays were significantly warmer on average than random arrays during the morning, at midday, and at night (Table 2). In contrast, nest arrays were significantly cooler than random arrays during the evening, which is when ambient temperatures are generally highest. At any given ambient temperature, the temperatures recorded at nest arrays were significantly cooler than those recorded at random arrays (28.96 ± 0.03, 29.35 ± 0.02, $p < 0.001$) (Figure 5), however, these differences in temperature were <0.5°C.

Preliminary analysis indicated that near (2 m from the nest bowl) and far (>2 m from the nest bowl) microsites were statistically similar to each other for all vegetation and thermal variables, therefore, we combined near and far microsites for the final analysis. Hereafter, all results presented for microsite characteristics represent both near and far microsites. At the microsite scale, we found that nest bowls differed from microsites in both vegetation and temperature. Nest bowls had greater cover of litter, grass, and shrubs than adjacent microsites

(Figure 6 and Table 3). Nest bowls also had less bare ground, taller live vegetation, and taller dead woody vegetation than microsites (Figure 6 and Table 3). No significant differences were detected for rock, forbs, litter depth, or slope between the nest bowl and adjacent microsites (Figure 6 and Table 3).

We found that thermal selection was much more pronounced at the scale of the nest bowl than at the scale of the nest array. At any given ambient temperature, nest bowls significantly moderated temperature relative to microsites (28.11±0.10, 29.85±0.03, $p<0.001$), with nest bowls being cooler under warm ambient conditions and slightly warmer under cool ambient conditions (Figure 7). Specifically, nest bowls were cooler than microsites during the morning, midday, and evening (Table 4 and Figure 8). At midday when the sun was at its highest angle, nest bowls remained approximately 5°C cooler on average than adjacent microsites (Figure 8). Nest bowls moderated temperatures at night by maintaining slightly warmer temperatures than adjacent microsites (Figure 8), although this trend was not statistically significant (Table 4).

Neither vegetation, topography, nor temperature appeared to have an influence on nest fate. Specifically, we did not detect any significant differences in vegetation cover, structure, or density; or topography between hatched and failed nests at either the scale of the nest bowl or the array scale (Table 5). Hatched and failed nests also did not differ significantly in temperature at any time of day (Table 6). However, hatched nest bowls showed a very slight trend towards warmer temperatures than failed nest bowls in the early morning before sunrise (02:00-06:00) and cooler temperatures than failed nest bowls in the afternoon and evening (13:00-21:00) (Figure 9). Similarly, hatched nests arrays moderated temperatures relative to failed nests at the array scale (29.85±0.05, 29.47±0.04, $p<0.001$) but at any given ambient temperature, nest bowl temperatures were not statistically different between nest fates (28±0.12, 28±0.10, $p=0.947$) (Figure 10).

Daily nest survival was not strongly influenced by any of the variables included in our nest survival models (Table 7). The null model received the greatest support ($\Delta \text{AIC}_C = 0$) within each of the eight model groups with the exception of the topography group. In the topography group, the best-supported model included slope at the nest bowl ($\Delta \text{AIC}_C = 0$), but the null model was still competitive ($\Delta \text{AIC}_C = 0.444$). Of the 38 models that we tested, 34 were considered competitive ($\Delta \text{AIC}_C < 2$).

Discussion

Our findings provide a more comprehensive perspective on how scaled quail select nest sites across their geographic distribution. Scaled quail clearly demonstrated preferences when choosing where to place their nests, and these preferences manifested differently at different spatial scales. Although we did not detect any influence of vegetation or temperature on nest survival, our results suggest that the availability of nesting substrate alone does not guarantee suitable nesting habitat. Rather, the characteristics of the area surrounding the nest also play an important role.

Nest site selection

We found that scaled quail showed consistent selection for certain vegetation features across scales. Specifically, they chose nest sites with greater horizontal cover of tall herbaceous vegetation, which suggests that this cover type provided important benefits for nesting quail. Shrub cover was also an important component of the nest bowl itself. Increased vegetation cover is generally associated with visual concealment of the nest from predators (Hernández et al. 2003, Townsend et al. 2001). However, we did not observe any difference in vertical obstruction between nests and random locations. This was surprising, given that vertical obstruction has been shown to play an important role in nest site selection and survival for other ground-nesting species including greater prairie-chickens (*Tympanuchus cupido*) (Grisham et al. 2016, Hovick et al. 2014) and sharp-tailed grouse (*T. phasianellus*) (Milligan et al. 2019). Vertical obstruction not only provides visual concealment, but is also positively related to turbulence intensity, which may increase olfactory concealment of the nest (Fogarty et al. 2018). Therefore, the lack of vertical obstruction at scaled quail nests suggests that nest sites were not selected primarily to reduce terrestrial predation risk. Rather, tall herbaceous vegetation and shrubs at the nest may have provided visual concealment from aerial predators, such as corvids (Rollins and Carroll 2001), or thermal screening, through increased vegetation height (Kline et al. 2019) and overhead obstruction (Tracol et al. 2011, Kopp et al. 1998).

Thermal screening at the nest bowl has important implications for nest survival. It is the temperatures in the nest bowl, rather than the surrounding air temperature, that have the greatest potential to directly influence survival of the embryos, the rate of embryonic development, and the behavior of the incubating adult; all of which could have serious implications for nest fate and eventual brood success (Belnap et al. 2019, French 2000, Reyna 2019, Webb 1987). Both adult quail and galliform embryos can experience hyperthermia at temperatures above 39°C (Guthery et al. 2005, Webb 1987). Choosing a nest sites that moderates temperature reduces the energy required for an incubating adult to thermoregulate, and may allow the adult to take longer, less frequent foraging bouts to reduce predation risk (DuRant et al. 2012, Thomson et al. 1998). We observed that nest bowls of scaled quail were roughly 5°C cooler on average than adjacent microsites during hours of peak heating (10:00-14:00), even when compared to microsites only 2 m away. This drastic change in temperature over such a short distance indicates extreme fine-scale thermal selection. Similar patterns related to temperature have been demonstrated for several species of ground-nesting birds across North America, including northern bobwhite (*Colinus virginianus*) (Carroll et al. 2015*a*), greater prairie-chicken (Hovick et al. 2014), and sharp-tailed grouse (Raynor et al. 2018). The consistency of these patterns across species further suggests that temperature is an important aspect of nest site selection at the scale of the nest bowl.

Although the exact mechanism behind these cooler temperatures has not been confirmed, several studies have suggested that shrub cover is an important source of thermal cover (Carroll et al. 2015*a*, Patten et al. 2005, Raynor et al. 2018). Shrubs provide a source of overhead shading that intercepts solar radiation and may decrease temperatures beneath the canopy (Geiger 1965). Given that scaled quail nests had significantly greater shrub cover and cooler temperatures than adjacent microsites, it is possible that shrub cover contributed to thermoregulation at the nest bowl through shading or other mechanisms. Regardless of the mechanism of selection, selected locations provided moderated temperatures relative to the surrounding landscape, providing a more favorable thermal environment for developing embryos and incubating adults.

Temperatures at the array scale appeared less favorable. Nest arrays tended to be warmer, with temperatures exceeding those at random arrays by as much as 1-2°C during the morning and midday. Furthermore, nest arrays experienced temperatures of over 40°C on average during the midday period. This pattern is counterintuitive, given the vulnerability of avian embryos to high temperatures. However, temperatures in the area surrounding the nest may not be biologically relevant. Incubating adults will spend most of their time on the nest bowl incubating the eggs, and even during foraging off-bouts they may avoid the nest area due to the risk of attracting visually-oriented predators (Bures and Pavel 2003, Burhans 2000). As long as the nest bowl itself maintains a suitable microclimate, temperatures outside of the nest may not directly influence the embryos or the incubating adult.

Warmer temperatures observed at the nest array may have been an artifact of selection for other nest site characteristics. For example, we saw clear selection for horizontal cover of herbaceous vegetation at nest arrays, a substrate that has been associated with higher temperatures than woody vegetation (Carroll et al. 2018). However, herbaceous vegetation can also provide important benefits in terms of visual (Townsend et al. 2001) or olfactory concealment (Fogarty et al. 2018). Warmer average temperatures at the array scale, therefore, may have been a by-product of selection for other beneficial site characteristics.

Time since fire did not influence scaled quail nest site selection or nest survival. Other studies have demonstrated both positive effects (Long et al. 2012) and negative effects (Sandercock et al. 2015) of recent burns on avian nest site selection and success, suggesting that the relationship between fire and nest site selection may be species-dependent (Long et al. 2012). Lack of response to time since fire has been documented in other ground-nesting species. Time since fire was not found to influence nest site selection of wild turkeys (*Meleagris gallopavo*) in a longleaf pine forest (Wood et al. 2019); rather, nest site selection was primarily driven by vegetation cover and structure at fine scales, and by proximity to roads at coarse scales. Northern bobwhite exhibit plasticity in nest site selection by choosing nest substrates based on availability within different times since fire, and these differences in selection did not influence nest success (Carroll et al. 2017*b*). Therefore, time since fire may only influence nest site selection of scaled quail insomuch as it influences the availability of suitable nest areas and nest bowl microclimates. We suspect that suitable nesting habitat was available for scaled quail in every time since fire at our study site. Due to the sparse vegetation structure at Sand Ranch ACEC, fuels were not continuous enough to burn entire pastures evenly. This created heterogeneous burns with "islands" of unburned vegetation throughout, which could have provided enough cover and structure for nesting quail. Effective investigations of the relationship between time since fire and nest site selection in sparsely vegetated landscapes may require a finer-scale approach to account for variation in completeness of burn across large areas.

Although site characteristics play an important role in shaping the nest microclimate, the nest location itself is only a part of what influences microclimate. Adult quail have been known to actively monitor and adjust egg temperatures throughout incubation. The presence of an incubating parent aided in optimizing egg incubation temperature when ambient temperatures fluctuated (Brown and Downs 2003, Carroll et al. 2018, Coe et al. 2015). Therefore, incubating adults must be careful about when and how long to leave the nest unattended during off-bouts. It is during these off-bouts that the characteristics of the nest bowl itself should be most important for moderating egg temperature. Previous work indicates that scaled quail time their off-bouts between 06:00-08:00 in the morning and 17:00-19:00 in the evening (Carroll et al. 2018). Our results suggested that temperatures at hatched nest bowls tended to be moderated relative to failed nest bowls during these off-bout periods. Specifically, hatched nests were slightly warmer right before the presumed morning off-bout (03:00-06:00) and slightly cooler right after the presumed afternoon off-bout (19:00-22:00). This pattern, although not statistically significant, may be biologically relevant. Changes in incubation temperature of less than 1°C have been shown to reduce hatchability and alter the duration of incubation in gallinaceous birds (Belnap et al. 2019, French 2000). A growing body of literature indicates that nest site selection is partially driven by temperature (Carroll et al. 2015*a*, Carroll et al. 2018, Hovick et al. 2014, Nelson and Martin 1999, Raynor et al. 2018). Therefore, although these slight differences in temperature were not statistically significant, further investigation is warranted to determine relevance for hatchability and nest survival.

Nest survival

Despite evidence for nest site selection at multiple spatial scales, none of the factors we evaluated were found to significantly influence nest fate. Several other studies on ground-nesting species have failed to detect a difference in vegetation between hatched and failed nests (Carroll et al. 2015*a*, Carroll et al. 2018, Hovick et al. 2014, Raynor et al. 2018); however, most of these studies observed that hatched nests provided cooler temperatures than failed nests (Carroll et al. 2015*a*, Hovick et al. 2014, Raynor et al. 2018). Previous work on scaled quail has also demonstrated a significant thermal difference between hatched and failed nests, although in this study hatched nests were significantly hotter than failed nests (Carroll et al. 2018). Weather variables have been shown to be the most important predictors of daily nest survival in other ground-nesting species. Survival probability of greater-prairie chickens in the Southern Great Plains was best predicted by solar radiation, which likely contributed to thermal differences between hatched and failed nests (Hovick et al. 2015). Vegetation height and linear temporal trends also played an important role, yet these variables explained much less of the variation in daily nest survival than did solar radiation. Weather variables related to moisture, specifically precipitation and relative humidity, were the best predictors of daily nest survival in northern bobwhite (Fogarty et al. 2017). These variables were believed to influence olfactory detection of nests by mammalian predators, as nests were more likely to survive on days with high moisture. Similarly, daily nest survival of northern bobwhite in Texas was most affected by maximum ambient temperature and precipitation, while vegetation variables played a lesser role (Rader et al. 2007). However, none of these weather variables influenced daily nest survival of scaled quail in our study, and neither did vegetation.

There are a few possible explanations for our findings related to nest fate. First, temperature and vegetation variables may truly be unrelated to nest fate. Rather, the greatest predictors of daily nest survival in our population may be factors that we did not account for in this study. For example, we did not measure humidity at the nest bowl or proximity to foraging resources, factors which may also play a role in adult behavior and nest survival (Grisham et al. 2016). Alternatively, our sample size (*n* = 39) may not have been adequate to detect an effect of these variables on daily nest survival. Given a larger sample size of nests over a greater period of time, our confidence in the results would increase, potentially revealing significant differences between hatched and failed nests. Another possibility is that nest site characteristics may only influence nest fate in scaled quail under certain conditions. The relative influence of vegetation and topography on temperature changes across days, seasons, and years (van Beest et al. 2012), and some features may become more important for thermal refuge in years with extreme conditions such as unusually high temperatures or extended drought. Even if those conditions occurred infrequently, extreme years could be enough to exert selection pressure on quail and influence natural selection at greater temporal scales (Brown and Brown 2000). Similarly, the importance of nest site characteristics may change in response to fluctuations of predator populations (Rauter et al. 2002) or populations of other prey species (Larsen 2000), causing some nests to become more vulnerable under greater pressure from predation. There is a paucity of information regarding nesting ecology of scaled quail, and further exploration is needed to understand the role of nest site characteristics, including temperature, in determining daily nest survival and ultimate nest fate.

Conclusion

Our findings provide a more comprehensive understanding of how scaled quail select habitat in the geographic core of their distribution. Consistent selection for tall, herbaceous cover at multiple spatial scales has important implications for management strategies such as grazing that can alter grass cover, at least in terms of nesting ecology. Similarly, shrub cover appears to be an important component of the nest structure itself, possibly providing both overhead concealment and thermal shading. Our results suggest that large-scale shrub removal may affect the availability of preferred nesting substrate for scaled quail, although the implications on nest fate are not clear. Nevertheless, managers should consider preserving a shrub component and residual herbaceous cover, thus maintaining suitable nesting cover. Our research fills geographical gaps in our understanding of scaled quail nest site selection, and emphasizes the importance of considering not only the characteristics of nest substrates, but also the structural, compositional, and thermal contexts in which those substrates occur.

Table 1. Differences in vegetation and topography between scaled quail (*Callipepla squamata*) nest arrays and random arrays. Significant differences ($p < 0.05$) are indicated by bolded font. Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

	Nest		Random			
	Mean	SE	Mean	SE	F	*p*
Bare ground cover (%)	40.74	2.63	51.98	2.04	11.40	**0.001**
Rock cover (%)	1.29	1.06	2.21	0.83	0.46	0.498
Litter cover (%)	46.12	2.61	34.84	2.02	11.70	**0.001**
Grass cover (%)	30.41	2.28	21.57	1.76	9.43	**0.002**
Forb cover (%)	5.49	0.85	4.50	0.66	0.84	0.358
Shrub cover (%)	19.79	1.88	15.58	1.46	3.14	0.077
Dead woody vegetation cover (%)	2.32	0.36	2.33	0.28	0.00	0.987
Vegetation height (mm)	515.12	21.48	416.73	16.64	13.11	**<0.001**
Dead woody vegetation height (mm)	398.55	24.69	323.10	20.07	5.63	**0.020**
Litter depth (mm)	17.24	1.78	17.86	1.38	0.08	0.781
Overhead obstruction (°)	81.74	2.43	30.99	1.88	273.40	**<0.001**
Vertical cover low: 0-4 dm (%)	82.20	1.29	45.52	2.85	93.51	**<0.001**
Vertical cover medium: 5-8 dm (%)	23.57	2.42	7.78	1.45	35.62	**<0.001**
Vertical cover high: 9-12 dm (%)	2.74	0.82	0.79	0.33	6.52	**0.011**
Local slope (°)	4.05	0.30	3.91	0.24	0.13	0.723
Tall mesquite (shrubs per ha)	6.07	1.63	3.04	1.27	2.15	0.142
Tall non-mesquite (shrubs per ha)	1.49	0.38	0.10	0.30	8.23	**0.004**

Table 2. Differences in temperature between scaled quail (*Callipepla squamata*) nest arrays and random arrays in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Significant differences (p < 0.05) are indicated by bolded font. For each set of comparisons, we evaluated thermal differences for 5 time periods: full (all hours), morning (06:00-08:00), midday (10:00-14:00), evening (17:00-19:00), and night (22:00-02:00).

	Nest		Random			
Time period	Mean	SE	Mean	SE	F	*p*
Full	29.71	0.16	29.22	0.12	6.09	**0.014**
Morning	23.10	0.15	21.98	0.12	35.88	**<0.001**
Midday	41.43	0.22	40.19	0.17	19.63	**<0.001**
Evening	34.62	0.25	35.44	0.19	6.92	**0.009**
Night	21.23	0.16	20.82	0.12	4.11	**0.043**

Table 3. Differences in vegetation and topography between scaled quail (*Callipepla squamata*) nest bowls and adjacent microsites (2-10 m away from the nest bowl). Significant differences ($p < 0.05$) are indicated by bolded font. Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

	Nest bowl		Microsites			
	Mean	SE	Mean	SE	F	*p*
Bare ground cover (%)	8.33	4.72	43.98	1.49	51.89	**<0.001**
Rock cover (%)	<0.01	1.54	1.42	0.49	0.77	0.380
Litter cover (%)	63.01	4.60	44.43	1.46	14.81	**<0.001**
Grass cover (%)	59.81	4.22	27.47	1.33	53.50	**<0.001**
Forb cover (%)	3.08	1.48	5.73	0.47	2.92	0.087
Shrub cover (%)	41.60	3.96	17.61	1.25	33.36	**<0.001**
Dead woody vegetation cover (%)	3.91	0.80	2.16	0.25	4.39	**0.036**
Vegetation height (mm)	722.87	37.88	494.92	12.03	32.90	**<0.001**
Dead woody vegetation height (mm)	490.47	43.26	367.59	14.92	7.21	**0.007**
Litter depth (mm)	25.64	2.86	16.69	0.93	8.88	**0.003**
Local slope (°)	3.72	0.66	4.08	0.21	0.27	0.603

Table 4. Differences in temperature between scaled quail (*Callipepla squamata*) nest bowls and adjacent microsites (2-10 m from the nest bowl) in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Significant differences (p < 0.05) are indicated by bolded font. For each set of comparisons, we evaluated thermal differences for 5 time periods: full (all hours), morning (06:00-08:00), midday (10:00-14:00), evening (17:00-19:00), and night (22:00-02:00).

	Nest		Random			
Time period	Mean	SE	Mean	SE	F	*p*
Full	28.07	0.35	29.87	0.11	24.43	**<0.001**
Morning	22.35	0.35	23.20	0.11	5.35	**0.021**
Midday	36.86	0.59	41.90	0.19	65.94	**<0.001**
Evening	32.19	0.70	34.87	0.23	13.23	**<0.001**
Night	21.30	0.43	20.54	0.14	2.81	0.094

Table 5. Differences in vegetation and topography between hatched and failed scaled quail (*Callipepla squamata*) nests at both the array scale and the microsite scale. Significant differences ($p < 0.05$) are indicated by bolded font. No significant differences were detected between hatched and failed nests for any of the variables tested. Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

		Hatched		Failed			
		Mean	SE	Mean	SE	F	*p*
Array scale	Bare ground cover (%)	37.81	3.99	43.01	3.51	0.96	0.327
	Rock cover (%)	2.55	1.56	0.32	1.37	1.16	0.282
	Litter cover (%)	45.82	4.12	46.35	3.62	0.01	0.922
	Grass cover (%)	31.70	3.93	29.42	3.45	0.19	0.663
	Forb cover (%)	5.91	1.33	5.17	1.17	0.18	0.675
	Shrub cover (%)	16.18	3.10	22.58	2.72	2.42	0.120
	Dead woody vegetation cover (%)	2.31	0.56	2.32	0.49	0.00	0.988
	Vegetation height (mm)	512.77	34.39	516.94	30.23	0.01	0.927
	Dead woody vegetation height (mm)	380.02	40.96	412.66	35.75	0.36	0.548
	Litter depth (mm)	18.68	2.03	16.12	1.78	0.90	0.342
	Overhead obstruction (°)	80.39	2.29	82.78	2.01	0.61	0.434
	Vertical cover low: 0-4 dm (%)	82.90	1.94	81.65	1.75	0.23	0.633
	Vertical cover medium: 5-8 dm (%)	22.94	4.15	24.06	2.94	0.05	0.821
	Vertical cover high: 9-12 dm (%)	2.87	1.45	2.64	0.95	0.02	0.892
	Local slope (°)	3.60	0.52	4.40	0.45	1.35	0.253
	Tall mesquite density (shrubs per ha)	3.85	2.49	7.79	2.19	1.41	0.235
	Tall non-mesquite density (shrubs per ha)	0.58	0.94	2.19	0.82	1.68	0.196
Microsite scale	Bare ground cover (%)	6.91	2.01	9.43	1.77	0.89	0.347
	Rock cover (%)	0.00	0.00	0.00	0.00	NA	NA
	Litter cover (%)	63.24	8.16	62.84	7.17	0.00	0.971
	Grass cover (%)	62.94	7.83	57.39	6.88	0.28	0.594
	Forb cover (%)	3.24	1.78	2.96	1.57	0.01	0.906
	Shrub cover (%)	39.71	8.56	43.07	7.53	0.09	0.768
	Dead woody vegetation cover (%)	2.50	1.85	5.00	1.63	1.03	0.311
	Vegetation height (mm)	753.29	54.24	699.36	47.68	0.56	0.455
	Dead woody vegetation height (mm)	483.86	99.27	495.10	83.06	0.01	0.931
	Litter depth (mm)	28.24	3.10	23.64	2.73	1.24	0.266
	Local slope (°)	2.79	0.95	4.45	0.84	1.70	0.192

Table 6. Differences in temperature between hatched and failed scaled quail (*Callipepla squamata*) nest arrays and hatched and failed nest bowls in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Significant differences ($p < 0.5$) are indicated by bolded font. For each set of comparisons, we evaluated thermal differences for 5 time periods: full (all hours), morning (06:00-08:00), midday (10:00-14:00), evening (17:00-19:00), and night (22:00-02:00).

		Nest		Random			
	Time period	Mean	SE	Mean	SE	F	*p*
Array scale	Full	29.57	0.17	29.72	0.15	0.47	0.492
	Morning	23.00	0.16	23.06	0.14	0.06	0.800
	Midday	41.21	0.30	41.40	0.26	0.23	0.629
	Evening	34.77	0.35	34.59	0.29	0.15	0.695
	Night	20.64	0.21	20.52	0.18	0.18	0.669
Microsite scale	Full	27.76	0.54	28.19	0.46	0.38	0.544
	Morning	22.24	0.46	22.17	0.40	0.01	0.910
	Midday	36.43	0.88	36.86	0.75	0.14	0.712
	Evening	31.85	0.97	32.40	0.82	0.19	0.668
	Night	21.28	0.67	21.32	0.57	0.00	0.956

Table 7. Models explaining the effects of nest site characteristics on daily survival probability of scaled quail (*Callipepla squamata*) nests in Chaves County, New Mexico, USA from 2018-2019.

Group	Model	ΔAICc	w	k
Vegetation	Null	0.000	0.307	1
	Shrub cover: array (%)	0.540	0.234	2
	Shrub cover: nest bowl (%)	1.158	0.172	2
	Tall mesquite density (shrubs per ha)	1.389	0.153	2
	Vegetation height: nest bowl (mm)	1.645	0.135	2
Quadratic vegetation	Null	0.000	0.362	1
	Vegetation height: nest bowl (mm)	1.356	0.184	2
	Shrub cover: array (%)	1.412	0.178	2
	Shrub cover: nest bowl (%)	1.836	0.144	2
	Tall mesquite density (shrubs per ha)	2.015	0.132	2
Visual Obstruction	Null	0.000	0.364	1
	Overhead angle of obstruction (°)	1.158	0.204	2
	Vertical cover low: 0-4 dm (%)	1.651	0.160	2
	Vertical cover medium: 5-8 dm (%)	1.948	0.138	2
	Vertical cover high: 9-12 dm (%)	1.999	0.134	2
Topography	Local slope: nest bowl (°)	0.000	0.350	2
	Null	0.444	0.281	1
	Local slope: array average (°)	1.910	0.135	2
	Rough topography	2.190	0.117	2
	Flat topography	2.190	0.117	2
Time since fire	Null	0.000	0.220	1
	1 year since fire	1.322	0.114	2
	3 years since fire	1.356	0.220	2
	2 years since fire	1.595	0.099	2
	0 years since fire (year of burn)	2.009	0.081	2
Microclimate	Null	0.000	0.469	1
	Mean nest bowl temperature (°C)	1.930	0.179	2
	Minimum nest bowl temperature (°C)	1.937	0.178	2
	Maximum nest bowl temperature (°C)	1.991	0.174	2
Weather	Null	0.000	0.347	1
	Daily mean relative humidity (%)	1.108	0.199	2
	Daily mean ambient temperature (°C)	1.125	0.198	2
	Daily precipitation (mm)	1.996	0.128	2
	Daily maximum solar radiation (W/m^2)	1.997	0.128	2
Temporal	Null	0.000	0.347	1
	Linear trend	1.301	0.181	2
	Quadratic trend	1.349	0.177	2
	Year	1.568	0.158	2

Table 8. Weekly nest initiation rates of scaled quail (*Callipepla squamata*) in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. In both years, nests were initiated over an 8-week period during which the number of live hens decreased. The number of live hens was adjusted based on DNA verification to account for 85% accuracy sexing scaled quail in the field, and this adjusted number was used to calculate rates of nest initiation and success. Note that nest monitoring ceased in early August of each year so potential nests initiated after than time are not accounted for.

Week	Dates	Year	Live Hens	Live Hens (Adjusted)	Nests Initiated	Initiation Rate	Successful Nests	Success Rate
1	May 1-7	2018	20	14	0	0.00	0	NA
2	May 8-14	2018	19	14	1	0.07	0	0.00
3	May 15-21	2018	19	14	2	0.14	0	0.00
4	May 22-28	2018	19	14	4	0.28	0	0.00
5	May 29-June 4	2018	19	14	5	0.36	4	0.80
6	June 5-11	2018	19	14	4	0.28	2	0.50
7	June 12-18	2018	19	14	0	0.00	0	NA
8	June 19-25	2018	19	14	0	0.00	0	NA
9	June 26-July 2	2018	19	14	1	0.07	1	1.00
10	July 3-9	2018	16	12	1	0.09	0	0.00
1	May 1-7	2019	33	26	5	0.20	1	0.20
2	May 8-14	2019	31	24	5	0.21	3	0.60
3	May 15-21	2019	30	24	4	0.17	3	0.75
4	May 22-28	2019	29	23	4	0.18	2	0.50
5	May 29-June 4	2019	28	22	4	0.18	1	0.25
6	June 5-11	2019	28	22	3	0.14	2	0.67
7	June 12-18	2019	27	21	2	0.10	1	0.50
8	June 19-25	2019	25	20	1	0.05	0	0.00
9	June 26-July 2	2019	25	20	2	0.10	2	1.00
10	July 3-9	2019	24	19	0	0.00	0	NA

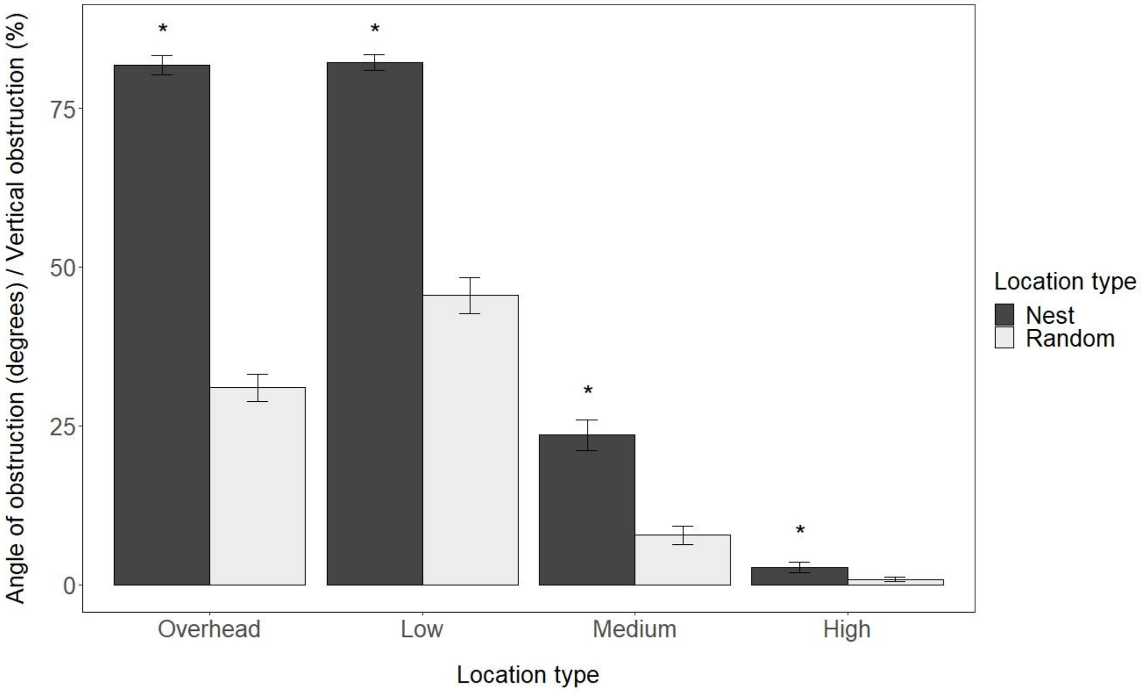

Figure 1. Mean values (along with standard errors) for overhead obstruction and vertical obstruction at scaled quail (*Callipepla squamata*) nest arrays and random arrays from 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Height categories for vertical obstruction included low (0-4 dm), medium (5-8 dm), and high (9-12 dm). Nest arrays had significantly greater overhead obstruction than random arrays. * denotes statistical significance at $p < 0.05$.

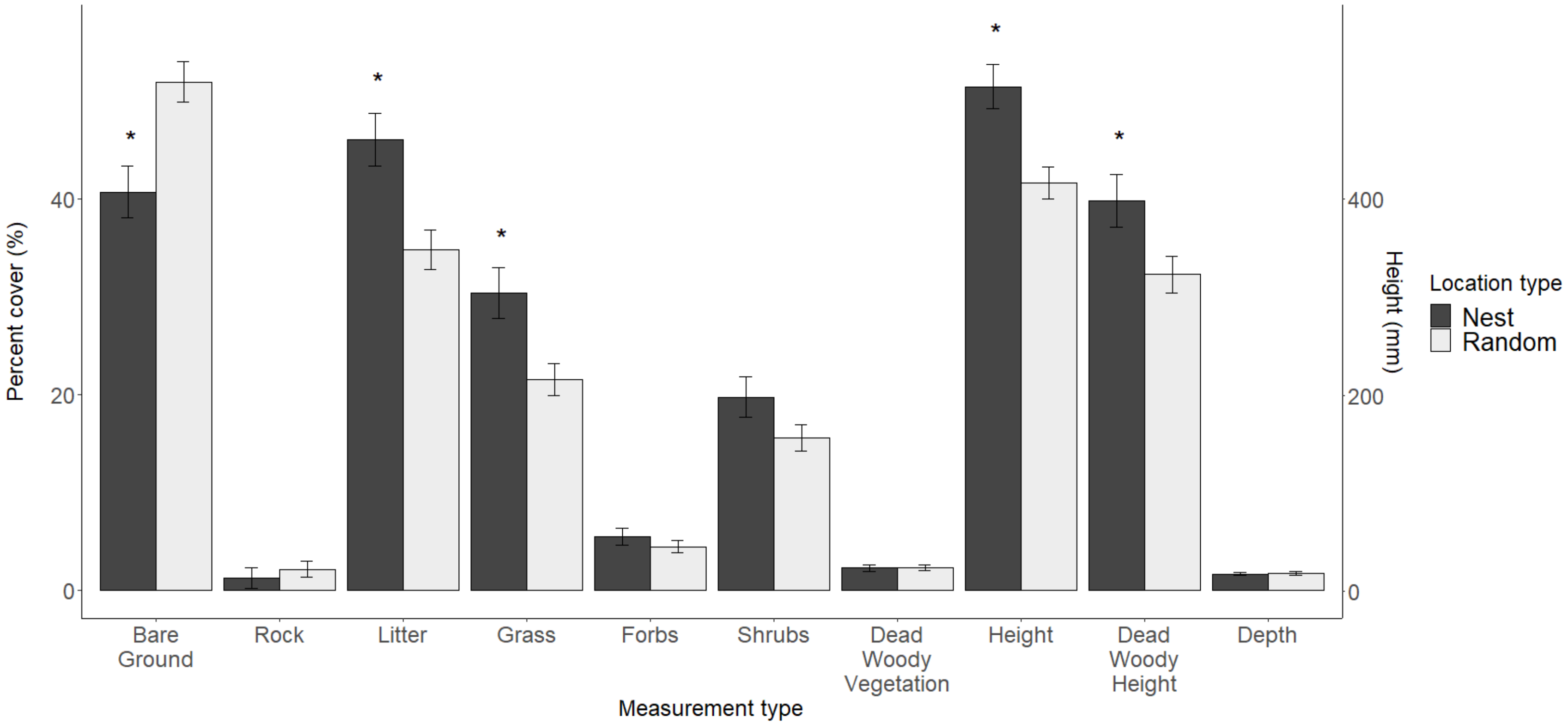

Figure 2. Mean vegetation cover and structure (along with standard errors) of scaled quail (*Callipepla squamata*) nest arrays and random arrays collected in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. The area around scaled quail nests had significantly greater cover of grass and litter, less bare ground cover, and taller vegetation than random locations. * denotes statistical significance at $p < 0.05$.

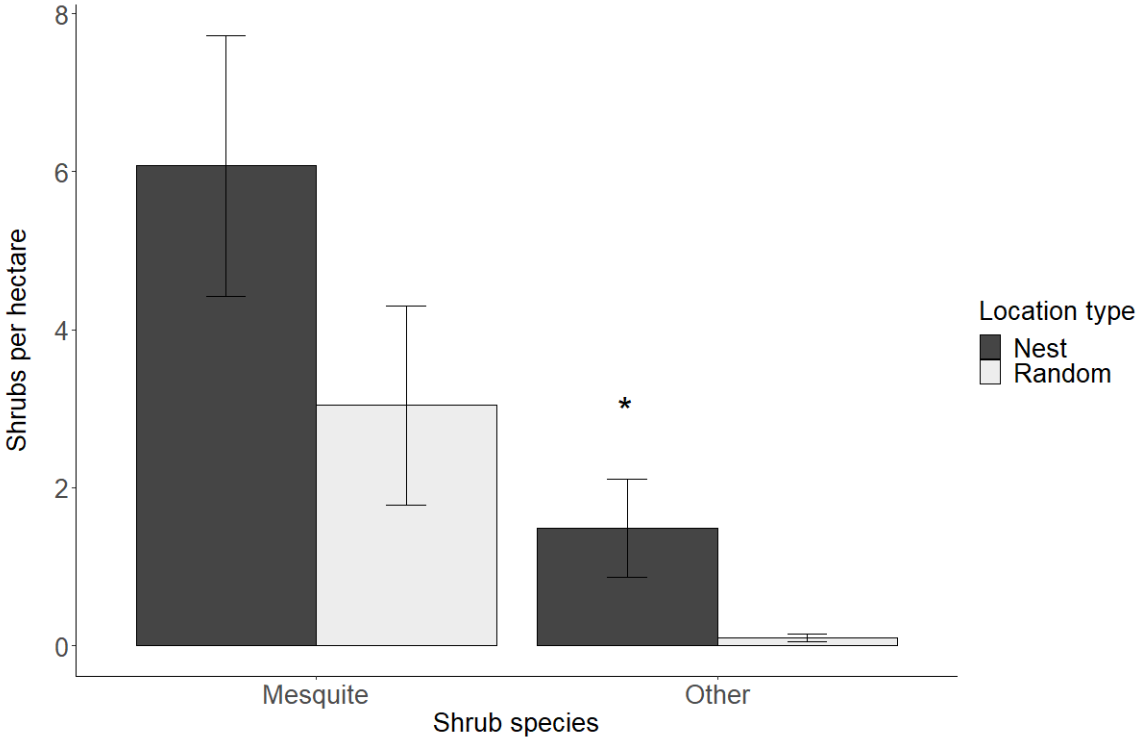

Figure 3. Mean density of tall (>1.5 m) shrubs at scaled quail (*Callipepla squamata*) nest arrays and random arrays in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Nest arrays had a greater density of tall non-mesquite shrubs than random arrays, but density of tall mesquite did not differ between the two array types. * denotes statistical significance at $p < 0.05$.

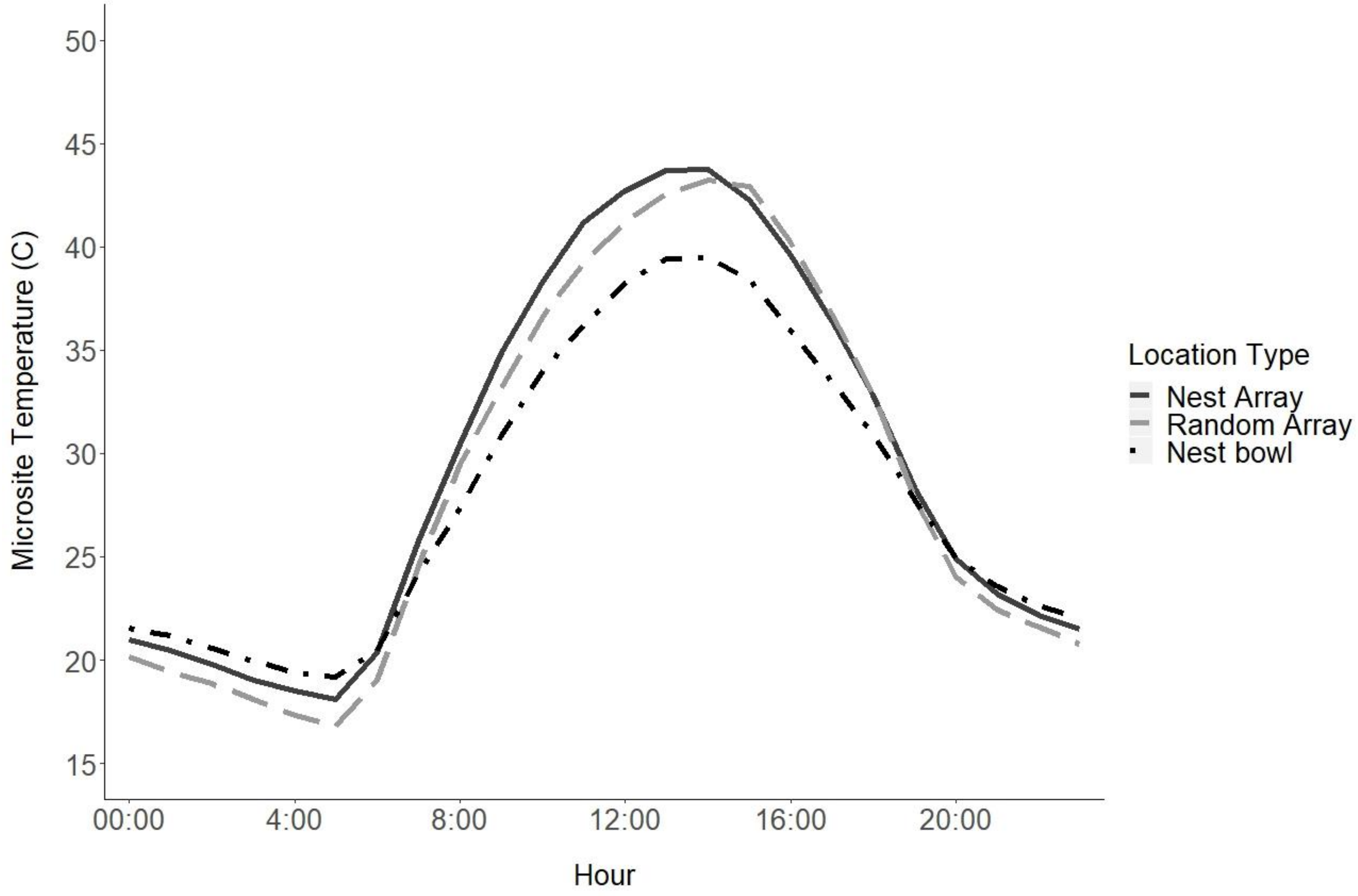

Figure 4. Average hourly temperatures at scaled quail (*Callipepla squamata*) nest arrays and random arrays at Sand Ranch in Chaves County, New Mexico, USA. Data was collected during the breeding seasons of 2018 and 2019. Hourly nest bowl temperatures are included for comparison. Nest arrays were significantly warmer than random arrays in the morning (06:00-08:00), at midday (10:00-14:00), and at night (22:00-02:00). Nest arrays were significantly cooler than random arrays in the evening (17:00-19:00).

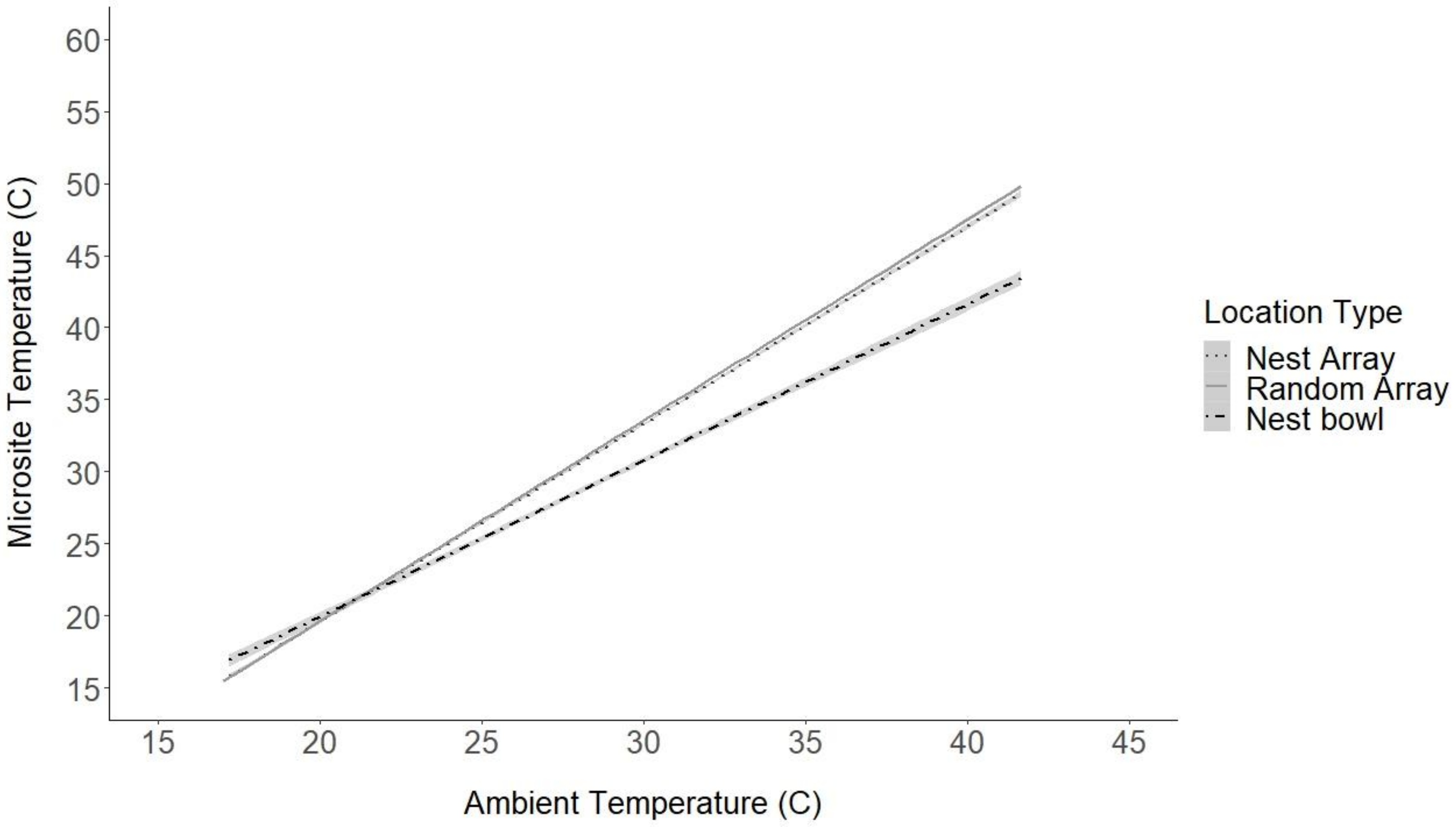

Figure 5. Linear regression explaining the relationship between ambient temperature and microsite temperatures between scaled quail (*Callipepla squamata*) nest arrays and random arrays (with nest bowl temperatures displayed for comparison). At any given ambient temperature, average microsite temperatures at nest arrays and random arrays were statistically different. However, these differences were so small that they not be biologically relevant. Thermal data was collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

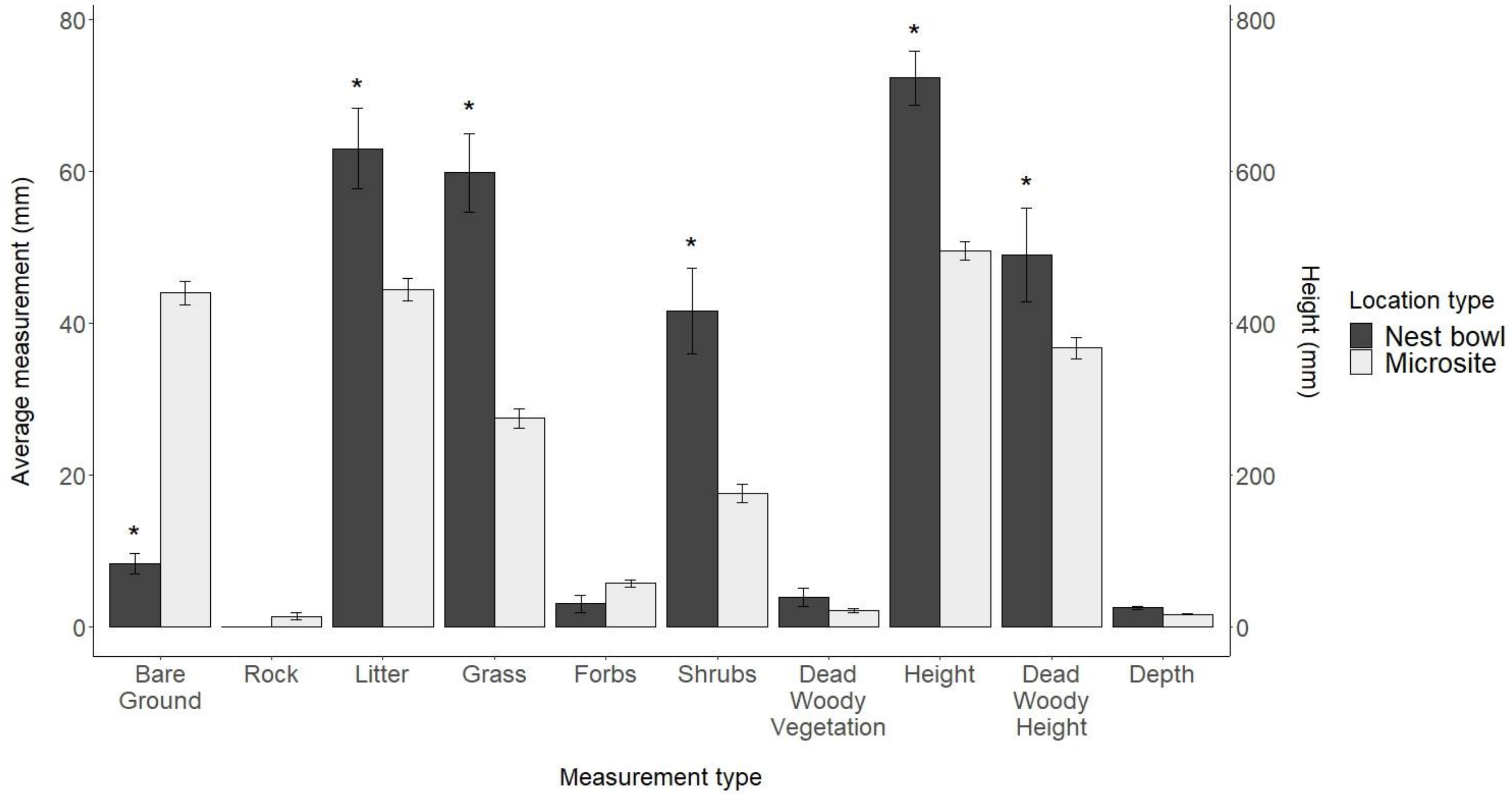

Figure 6. Mean vegetation cover and structure (along with standard errors) of scaled quail (*Callipepla squamata*) nest bowls and adjacent microsites (2-10 m) collected in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Scaled quail nest bowls had significantly greater cover of grass, litter, and shrubs; less bare ground cover; and taller vegetation than adjacent microsites. * denotes statistical significance at $p < 0.05$.

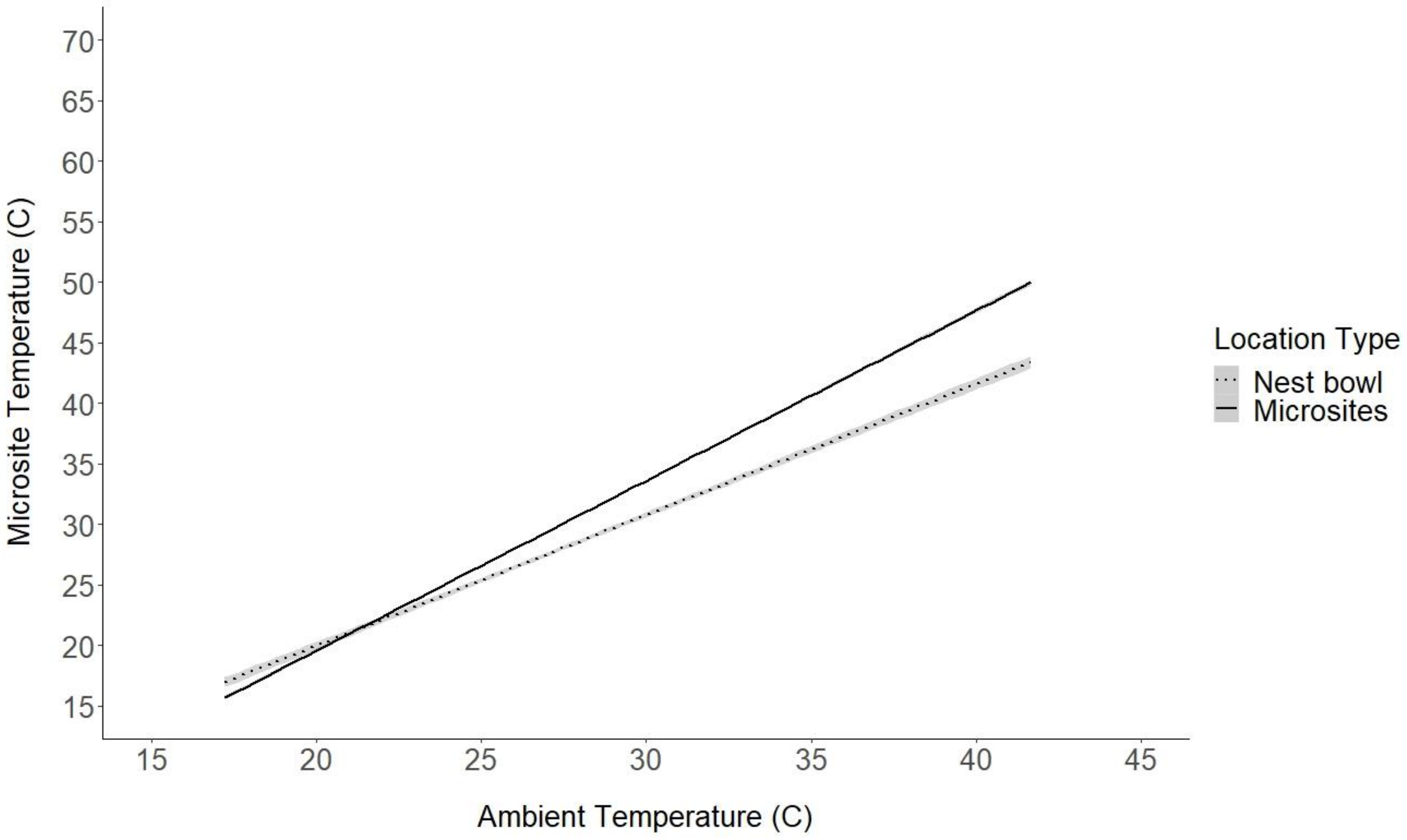

Figure 7. Linear regression explaining the relationship between ambient temperature and microsite temperatures between nest bowls and adjacent microsites (2-10 m). Nest bowls moderated temperature relative to adjacent microsites at ambient temperatures greater than 23°C. Thermal data was collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

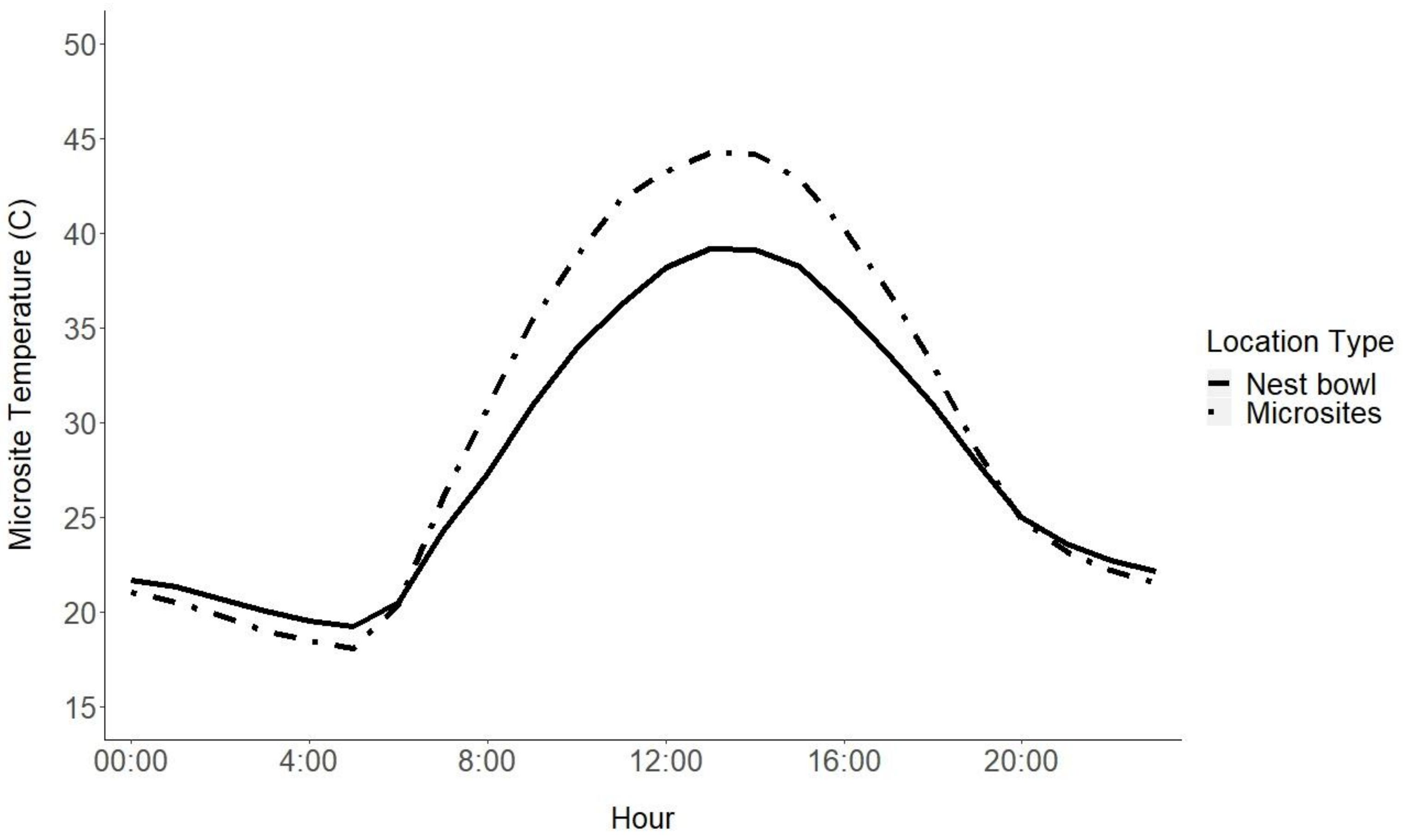

Figure 8. Average hourly temperatures at scaled quail (*Callipepla squamata*) nest bowls and adjacent microsites (2-10 m) at Sand Ranch in Chaves County, New Mexico, USA. Data was collected during the breeding seasons of 2018 and 2019. Nest bowls were significantly cooler than microsites during daylight hours (06:00-19:00), and significantly warmer than microsites at night (22:00-02:00). This suggests that nest sites moderate temperature at fine spatial scales.

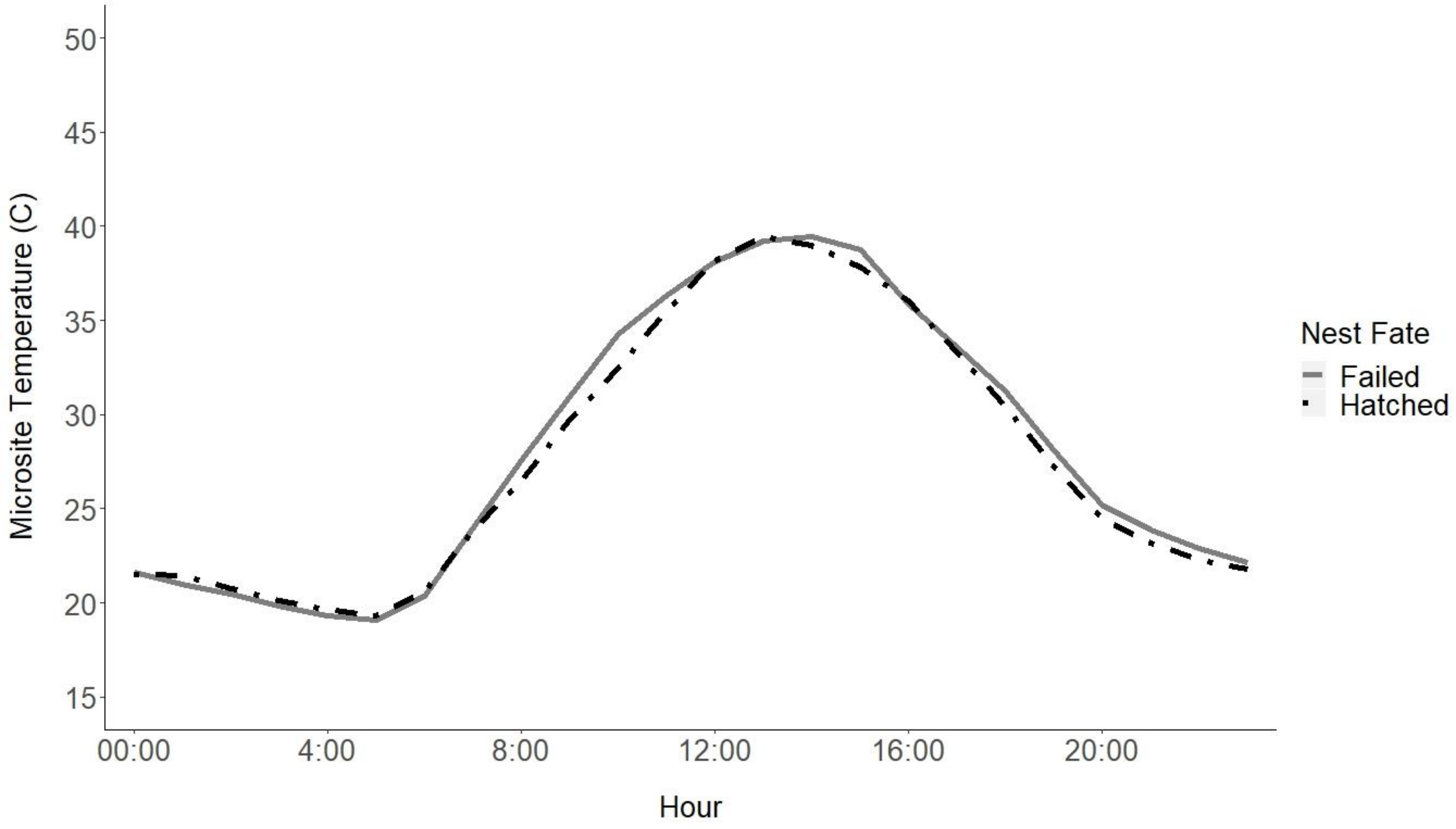

Figure 9. Average hourly temperatures at hatched (n=17) and failed (n=22) scaled quail (*Callipepla squamata*) nest bowls at Sand Ranch in Chaves County, New Mexico, USA in 2018 and 2019. Although nest temperatures were not significantly different between nest fates, hatched nest bowls tended to moderate temperature more effectively than failed nest bowls by remaining slightly warmer in the early morning (02:00-07:00) and slightly cooler in the late afternoon and evening (16:00-20:00).

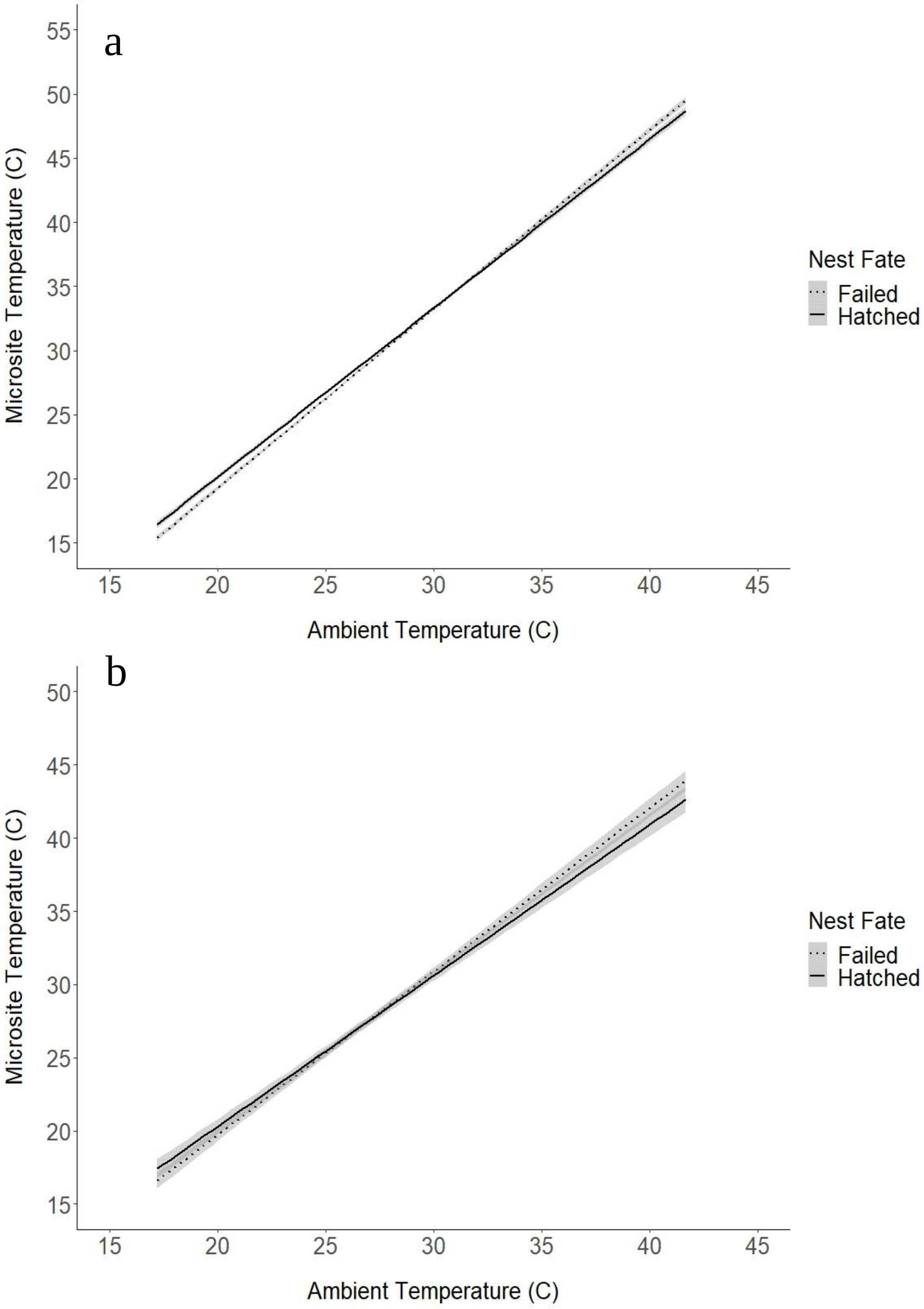

Figure 10. Linear regression explaining the relationship between ambient temperature and microsite temperatures between hatched and failed nests at a) the array scale and b) the nest bowl scale. Hatched nests significantly moderated temperature relative to failed nests at the array scale, but at any given ambient temperature the temperatures in hatched and failed nest bowls were not statistically different. Thermal data was collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

CHAPTER II

SCALED QUAIL HABITAT USE AND SURVIVAL DURING THE BREEDING SEASON

Abstract

Scaled quail (*Callipepla squamata*) have experienced range-wide declines over the last few decades. Despite interest in managing for this species, very little is known about scaled quail habitat use and response to management. We investigated breeding season habitat use and survival of scaled quail in response to vegetation, temperature, and time since fire, and anthropogenic structures. We captured and radio-marked adult scaled quail in Chaves County, New Mexico during the breeding seasons of 2018 and 2019. We monitored both adults and broods using radio-telemetry and paired this with vegetation and thermal data at locations of non-brooding adults, brooding adults, and stratified random locations. We used a series of univariate candidate models to evaluate factors influencing daily survival rate of adults and broods. Locations of both brooding and non-brooding adults had greater vertical obstruction and a higher density of tall (≥1.5 m) shrubs than random locations. In particular, density of tall honey mesquite (*Prosopis glandulosa*) at locations of non-brooding adults was almost 20 times greater than at random locations. Both brooding and non-brooding adults showed selection for cover of mesquite, although selection was weaker for brooding adults than non-brooding adults. The response of scaled quail to fire was less clear, likely due to the non-random nature of prescribed fire treatments, which were biased towards dense mesquite. Weather explained more variation in survival than vegetation, time since fire, or anthropogenic structures. Specifically, non-brooding adult survival was negatively related to average daily temperature, brooding adult survival was negatively related to precipitation, and brood survival was negatively related to maximum daily solar radiation. These results highlight the importance of vegetation structure and temperature in providing habitat for scaled quail, and suggest that quail are likely to respond to management practices that alter the availability of tall shrub cover and microclimate.

Introduction

Scaled quail (*Callipepla squamata*) are ground-dwelling birds native to semiarid grasslands and shrublands. Their geographic distribution spans both northern Mexico and the southwestern United States including parts of Texas, New Mexico, Arizona, Colorado, Kansas, and Oklahoma. Scaled quail populations have been declining throughout much of this region since the 1960s (Brennan et al. 1994, Rollins 2000, Pardieck et al. 2019), and although the causes of declines are unknown, they are often attributed to changes in land cover resulting from heavy livestock grazing, fire suppression, and energy development (Brennan 1994, Rollins 2000, Pleasant et al. 2006). Brush management is also common throughout the region, which may alter availability of shrubs used by scaled quail (Bestelmeyer et al. 2018, Coffman et al. 2014). Due to the popularity of scaled quail as a game species, long-term declines are an important concern for both agencies and landowners.

Very little is known about scaled quail and their response to management practices (Fulbright et al. 2019, Rollins 2000). Although habitat use and population dynamics have previously been investigated, the bulk of our knowledge of scaled quail habitat comes from a limited number of sources (Guthery et al. 2001, Campbell et al. 1973, Schemnitz 1964, Schemnitz 1961, Wilson and Crawford 1987). This irregular distribution of research effort has implications for how we understand scaled quail habitat and, consequently, how we manage for scaled quail. Furthermore, many previous studies of scaled quail habitat selection have relied on flush counts (Bristow and Ockenfels 2006, Wilson and Crawford 1987), transect surveys (Saiwana et al. 1998, Campbell et al. 1973, Reid et al. 1993), or sign (Guthery et al. 2001, Schemnitz 1961) to determine habitat associations, rather than telemetry studies.

Considerable variation exists not only in the plant communities inhabited by scaled quail but also in the habitat preferences of the four subspecies. Chestnut-bellied scaled quail (*C.s.*

castanogastris) use relatively dense thorn-scrub vegetation in south Texas, while the other three subspecies are associated with landscapes dominated by herbaceous vegetation and scattered shrubs (Rho et al. 2015, Silvy et al. 2007, Guthery et al. 2001). Although there are common characteristics preferred by all four subspecies including shrubs, extensive bare ground, and a diversity of forbs (Schemnitz 1961, Campbell et al. 1973, Saiwana et al. 1998), regional differences suggest that more research is needed to better understand spatial variation in scaled quail habitat use.

Recent research indicates that near-ground temperatures are an important component of scaled quail habitat. Exposure to temperatures outside of their thermoneutral zone (25-35°C, Henderson 1971) could lead to physiological stress, altered behavior and movement patterns, or reduced survival, as has been observed with several other species of ground-dwelling birds (Rakowski et al. 2018, Carroll et al. 2015*b*, Guthery et al. 2005, Patten et al. 2005, Goldstein 1984). Therefore, the availability of favorable microclimates may be an important determinant of habitat. For example, in the South Texas Plains, scaled quail avoided locations where ground surface temperatures exceeded 43°C during the hottest part of the day (Kline et al. 2019). These temperatures were strongly influenced by the degree of vertical obstruction provided by surrounding vegetation (Kline et al. 2019). Temperature also played an important role in nest site selection of scaled quail in the Oklahoma Panhandle, where nesting quail selected locations that provided significantly cooler temperatures than microsites less than 2 m away (Carroll et al. 2018). Nest temperatures varied by substrate, with nests in yucca (*Yucca glauca*) being cooler than nests in sand sagebrush (*Artemisia filifolia*) or herbaceous cover (Carroll et al. 2018). These studies indicate that the interaction between vegetation and temperature is also likely to influence scaled quail habitat in populations farther west.

Scaled quail, like many other quail species, exhibit boom-bust population dynamics characterized by striking year-to-year variation population size (Pardieck et al. 2019, Campbell et al. 1973). To better understand factors influencing population dynamics, much attention has been given to the influence of weather variables. Scaled quail hunter harvest has been shown to be positively related to spring and summer rainfall in southeastern New Mexico (Campbell 1973, Campbell 1968), and drought indices have been linked to scaled quail population trends in Texas (Bridges et al. 2001). To remedy the potential impacts of rainfall and drought on quail, constructing artificial water sources is a common management practice in arid and semiarid rangelands (Campbell 1960, Rosenstock et al. 1999). However, the role of surface water in scaled quail management remains unclear. Although the space use of scaled quail is influenced by surface water (Tanner et al. 2019, Rollins et al. 2006, Schemnitz 1961), there is no evidence that access to standing water increases reproduction or survival (Tanner et al. 2019). Similarly, scaled quail are known to use man-made structures for cover including: junk piles, old machinery, and fencerows (Schemnitz 1961). Based on these observations, the construction of artificial structures is recommended to increase available scaled quail habitat (Schemnitz 1961). However, the influence of such structures on survival have not been explored.

Shrub cover is another important consideration for scaled quail management. The geographic distribution of scaled quail roughly coincides with the Chihuahuan desert grasslands (Johnsgard 2017), and since the late 19th century much of this region has experienced a regime shift from grasslands to shrublands (Bestelmeyer et al. 2018, Van Auken 2000). One of the more prolific encroaching shrubs in this region is mesquite (*Prosopis* spp.) (Van Auken 2000). Mesquite can alter soil properties and microbial communities (Tiedemann and Klemmedson 1977, Tiedemann and Klemmedson 1973, Hollister et al. 2010), and compete with herbaceous species for resources (Ansley et al. 2013, Tiedemann and Klemmedson 1977), altering the vegetation community. Increased shrub cover may also provide perches or cover for predators (Behny et al. 2012), influencing quail space use and survival. A variety of management practices are used to reduce shrub density and restore grassland communities including mechanical removal, targeted herbicide treatments, prescribed fires, or combinations thereof. Prescribed fire is believed to benefit areas were shrub expansion has been facilitated by fire suppression. Fire clears out litter, stimulates growth of forbs, and increases some grass species (Boyd and Bidwell 2001, Monasmith et al. 2010, Guthery 1986), all of which may benefit scaled quail. However, while fires impede seedling establishment and may kill young mesquite shrubs, mature individuals are often only top-killed and re-sprout from underground stems (Cable 1967, Young et al.1947). For this reason, the use of herbicides is a common method of shrub control, either alone or in conjunction with prescribed fires. Herbicide may also be more effective in areas where there are not enough fine fuels to effectively carry a fire (Coffman et al. 2014). Herbicides have a longer treatment life than prescribed fires (Ansley et al. 2004), however, the defoliated woody stems still remain. Herbicide treatments also have implications for scaled quail, as they use mesquite extensively for cover when available (Saiwana et al. 1998, Germano et al. 1983, Stormer 1981), and defoliated shrubs are unlikely to provide sufficient thermal buffering or predator screening. Without a greater understanding of how scaled quail use mesquite in desert grasslands, it is unclear how shrub management projects in this region may affect available habitat.

To better understand how scaled quail use habitat in the core of their distribution, and how their space use influences survival, we monitored scaled quail adults and broods in southeastern New Mexico. Our objectives were to 1) evaluate the influence of time since fire on vegetation composition, vegetation structure, and near-ground temperatures; 2) characterize breeding-season habitat use of both brooding and non-brooding scaled quail in terms of vegetation, temperature, and time since fire; and 3) evaluate the influence of time since fire, mesquite cover, weather, and anthropogenic features on the survival of scaled quail adults and broods.

Methods

Study site

Our study was conducted at the Sand Ranch Area of Critical Environmental Concern (ACEC) in Chaves County, New Mexico. The property is over 23,000 hectares in size and is managed cooperatively by the Bureau of Land Management and the New Mexico Department of Game and Fish. Management practices at the site include dormant season prescribed fire, livestock grazing, and mesquite control. Prescribed fires were conducted in 2016, 2017, and 2019 on specific pastures within the ACEC, but were not conducted in 2018 due to dry conditions. Two unplanned wildfires also occurred on the property during this study: East Cato wildfire (2017, 153.0 hectares) and Cato wildfire (2018, 33.6 hectares). Herbicide control of mesquite and other shrubs has occurred intermittently throughout the past several decades, resulting in a mosaic of shrub density and distribution.

As a result of variation in past management, soil differences, and topography, the vegetation on the ACEC is heterogeneous. The primary plant communities consist of sand shinnery oak (*Quercus havardii*) and honey mesquite (*Prosopis glandulosa*) shrublands. Other prominent woody species include sand sagebrush (*Artemisia filifolia*), four-wing saltbush (*Atriplex canescens*), soapweed yucca (*Yucca glauca*), broom snakeweed (*Gutierrezia sarothrae*), and prickly pear (*Opuntia* spp.). Prevalent forbs include western ragweed (*Ambrosia psilostachya*), croton (*Croton* spp.), evening primrose (*Oenothera* sp.), catclaw sensitive briar (*Acacia greggi*), daisy fleabane (*Erigeron* sp.), phlox (*Phlox* sp.), wild buckwheat (*Eriogonum annum*), ratany (*Krameria* spp.), and broom groundsel (*Senecio spartioides*) (Davis et al. 1979). Dominant grasses include sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), three-awn (*Aristida* spp.), sand dropseed (*Sporobolus cryptandrus*), red lovegrass (*Eragrostis secundiflora*), and hairy grama (*Bouteloua hirsuta*). The general topography consists of undulating sand dunes interspersed with flat areas of finer soil types (Davis et al. 1979). Major soil types include Roswell, Roswell-Jalmar, and Faskin fine sands (NRCS 2017). The climate is semiarid with an average annual precipitation of 39.2 cm and mean annual maximum and minimum temperatures of 6.6°C and 23.6°C (PRISM Climate Group 2019). The site received 36.2 cm of precipitation in 2018 and 55.6 cm in 2019, most of which occurred from July through October, coinciding with monsoonal weather patterns. Ambient temperatures during the study period (February –August) ranged from -7.8 to 41.7°C in 2018 and -9.4 to 39.4°C in 2019 (Horel et al. 2002).

Quail capture and monitoring

We captured adult scaled quail using walk-in funnel traps (Stoddard 1931). Trapping began in mid-February and continued through late April of both years. Traps were constructed of wire mesh, baited with cracked corn and milo, and shaded with burlap and native plant materials to reduce stress and predation of trapped birds. We checked traps at least twice per day to reduce the risk of exposing trapped quail to predators and adverse weather. For every captured scaled quail, we determined sex and age (yearling vs. adult), collected morphometric data, and attached a uniquely numbered aluminum leg band (size 7, National Band & Tag Company, Newport, Kentucky, USA). We fitted all scaled quail weighing ≥120 g (both male and female) with necklace-style radio transmitters weighing approximately 6-7 grams with an expected battery life of 11 months (American Wildlife Enterprises, Monticello, FL and Advanced Telemetry Systems, Isanti, MN). Quail weighing less than 120 g received only a leg band. We released captured quail at their respective trap sites after processing. Capture and handling protocols were approved by the Oklahoma State University Institutional Animal Care and Use Committee (Protocol No. AG-17-23).

Each radio-marked quail was located 2-3 times per week using a homing method (White and Garrot 1990) and circled at a distance of 15-20 m. Quail locations were estimated by measuring the azimuth and distance to the bird from the observer. We determined a quail to be on nest when it had been located at the same point for three consecutive telemetry checks. Once a nest was confirmed, we calculated the forecasted hatch date by projecting 23 days (Johnsgard 2017) forward from the estimated start of incubation. Nesting quail were checked 3 times per week until the nest either hatched or failed. We considered a nest successful if at least 1 egg hatched. Quail with successful nests were located with their broods 2-3 times per week using the same homing protocol. These locations were considered brood locations until evidence of brood failure. We flushed each brood once per week to determine brood presence. If any chicks were present with the brooding adult during the flush count, then the brood was considered to be surviving. We considered a brood successful if at least one chick was still present with the brooding adult 30 days after hatch (Lusk et al. 2005, Borchelt and Ringer 1973).

Thermal and weather sampling

We collected thermal data at a subset of locations for both brooding and non-brooding adults and stratified random locations to evaluate habitat use during the breeding season. We randomly selected non-brooding adult telemetry locations for sampling based on the available population of non-nesting, non-brooding adults. We sampled one telemetry location from each adult with a surviving brood every 1-2 weeks. We sampled all quail locations within 1-2 days of quail use in order to minimize potential changes in site characteristics over time. We used stratified random sampling across the entire ACEC to select random sample points from every TSF. For both years of the study, random locations were sampled during the same time of year as quail locations (May—July).

At both quail locations and random locations, we established 20 m arrays centered on the sample point (the estimated quail location or the random point) and extending away from the sample point in the directions of a random azimuth and 180° from the random azimuth. We characterized the thermal environment using self-contained temperature data-loggers

(Thermochron ibuttons, Mouser Electronics, Inc., Mansfield, Texas, USA; hereafter, ibuttons) programmed with a 15-minute sampling rate. We deployed ibuttons by attaching them to metal stakes using double-sided mounting tape. We pushed the stakes into the soil so that each ibutton was located at a height of 10 cm above the ground surface to approximate temperatures experienced at the height of an adult quail's body core. We placed one ibutton at the sample point and then every 2 m along the array for a total of 11 ibuttons per array. Each ibutton location constituted a "microsite." We collected temperature data for 48 hours at each array. We compared this temperature data with weather data recorded hourly by an on-site weather station (33°29'59 N, -103°55'5.40 W) (Horel et al. 2002). The weather station recorded ambient temperature, solar radiation, relative humidity, and precipitation.

Vegetation sampling

After 48 hours of thermal data collection, we returned to each array to retrieve the ibuttons and collect data on vegetation cover and structure. We estimated vertical obstruction at the center of each array using a Nudds profile board (Nudds 1977) modified for use in a sand shinnery oak community (Guthery 1981). We collected the Nudds board readings at the center point for each non-brooding, brooding, and random array.

To quantify the density of tall woody vegetation surrounding each sample point, we used a point-centered quarter method (Cottam and Curtis 1956) at the center point of each array. In each quarter, we measured the distance to the nearest tall mesquite shrub (>1.5 m) and the nearest tall non-mesquite shrub (>1.5 m) using a laser rangefinder, truncated to 100 m from the sample point. We selected 1.5 m as our threshold based on previous research that indicated scaled quail prefer to loaf under shrubs ranging from 0.5 to 1.5 m tall (Goodwin and Hungerford 1977, Stormer 1981). However, anecdotal evidence suggests that scaled quail frequently use tall shrubs for cover and perching. Therefore, we used a height of 1.5 m as a threshold to test whether tall shrub cover is selected for or avoided during the breeding season.

At each individual microsite (11 per array) within non-brooding, brooding, and random arrays, we measured horizontal vegetation cover and structure. We estimated horizontal ground cover composition using a 0.5 m x 0.5 m cover frame centered over each ibutton location. Within the frame we visually estimated percent cover of 7 functional groups (bare ground, rock, litter, grass, forbs, shrubs, and dead woody vegetation) using the cover classes described by Daubenmire (1959). We defined dead woody vegetation as any defoliated, dead woody stems that stood at least 10 cm tall. If a dead woody stem was less than 10 cm tall, we considered it litter because it did not provide overhead structure from the perspective of a quail. We defined litter as any dead plant material on the soil surface which was not rooted in the ground. We also measured the height of the tallest living vegetation in the frame, height of the tallest dead woody vegetation within the frame, and litter depth at the center of the frame.

At random arrays only, we collected an index of the three-dimensional structure surrounding each microsite (Kopp et al. 1998, Harrell and Fuhlendorf 2002) that was used to compare vegetation structure between TSF categories. We attached a digital level to the Nudds profile board to measure the angle of overhead obstruction at every microsite within each random array to produce a total of 11 readings per array. We then collected angle measurements in 8 evenly-spaced cardinal directions by placing one end of the profile board at the microsite and tilting the board until it hit the top of the nearest obstructing vegetation. We averaged the 88 total angles collected at each array to determine the average angle of obstruction for each random sample point.

Statistical analysis

To evaluate habitat use by brooding and non-brooding adult scaled quail, we used generalized linear models (GLM) and post-hoc Tukey tests to compare mean differences in vegetation cover and structure between used and random locations. To analyze vertical obstruction, we combined the Nudds strata into three groups that approximated the height of the line of sight for potential terrestrial predators: low (<4.0 dm; American badger [Taxidea taxus], striped skunk [Mephitis mephitis], and swift fox [Vulpes velox]), medium (4.0-8.0 dm; coyote [Canis latrans] and javelina [Tayassu tajacu]), and high (>8.0 dm, above the line of sight for most terrestrial predators).

To determine habitat use in relation to mesquite cover and time since fire, we used Jacob's electivity index (Jacobs 1974), which ranges from -1.0 to +1.0 with negative values indicating avoidance and positive values indicating selection. Spatial data delineating prescribed fire units and mesquite density were provided by the BLM Roswell Field Office in Roswell, New Mexico. We edited the spatial layer for burn units to create a unique fire history for each year of the study. We then determined the number of months since fire for each unit, and each unit was assigned a value representing a discrete TSF category (0 = 0-11 months since fire, 1 = 12-23 months since fire, 2 = 24-35 months since fire, 3 = ≥36 months since fire). Mesquite density was represented by a 30 m x 30 m raster. Each pixel in the raster represented one of seven discrete canopy cover classes (0 = <1%, 1 = 1-5%, 2 = 5-10%, 3 = 10-15%, 4 = 15-30%, 5 = 30-50%, 6 = >50%). We reclassified pixels with values from 0-2 (0-10% mesquite cover) as "0" to indicate mesquite absence, while pixels with values from 3-6 (>10% mesquite cover) were reclassified as "1" to indicate mesquite presence. We selected 10% as our threshold for mesquite presence because the subspecies at our site, the Arizona scaled quail (C.s. pallida), is thought to use grasslands with 10-15% shrub cover (Silvy et al. 2007), so using 10% as our threshold allowed us to determine whether higher densities of mesquite were selected or avoided. We extracted the pixels for mesquite presence from the raster and converted to a polygon data format. We placed a buffer of 20 m around the resulting mesquite presence polygon, which allowed us to account for telemetry error within our 20 m homing radius. Because the mesquite raster represented mesquite density observed in 2011, we modified the raster to estimate mesquite cover at the time of this study. We used a polygon of mesquite treatments provided by the BLM Roswell Field Office in Roswell, New Mexico, to remove areas from the mesquite density raster that received herbicide treatments targeting mesquite from 2011 to 2016. This methodology assumes that the herbicide treatments were 100% effective at killing mesquite in every area treated. Because both the original mesquite raster and the modified mesquite raster were likely to approximate the mesquite cover actually present during our study, we conducted analyses using both rasters to compare the results.

We placed a 1 km buffer around all quail locations to limit the potential landscape that was available for habitat selection analyses. This distance was selected because it was believed to encompass the average daily movements of a scaled quail (160 acres, Wallmo 1956).

For all thermal analyses, we extracted the microsite temperatures that were recorded closest to the hour so that each microsite had only one temperature per hour. This allowed us to compare microsite temperatures with the concurrent ambient temperatures, which were recorded once per hour by the on-site weather station, at the same temporal scale. We used these data to evaluate thermal differences between quail and random locations using a one-way repeated measures mixed-model ANOVA. Because we expected thermal relationships to change across the diel cycle, we ran separate tests for four discrete time periods: morning (06:00-08:00), midday (10:00-14:00), evening (17:00-19:00), and night (22:00-02:00).

Survival analysis

We analyzed spatial factors influencing adult and brood survival using the nest survival model in Program MARK (version 6.2, Cooch and White 2019). This model allowed us to account for irregular time intervals between telemetry locations (Dinsmore et al. 2002, Tanner et al. 2019). We included spatial variables that were hypothesized to influence daily survival probability of scaled quail either based on previous research (Bridges et al. 2001, Campbell 1968, Duquette et al. 2019, Henderson 1971, Kline et al. 2019, Tanner et al. 2015) or based on our observations of habitat use. We obtained spatial data for this analysis from the BLM Roswell Field Office. These included feature classes for roads, oil and gas infrastructure, range improvement structures, and prescribed fire units on the ACEC.

The majority of roads at Sand Ranch are caliche roads and two-track roads. With the exception of one caliche road, which runs north to south across the west side of the ACEC and is used for oil and gas activities, the majority of roads are very lightly travelled. A few of these roads are only accessible by all-terrain vehicles. In contrast, the southern boundary of the ACEC is formed by a highway which receives steady traffic. We first examined roads by Census Feature Class Code (CFCC) (US Census Bureau 2019), and extracted roads classified as “primary” (CFCC A21) and “secondary” (CFCC A31) roads and combined them into a single class of high-traffic roads labeled “Highway”. We also investigated quail survival in response to all roads on Sand Ranch including primary and secondary roads (described above as “Highway”), county roads, and two-tracks. This resulted in two spatial layers for roads: 1) Highway and 2) All Roads.

To examine the influence of standing water on scaled quail survival, we used the range improvement points dataset to derive a layer for water sources only. The range improvement points dataset included both structures that were associated with accessible standing water (livestock troughs, wildlife drinkers and catchments, retention dams, etc.) and structures that were not (corrals, air vents, shut-off valves, etc.). We identified water sources using attribute data and confirmed them using aerial imagery and ground-truthing. We extracted the confirmed water sources from the range improvement points dataset to produce two spatial layers for range improvement structures: 1) All Range Structures and 2) Water Sources Only. We retained data for water sources within the All Range Structures layer to examine how man-made structures in general influenced quail survival. Therefore, there was overlap between the two layers.

This All Range Structures dataset included only structures associated with range improvement, and did not include structures associated with oil and gas development. Locations of oil and gas wells were stored in a separate dataset labeled as “Oil and Gas Wells,” and included both active and inactive wells.

To determine distance to the nearest edge of a burn, we combined the TSF categories for 0-11, 12-23, and 24-35 months since fire to represent “burned” areas, while the TSF category for ≥36 months since fire represented “unburned” areas. We used the Polygon to Line tool in ArcGIS Pro to create a dataset representing the boundaries between burned and unburned areas. The resulting spatial layer was used to examine if scaled quail survival was influenced by Edge of Burn.

We used the Euclidean Distance tool in ArcGIS Pro (ESRI 2020) to create a raster for each of the six spatial layers: Highway, All Roads, All Range Structures, Water Sources Only, Oil and Gas Wells, and Edge of Burn. Each pixel in the resulting Euclidean distance rasters represented the distance from that pixel to the nearest feature of interest.

We conducted survival analyses for all adults combined (n = 71), non-brooding adults only (n = 45), and brooding adults only (n = 26) at both the location scale and the home range scale, as selection likely differs across scales. For both scales, we only included individuals with at least 20 relocations. While a minimum of 20 relocations is only necessary for home range analysis (Carroll et al. 2017*a*, Aebischer et al. 1993), we used the same dataset for analyses at the location scale to ensure that responses observed across scales were a result of differences in scale, and not a result of differences in the datasets. We calculated home ranges using the adehabitatHR package in Program R (Calenge 2006, R Core Team 2019) to create a 95% volume contour of all relocations for each individual. We conducted these same analyses for broods using all brood relocations; however, due to the small number of relocations for each brood, we were not able to analyze survival at the home range scale.

We plotted both quail (adult and brood) locations and home range polygons in ArcGIS Pro. For each point location, we extracted distance values from the Euclidean distance rasters for Highway, All Road, Oil and Gas Wells, All Range Structures, Water Sources Only, and Edge of Burn. We used the extracted values to calculate the average distance to the nearest feature of interest for each individual. These location-scale averages were used as individual covariates in the survival analysis. We also extracted the values representing TSF category (0, 1, 2, or 3) and mesquite presence (0 or 1) for each point. For each individual quail we determined the proportion of its relocations in each TSF category and the proportion of its relocations in mesquite cover. These proportions were used as individual covariates for the survival analysis.

At the home range scale, we used the Zonal Statistics tool in ArcGIS Pro and the Euclidean distance rasters to calculate the average distance to each feature of interest within each home range. We used the Tabulate Intersection tool to calculate the proportion of each home range that fell within each TSF category and the proportion of each home range covered by mesquite. These home range-scale averages and proportions were included as individual covariates in the survival analysis.

For each of the 3 analyses (all adults, non-brooding, and brooding) we created 37 univariate candidate models using the derived spatial covariates, weather variables collected at the on-site weather station (average daily temperature, daily variation in temperature, maximum daily solar radiation, average daily humidity, and daily precipitation), and individual quail characteristics including age (adult or juvenile) and sex. Brood status was included as a covariate only in the combined analysis. We divided these models into 10 model groups (Tables 4 - 6) and evaluated each model group separately using Akaike Information Criterion adjusted for small sample sizes (AICC). We considered a model to be competitive if ΔAICC < 2, and significant if 95% confidence intervals for the β estimate did not overlap zero (Burnham and Anderson 2002). For models that were highly competitive or significant, we used the model output to plot the covariates against daily survival rate to visualize the relationship.

We conducted the same analysis for brood survival (n = 22) using 21 univariate models divided into 7 model groups (Table 7). Due to the small sample size of broods, model groups for broods were limited to no more than 3 individual covariates.

Results

During the breeding seasons of 2018 and 2019, we captured and radio-marked 183 adult scaled quail (n = 85 in 2018 and n = 98 in 2019) and monitored 22 broods (n = 6 in 2018 and n = 16 in 2019). We measured thermal and vegetation characteristics at a total of 38 non-brooding adult locations, 24 brooding adult locations, and 65 stratified random locations.

Vegetation use and selection

Non-brooding adult quail locations were similar to random locations in terms of vegetation for most measures (Figure 1), however, there were notable exceptions. Locations of non-brooding adults had significantly greater density of both tall mesquite shrubs and tall non-mesquite shrubs compared to random locations (Table 1, Figure 2). They also had greater visual obstruction at all three heights (low, medium, and high) than random locations (Table 1).

Brooding and non-brooding adult locations were not significantly different in terms of vegetation, but they were significantly different from random locations, exhibiting greater cover of forbs, litter, and dead woody vegetation (Figure 1). Both live vegetation and dead woody vegetation were significantly taller at locations of brooding adults than they were at random locations (Figure 1). Similar to non-brooding adults, brooding adult locations had greater density of tall mesquite shrubs and tall non-mesquite shrubs than random locations (Figure 2).

Adult scaled quail showed moderate selection for greater TSF (Table 2, Figure 3). In 2018, non-brooding adults selected for unburned areas (D = 0.34), while brooding adults avoided unburned areas (D = -0.20) and selected for 12-23 months since fire (D = 0.25). In 2019, brooding adults selected for 24-35 months since fire (D = 0.38). Non-brooding adults also selected for 24-35 since fire (D = 0.27), but appeared to select for recently burned units (0-11 months since fire) to a similar extent (D = 0.28). All adults completely avoided recently burned units in 2018 (D = -1.00); however, this is likely a result of the very low availability of that TSF in 2018 rather than biological relevance (Figure 3).

Not only did scaled quail select for tall mesquite, but both brooding and non-brooding adults selected for total mesquite cover (Table 2, Figure 4). Brooding adults exhibited stronger selection for mesquite cover than non-brooding adults using both the pre-treatment mesquite layer ($D_{\text{Brooding}} = 0.71$, $D_{\text{Non-brooding}} = 0.64$) and the post-treatment mesquite layer ($D_{\text{Brooding}} = 0.56$, $D_{\text{Non-brooding}} = 0.48$) (Figure 4).

Temperature use

Thermal relationships between non-brooding, brooding, and random locations changed across the diel cycle. Thermal differences were most pronounced during midday and least pronounced at night (Table 3). Locations of non-brooding adults were significantly cooler than random locations during the morning, evening, and night (Table 3), while temperatures at brooding adult locations remained significantly warmer than random locations across all time periods (Table 3).

Adult and brood survival

Factors influencing survival were similar between non-brooding adults and all adults combined. For these two groups, the null model was the top model in most analyses except for those of weather, time since fire, and oil and gas (Tables 4 and 5). Average daily temperature was the only variable that had a significant relationship with adult survival, as daily survival rates of all adults combined ($\beta = -0.52$) and non-brooding adults only ($\beta = -0.77$) decreased with increasing temperature (Tables 4 and 5, Figure 5). Other variables that explained variation in daily survival rate for these two groups included density of oil and gas wells within the home range ($\beta_{\text{Non-brooding}} = 117.697$, $\beta_{\text{All}} = 123.021$), total number of oil and gas wells within the home range ($\beta_{\text{Non-brooding}} = 0.596$, $\beta_{\text{All}} = 0.566$), and the proportion of locations ($\beta_{\text{Non-brooding}} = -5.356$, $\beta_{\text{All}} = -5.851$) and individual home ranges ($\beta_{\text{Non-brooding}} = -0.036$, $\beta_{\text{All}} = -0.039$) in burned areas. However, the relationships of these variables with daily survival rate were not significant (Tables 4 and 5).

Average daily temperature did not explain as much variation in DSR for brooding adults. Competitive models for brooding adults included daily precipitation ($\beta = -0.119$), distance to highways at both the location scale ($\beta = -0.002$) and the home range scale ($\beta = -0.001$), proportion of locations ($\beta = -337.911$) and home range ($\beta = -0.080$) in unburned areas, and post-treatment mesquite cover at the location scale ($\beta = -332.790$) (Table 6). Specifically, brooding adult DSR had significant negative relationships with daily precipitation, the proportion of locations in unburned areas, and post-treatment mesquite cover.

The null model performed best in every model group except for the temporal group for survival of broods (Table 7). Nevertheless, the null model was still competitive ($\Delta\text{AIC}_\text{C} = 0.56$). Maximum solar radiation and sex of the brooding adult were the only two variables that had a significant relationship with daily survival rate, and although these models were competitive, they were both out-performed by the null model (Table 7). Maximum daily solar radiation was negatively related to daily survival rate of broods ($\beta = -0.02$) (Table 7, Figure 6).

Influence of time since fire

Vegetation composition and structure were relatively similar across times since fire, with the exception of herbaceous vegetation and dead woody vegetation (Table 8, Figure 7). Cover of grasses was greatest in TSF >23 months after fire, while cover of forbs was lowest 12-23 months after fire (Figure 7). Cover and height of dead woody vegetation was generally greatest in both recently burned (0-11 months since fire) and unburned units, although these trends were not significant for all comparisons (Figure 7). Vertical obstruction tended to be greatest in unburned units while overhead obstruction was greatest in units 12-23 months since fire (Table 8). Density of tall mesquite was greatest in units burned 24-35 months prior (7.51 shrubs per ha ± 5.21) and lowest in units burned 12-23 months prior (0.72 shrubs per ha ± 0.42) (Table 8). Similarly, the total proportion of mesquite cover in 2018 was greatest within units 24-35 months since fire (79.97%) and least in units 12-23 months since fire (33.79%) (Figures 8 and 9). In 2019 the greatest mesquite cover was observed in units 0-11 months since fire (91.31%) and the least was in units 24-35 months since fire (33.80%) (Figures 8 and 9). Temperatures were similar between recently burned (0-11 months since fire) and unburned units, both of which were significantly cooler than other times since fire for all time periods (Table 9).

Discussion

Our findings highlight the importance of vegetation structure, particularly tall shrubs, for scaled quail during the breeding season. Both brooding and non-brooding adults selected for mesquite cover, vertical obstruction, and high density tall shrubs. Although mesquite cover did not appear to influence survival, it may play a role in providing thermal refuge for quail. The availability of thermal cover appears to be important given that survival of non-brooding adults declined significantly with increasing average daily temperatures, and survival of broods showed similar declines with increasing levels of solar radiation.

Habitat use

Although locations used by non-brooding adults were generally similar to random locations, they were distinct in some aspects. First, non-brooding adult locations had greater visual obstruction at all three height categories. The semiarid landscapes inhabited by scaled quail are generally characterized by an open vegetation structure (Silvy et al. 2007, Schemnitz 1964), so vertical cover may provide important concealment from predators when available (Hiller and Guthery 2005, Kopp et al. 1998). Scaled quail use a variety of structures for loafing and escape cover including shrub species such as cholla (*Opuntia imbricata*) and yucca (*Yucca glauca*), or man-made structures (Stormer 1981, Schemnitz 1961). This cover provides complex structure that may create greater vertical obstruction. A less recognized benefit of vertical obstruction is thermal buffering. In the South Texas Plains, vertical obstruction was identified as one of the greatest predictors of relative probability of use for scaled quail (Kline et al. 2019). Ground surface temperatures also decreased with increasing vertical obstruction, and the authors hypothesized that vertical obstruction blocks solar radiation when the sun is at lower angles (Kline et al. 2019). This relationship between vertical obstruction and temperature could account in part for the cooler temperatures observed at adult locations in our study. Non-brooding adult locations were significantly cooler than random locations at low solar angles (06:00 to 08:00 and 17:00-19:00), and although these differences were only 0.5 to 2.0°C, this may have important implications for thermoregulation of scaled quail at high ambient temperatures.

Scaled quail tended to select for areas on the landscape with mesquite cover. Specifically, locations used by non-brooding adult quail had high densities of tall mesquite shrubs. On average, the density of tall mesquite at non-brooding adult locations was almost 20 times greater than at random locations. Tall mesquite density at brooding adult locations was less than that of non-brooding adults, but it was still more than 8 times greater than the density at random locations. These patterns suggest that mesquite cover, especially tall mesquite (i.e. >1.5m), is an important component of scaled quail habitat. We also observed significantly greater densities of tall non-mesquite shrubs at used quail locations, although densities of these species were not as high as those of mesquite. This apparent preference for tall mesquite over other tall shrub species may reflect availability rather than selection for a particular shrub species. The two dominant shrub species at Sand Ranch were mesquite and sand shinnery oak, but shinnery oak rarely occurred >1 m in height (Peterson and Boyd 1998). Although other shrub species such as four-wing saltbush (*Atriplex canescens*), western soapberry (*Sapindus saponaria*), and sandsage (*Artemisia filifolia*) occasionally reached 1.5 m in height, these species did not occur as frequently as mesquite. Based on our results, it is unclear whether scaled quail would have used areas of high density non-mesquite shrubs if they occurred more frequently on the landscape. Previous work conducted in Arizona (Goodwin and Hungerford 1977) and Texas (Stormer 1981) indicated that scaled quail preferred to use shrubs 0.5 to 1.5 m tall. In southeastern Arizona, measurements from five 0.4-hectare plots found that on average, only 2 shrubs per plot (including mesquite [*Prosopis juliflora*], hackberry [*Celtis reticulata*], and wolfberry [*Lycium* spp.]) were over 2 feet (0.61 m) tall, a density of approximately 5 shrubs per hectare (Goodwin and Hungerford 1977). This is only slightly greater than mesquite densities observed at random locations in our study area. The findings from our study may therefore reflect differences in availability of tall shrubs or differences in shrub species composition across the geographic distribution of scaled quail.

There are several potential reasons that scaled quail may select for tall mesquite cover. These tall shrubs may provide important benefits through increased canopy cover and structure, which can provide moderate microclimates (Kline et al. 2019) and predator screening (Kopp et al. 1998). Additionally, the presence of tall shrubs may aid in predator and/or conspecific detection through vigilance of scaled quail. We frequently observed scaled quail perching on and calling from tall shrubs.

Brooding adult locations, although similar to non-brooding adult locations, were more distinct from the rest of the landscape. While brooding adults also tended to use greater vertical cover and higher densities of tall shrubs, their locations had additional characteristics which may provide important resources for broods. Significantly taller live and dead vegetation at brooding adult locations may provide additional concealment from predators for vulnerable chicks. We expected that increased vertical obstruction and taller vegetation at brood locations would buffer ambient temperatures (Kline et al. 2019) to provide cooler microclimates for young chicks that cannot yet thermoregulate on their own. However, we observed warmer temperatures at brooding adult locations than at random locations. This was even more surprising given that non-brooding adults used locations that provided cooler temperatures. There are a couple of possible explanations for this observation. The first is related to the potential trade-offs between the needs of the chicks and the needs of the brooding adult (Ghalambor and Martin 2001). Due to the nutritional needs of developing quail chicks, brooding habitat should provide high arthropod densities and enough bare ground to facilitate movement of small chicks (Hurst 1972, Doxon and Carroll 2010). Forbs are associated with higher densities of arthropods, a food which is important for meeting the high protein needs of young quail chicks (Guthery 1986, Hurst 1972). However, patches of forbs and bare ground may not provide sufficient thermal cover or predator screening for the brooding adult. Locations of brooding adults in our study had significantly greater forb cover than random locations, however, they did not have less cover of shrubs or grass and they had much taller vegetation. This suggests that sufficient cover would have been available for brooding adults, and accordingly, our survival analysis indicated that brood status did not influence adult survival. Similar results were observed in the Oklahoma panhandle, where brooding scaled quail were not found to incur a survival cost relative to non-brooding quail (Tanner et al. 2019). A second explanation for the warmer temperatures at brooding adult locations is the scale of observation. Our results reflect the average temperature found within the area surrounding the brooding adult’s location, but within this area there may be considerable opportunities for thermal refuge at fine scales. Thermal differences of several degrees can occur within <2 m (Carroll et al. 2018, Hovick et al. 2014), and even a large leaf may provide sufficient refuge for a small quail chick. Therefore, brooding adults may be selecting for temperature at finer scales than what we were able to measure due to telemetry error or the scale at which we chose to monitor temperature.

Apparent selection for time since fire was different between years. In 2018, non-brooding adults selected for unburned areas, despite the fact that these areas did not have high densities of tall mesquite or a large proportion of mesquite cover. However, many of the features used by non-brooding adult quail, including vertical obstruction and cooler temperatures, were also characteristic of unburned areas. This pattern changed in 2019, when all adult quail combined selected instead for areas burned 24-35 months prior. This TSF had the lowest frequency of mesquite presence in 2019, suggesting that the change in selection was not driven by mesquite cover. Based on our data, it is unclear why selection patterns switched between years. This leads us to hypothesize that scaled quail were not responding to TSF, rather, there may have been an element of site fidelity influencing selection. Covey home ranges do not change significantly between years (Schemnitz 1961, Wallmo 1956), and winter home ranges in Oklahoma were found to be nested within summer home ranges (Schemnitz 1961). Extreme movements (>10 miles) do occur (Campbell and Harris 1965), but most daily movements occur within a relatively small area (Schemnitz 1961, Wallmo 1956). Due to the large size of the prescribed fire units at Sand Ranch (221 ha—5,066 ha), options between different TSF were not readily available to all individuals. However, there may have been enough variation within each TSF to meet the habitat requirements of scaled quail. Northern bobwhites responded to prescribed fires through plasticity in choice of nest substrates, selecting nest sites with particular structural characteristics regardless of TSF (Carroll et al. 2017*b*). This plastic response allowed bobwhites to maintain high nest success across all TSF categories. Scaled quail seem likely to exhibit similar plasticity given their ability to make use of unconventional sources of cover (e.g. junk piles, machinery). Therefore, as long as habitat requirements can be met within their current home ranges, TSF may not be important for quail space use when burns are conducted at large spatial scales. Additionally, the prescribed fires on Sand Ranch were not random. They were targeted toward areas with high mesquite cover. As we found that scaled quail selected areas with higher mesquite cover, it is possible that site fidelity confounded apparent selection of TSF categories.

Adult and brood survival

Despite strong selection for mesquite cover including tall mesquite, selection for mesquite cover did not influence survival. Rather, survival of both adults and broods was best explained by weather. Similar findings have been previously reported for scaled quail (Tanner et al. 2017). Survival of non-brooding adults and all adults combined was significantly and negatively related to average daily temperature. By modeling daily survival rate as a function of average daily temperature, we observed that survival began to drop between 25 and 30°C. This range is within the thermoneutral zone reported for scaled quail by Henderson (1971) (25-35°C), and it is at approximately these temperatures that incubating northern bobwhites (*Colinus virginianus*) have been observed to begin gular flutter (Guthery et al. 2005), a strategy used to dissipate heat. Therefore, scaled quail may experience heat stress at temperatures above this threshold, leading to increased mortality risk. Animals experiencing heat stress must either divert resources to reduce body temperatures through metabolism (Wolf 2000), increase food intake (Du et al. 2000), or move to cooler microclimates on the landscape (Rakowski et al. 2018, Carroll et al. 2015*b*, van Beest et al. 2012), strategies which may expose them to predators through increased movement. Although the mechanisms by which temperature influences daily survival rate are beyond the scope of our study, these results indicate that temperature plays an important role in mortality risk of scaled quail, either directly or indirectly.

The primary weather variable influencing survival in brooding adults was daily precipitation. The boom bust population dynamics of quail have frequently been associated with annual variation in the timing and quantity of precipitation (Lusk et al. 2002, Giuliano and Lutz 1993, Campbell et al. 1973), with spring and summer rainfall being most important for production (Campbell et al. 1973, Campbell 1968). However, precipitation is primarily thought to influence populations positively by increasing the availability of resources such as vegetation (Campbell et al. 1973) and insects (Roseberry and Klimstra 1984), thereby increasing reproductive effort and recruitment. However, our results for brooding adults indicated a significant negative response. Nests and chicks are thought to be vulnerable to exposure (Stoddard 1931) during precipitation events, and fall and winter precipitation has been shown to negatively influence scaled quail abundance (Lusk et al. 2002, Giuliano and Lutz 1993). However, a negative response by adult quail during the breeding season has not previously been documented. It is unclear why brooding adults were the only group in our study to respond to precipitation. Our data did not indicate that brood status influenced survival, yet survival of brooding and non-brooding adults appeared to be influenced by different weather variables. Given the small sample size of brooding adults, further investigation is needed to better understand the role of precipitation and brood status in adult survival.

Survival of both brooding and non-brooding adults decreased with increasing use of unburned areas at both the location scale and the home range scale. This was surprising given that unburned areas had greater vertical obstruction and cooler temperatures than other TSF, features which were characteristic of locations used by non-brooding adults. Yet unburned areas were avoided by brooding adults in 2018, and avoided by all adults in 2019. As discussed previously, these selection patterns may have less to do with current vegetation and temperature characteristics and more to do with pre-burn conditions and site fidelity. Because prescribed fire units were non-randomly selected to target high density mesquite, these selected units may have been preferred by quail prior to the burns. Given that vegetation characteristics between TSF were generally similar, quail within the burned areas may not have had any reason to alter their space use after the burn. Selection for recently burned areas seems to indicate that there is enough variation present in these areas to provide habitat for scaled quail.

In general, range structures had minimal influence on quail survival. The lack of response to water sources was expected based on previous research. Scaled quail are well-adapted to arid and semiarid climates and can meet their water requirements through their diet (Campbell et al. 1973). Although they do drink from standing water sources when available (Campbell et al. 1973), there is no evidence that providing supplemental surface water benefits quail through increased survival or reproductive success. Tanner et al. (2019) determined that scaled quail strongly selected for areas 100-650 m from water sources during the breeding season. This selection appeared to be driven specifically by the water sources rather than by associated vegetation. Similar findings were documented by Rollins et al. (2006) and Schemnitz (1961), who found that water influenced scaled quail space use but not survival or reproduction.

We observed a positive relationship between survival of non-brooding adults and density of oil and gas wells. Very little research has examined the effects of oil and gas infrastructure on quail, and most studies have reported a neutral response (Tanner et al. 2016, Dunkin et al. 2009). An exception was documented by Duquette et al. (2019), who found that northern bobwhites avoided high densities of oil pads at the home range scale. However, they did not avoid oil pads within their home range, suggesting that bobwhites tolerate oil pads up to a certain threshold. Therefore, the apparent benefit of oil pad density for scaled quail survival is unusual. This may be due in part to the activity level and spatial distribution of oil and gas extraction at Sand Ranch. Although some active wells persist within the ACEC, most existing well pads are no longer active. The majority of oil and gas activity occurs on the west side of the study area along Cato Road, a caliche road that transects the ACEC from north to south and provides access to the Cato

Oil Fields to the north. The west side of the ACEC is also an area with high density mesquite. We did not find a correlation between oil pad density and mesquite presence, but our analysis used 10% mesquite cover as the threshold for determining mesquite presence. Therefore, the presence of mesquite in our analysis could represent anywhere from 10-100% cover of mesquite within a 30 x 30 m area. Areas with high densities of mesquite present may provide more thermal options than areas with low densities present, allowing quail to seek refuge during extreme temperatures. Furthermore, scaled quail may be using the structures on oil pads for cover, as they are known to use man-made objects including machinery (Schemnitz 1961). structures on oil pads may be used as cover. Therefore, oil pad density may be confounded by other spatial features which have a direct influence on quail survival.

Brood survival was best explained by maximum solar radiation, with a significant negative relationship. Solar radiation can intensify temperatures experienced near the ground (Bakken 1992), resulting in hyperthermia even when air temperatures are otherwise suitable for survival. At our study site, solar radiation was greatest from late April to late June prior to the monsoonal rains. This timing coincides with the peak of the nesting season, which may impact survival of early broods and annual recruitment. The taller vegetation and increased vertical obstruction at brooding adult locations may serve to reduce exposure to solar radiation (Kline et al. 2019). However, we found that brooding adult locations experienced hotter temperatures than random locations. It is possible that scaled quail are selecting areas with more food resources (forbs) at a cost of higher temperatures. Therefore, high temperature at brooding adult locations may not indicate selection for temperature, but instead may be a result of factors such as reduced air flow or increased litter cover, which may help hold heat even while tall vegetation blocks solar radiation. Further study is needed to fully understand the role and relationships of weather, cover, and food resources in brood survival and the associated impacts on brood space use.

Influence of time since fire

We observed minimal differences in vegetation composition and structure across different times since fire. Herbaceous vegetation and dead woody vegetation were the features most responsive to time since fire. This is not surprising, given that fire is known to influence herbaceous cover by removing accumulated litter and stimulating growth of grass and annual forbs (Campbell et al. 1977, Boyd and Bidwell 2001, Monasmith et al. 2010, Guthery 1986). However, we observed the greatest grass cover in units >23 months since fire. This is likely due to a buildup of senescent grass in the absence of fire. Fire removes litter and standing dead vegetation, decreasing the overall ground cover but increasing productivity of the live herbaceous vegetation (Campbell et al. 1977). Fire may also stimulate the growth of fire-adapted annual forb species (Campbell et al. 1977, Boyd and Bidwell 2001, Monasmith et al. 2010), which provide food and concealment for wildlife. However, we did not observe greater forb cover in recently burned units than in others. Forb cover was nearly identical across times since fire with the exception of units burned 12-23 months prior, which had significantly less forb cover. Similar patterns have been observed in the shortgrass prairie of northern Texas, where forb cover did not vary significantly between prescribed fire treatments (fires every 2 years, 4 years, or 10 years) (Long et al. 2012). However, in sand shinnery oak prairie (Boyd and Bidwell 2001) and semidesert grassland (Monasmith et al. 2010), fire promoted growth of forbs, possibly by reducing competition from grasses and shrubs.

The responses of live and dead woody vegetation to time since fire were unclear. Because prescribed fires targeted woody cover, we expected shrub cover and structure, particularly of mesquite, to show a positive relationship with time since fire. However, this was not the case. Long et al. (2012) also noted a lack of clear shrub response to fire treatments in experimental plots, suggesting that the patterns observed in our study are not unusual. Ultimately, differences (or lack thereof) in woody vegetation may have resulted from conditions that existed prior to burning. Prescribed fire units at the site were selected non-randomly in an effort to manage shrub cover. Therefore, burned units were more likely to have higher densities of mesquite than areas not selected for treatment. Furthermore, prescribed fires may not necessarily impact all shrubs within a given unit. In communities characterized by sparse vegetation, burns may be uneven or incomplete due to the patchy distribution of fuels (Coffman et al. 2014, Gibbens et al. 1986). Fires are most likely to affect young shrubs under a certain size, but once mature, mesquite shrubs are highly adapted to disturbance and will re-sprout following fire (Cable 1967, Young et al.1947). These considerations may have confounded the influence of fire on woody cover between times since fire at our site.

Thermal differences between times since fire followed a counterintuitive pattern. Both unburned and recently burned (0-11 months since fire) units experienced significantly cooler temperatures throughout the day relative to the intermediate two TSF categories. The drivers of thermal variation near the ground are complex, with contributions from both biotic and abiotic features (Rich et al. 1995, Geiger 1965). However, we would expect fire to influence near-ground temperatures primarily through its effects on vegetation composition and structure. The taller vegetation and increased grass cover in unburned areas may have provided overhead and vertical cover that blocked solar radiation (Kline et al. 2019), creating cooler microclimates beneath the canopy (Rich et al. 1993). Although overhead obstruction was not significantly greater in unburned units than in any of the burned units, overhead obstruction in combination with vertical obstruction and grass cover may provide different microclimates than overhead cover alone (Kline et al. 2019). Cooler temperatures in recently burned areas may be a result of increased bare ground and a more open vegetation structure. Recently burned units (0-11 months since fire) tended to have greater cover of bare ground, less grass cover, and greater shrub cover than other TSF categories. These conditions could have provided cooler microclimates through overhead shading (Geiger 1965). Despite being statistically significant, there may not have been any biological significance to the thermal differences we observed between times since fire. Most of the thermal differences between TSF categories were only 1-2°C in magnitude, raising the possibility that the statistical significance we observed may have been a product of large sample sizes rather than an indication of true thermal differences caused by time since fire. Furthermore, the lack of clear differences in vegetation between TSF and the non-random nature of the prescribed fires may further confound the influence of TSF on near-ground temperatures.

Conclusion

Although we did not observe a clear response of scaled quail to time since fire, our findings indicate that shrubs, particularly tall shrubs, are important for scaled quail. Therefore, management practices that alter shrub cover may affect space use of quail and determine the amount of usable space on the landscape. Tall, dense shrubs appear to form a critical component of scaled quail habitat, potentially due to screening cover, thermal cover, and vigilance. Our findings emphasize the importance of tall shrubs for scaled quail during the breeding season, particularly for non-brooding adults. Land managers suppressing shrub cover should consider the intensity and distribution of shrub control practices, maintaining compositional and structural diversity of vegetation on the landscape to meet the needs of non-target wildlife while still achieving management goals. We did not find any evidence that artificial water sources influenced survival during the breeding season, suggesting that wildlife water installations are not an effective tool for increasing quail numbers, which is supported by previous research. Rather, resources for management would be better directed towards establishing and maintaining structural and compositional diversity of vegetation.

Table 1. Mean differences in vegetation structure and composition (along with standard errors) between non-brooding adult scaled quail (*Callipepla squamata*) locations, brooding scaled quail locations, and random locations at Sand Ranch in Chaves County, New Mexico, USA. Data were collected during the breeding seasons of 2018 and 2019. Significant differences ($p < 0.05$) are indicated in bold.

Variable	Location type	Mean	SE	Adult	Brood
Bare ground cover (%)	Adult	48.31	2.85	-	
	Brood	47.26	2.83	0.805	-
	Random	51.98	2.04	0.286	0.211
Rock cover (%)	Adult	0.17	0.07	-	
	Brood	0.63	0.31	0.080	-
	Random	2.21	0.84	0.065	0.258
Litter cover (%)	Adult	36.91	2.44	-	
	Brood	42.62	3.26	0.155	-
	Random	34.84	1.98	0.516	**0.042**
Grass cover (%)	Adult	21.98	2.35	-	
	Brood	21.69	2.55	0.935	-
	Random	21.57	1.62	0.883	0.970
Forb cover (%)	Adult	5.57	0.78	-	
	Brood	7.12	1.14	0.245	-
	Random	4.50	0.65	0.304	**0.039**
Shrub cover (%)	Adult	18.32	2.03	-	
	Brood	15.06	1.85	0.269	-
	Random	15.58	1.35	0.245	0.833
Dead woody vegetation cover (%)	Adult	2.86	0.59	-	
	Brood	4.59	1.09	0.130	-
	Random	2.33	0.28	0.365	**0.005**
Vegetation height (mm)	Adult	45.95	2.23	-	
	Brood	54.77	2.39	**0.009**	-
	Random	41.67	1.62	0.116	**<0.001**
Dead woody vegetation height (mm)	Adult	40.18	3.01	-	
	Brood	46.41	3.51	0.182	-
	Random	32.31	1.89	**0.020**	**<0.001**
Litter depth (mm)	Adult	2.03	0.22	-	
	Brood	1.41	0.18	**0.046**	-
	Random	1.79	0.15	0.349	0.173
Vertical cover low: 0-4 dm (%)	Adult	57.66	2.72	-	
	Brood	66.95	3.58	**0.037**	-
	Random	45.52	2.85	**0.004**	**<0.001**
Vertical cover medium: 5-8 dm (%)	Adult	21.41	3.59	-	
	Brood	30.70	5.06	0.125	-
	Random	7.78	1.45	**<0.001**	**<0.001**

Vertical cover high: 9-12 dm (%)	Adult	10.87	3.24	-	
	Brood	13.80	3.63	0.557	-
	Random	0.79	0.33	**<0.001**	**<0.001**
Tall mesquite (shrubs per ha)	Adult	60.16	24.24	-	
	Brood	26.53	12.38	0.298	-
	Random	3.04	1.26	**0.002**	**0.002**
Other tall shrubs (shrubs per ha)	Adult	3.05	1.63	-	
	Brood	3.07	2.22	0.993	-
	Random	0.10	0.05	**0.018**	**0.026**

Table 2. Jacob's electivity index for use of mesquite cover and time since fire (TSF) by scaled quail (*Callipepla squamata*) at Sand Ranch in Chaves County, New Mexico, USA. Positive values indicate selection and are highlighted in bold, while negative values indicate avoidance. Data were collected during the breeding seasons of 2018 (February—July) and 2019 (February—August) for all adults combined, non-brooding adults, brooding adults, and for broods only.

		Electivity Index		
Year		All adults	Non-brooding adults	Brooding adults
2018	Mesquite (pre-treatment)	**0.65**	**0.64**	**0.71**
	Mesquite (post-treatment)	**0.50**	**0.48**	**0.56**
2019	Mesquite (pre-treatment)	**0.56**	**0.79**	**0.40**
	Mesquite (post-treatment)	**0.32**	**0.48**	**0.18**
2018	0-11 months since fire	-1.00	-1.00	-1.00
	12-23 months since fire	-0.17	-0.28	**0.25**
	24-35 months since fire	-0.29	-0.36	-0.02
	≥36 months since fire	**0.23**	**0.34**	-0.20
2019	0-11 months since fire	-0.02	**0.28**	-0.40
	12-23 months since fire	-0.36	**0.07**	-1.00
	24-35 months since fire	**0.33**	**0.27**	**0.38**
	≥36 months since fire	-0.31	-0.30	-0.32

Table 3. Differences in temperature between non-brooding adult scaled quail (*Callipepla squamata*) locations, brooding scaled quail locations, and random locations at Sand Ranch in Chaves County, New Mexico, USA. Data were collected during the breeding seasons of 2018 and 2019. Significant differences (p<0.05) are indicated in bold. We evaluated thermal differences for 5 time periods: full (all hours), morning (06:00-08:00), midday (10:00-14:00), evening (17:00-19:00), and night (22:00-02:00).

Time period		Mean	SE	Adult	Brood	Random
Morning	Adult	21.30	0.14	-		
	Brood	24.20	0.17	**<0.001**	-	
	Random	22.00	0.12	**0.001**	**<0.001**	-
Midday	Adult	40.20	0.19	-		
	Brood	42.50	0.23	**<0.001**	-	
	Random	40.20	0.17	0.859	**<0.001**	-
Evening	Adult	33.70	0.23	-		
	Brood	36.70	0.28	**<0.001**	-	
	Random	35.40	0.20	**<0.001**	**<0.001**	-
Night	Adult	19.50	0.14	-		
	Brood	23.40	0.18	**<0.001**	-	
	Random	20.80	0.13	**<0.001**	**<0.001**	-

Table 4. Models explaining the effects of landscape features, weather, and other factors on daily survival probability of adult scaled quail (*Callipepla squamata*) (both brooding and non-brooding combined) in Chaves County, New Mexico, USA, during the breeding seasons of 2018 and 2019. Survival was analyzed at both the location scale and the home range scale. Significant relationships ($\beta_1 \neq 0$) are indicated in bold.

Group	Model	ΔAICc	w	K	B_1	UCI	LCI
Individual	Null	0.000	0.388	1	-	-	-
	Brood status	0.767	0.264	2	0.833	-0.739	2.405
	Age	1.316	0.201	2	0.553	-0.762	1.869
	Sex	1.932	0.147	2	0.175	-1.140	1.491
Temporal	Null	0.000	0.394	1	-	-	-
	Year	0.584	0.294	2	-0.788	-2.142	0.565
	Linear time	1.783	0.161	2	-0.001	-0.007	0.005
	Quadratic time	1.917	0.151	2	- <0.001	- <0.001	<0.001
Weather	Average daily temperature	0.000	0.992	2	**-0.516**	**-0.880**	**-0.153**
	Daily variation in temperature	11.618	0.003	2	0.414	-0.074	0.903
	Null	12.102	0.002	1	-	-	-
	Average daily humidity	13.740	0.001	2	-0.014	-0.061	0.032
	Maximum daily solar radiation	13.824	<0.001	2	-0.003	-0.015	0.009
	Daily precipitation	13.861	<0.001	2	-0.033	-0.136	0.070
Time since fire: Location scale	>36 months since fire	0.000	0.711	2	-5.851	-13.993	2.291
	24-35 months since fire	3.569	0.119	2	5.113	-4.371	14.597
	12-23 months since fire	3.784	0.107	2	368.216	-318030.020	318766.450
	Null	5.975	0.036	1	-	-	-
	Distance to edge of burn	7.963	0.013	2	- <0.001	- <0.001	<0.001
	0-11 months since fire	7.974	0.013	2	0.208	-9.758	10.173
Time since fire: Home range scale	>36 months since fire	0.000	0.622	2	-0.039	-0.084	0.005
	24-35 months since fire	3.198	0.126	2	0.030	-0.019	0.080
	12-23 months since fire	3.362	0.116	2	0.066	-0.083	0.215
	Null	4.170	0.077	1	-	-	-
	0-11 months since fire	6.003	0.031	2	-0.019	-0.102	0.064
	Distance to edge of burn	6.132	0.029	2	- <0.001	- <0.001	<0.001
All range structures: Location scale	Null	0.000	0.308	1	-	-	-
	Distance to oil and gas wells	1.278	0.162	2	- <0.001	-0.001	<0.001
	Distance to highway	1.548	0.142	2	- <0.001	- <0.001	<0.001

	Distance to water source	1.606	0.138	2	<0.001	-0.001	0.002
	Distance to all roads	1.721	0.130	2	- <0.001	-0.003	0.002
	Distance to range structures	1.886	0.120	2	- <0.001	-0.002	0.001
All range structures: Home range scale	Null	0.000	0.369	1	-	-	-
	Distance to highway	1.550	0.170	2	- <0.001	- <0.001	<0.001
	Distance to water sources only	1.705	0.157	2	<0.001	-0.001	0.003
	Distance to range structures	1.732	0.155	2	- <0.001	-0.003	0.002
	Distance to all roads	1.820	0.149	2	- <0.001	-0.003	0.002
Oil and gas: Home range scale	Wells per hectare in home range	0.000	0.442	2	123.021	-74.517	320.560
	Total wells in home range	0.851	0.289	2	0.566	-0.315	1.448
	Null	2.429	0.131	1	-	-	-
	Distance to oil and gas wells	3.547	0.075	2	- <0.001	-0.001	<0.001
	Home range area	3.926	0.062	2	- <0.001	-0.001	<0.001
Mesquite: Location scale	Null	0.000	0.486	1	-	-	-
	Proportion in mesquite cover (post-treatment)	0.749	0.334	2	-0.906	-2.521	0.710
	Proportion in mesquite cover (pre-treatment)	1.979	0.181	2	-0.167	-2.379	2.046
Mesquite: Home range scale	Null	0.000	0.514	1	-	-	-
	Proportion in mesquite cover (post-treatment)	1.362	0.260	2	-0.007	-0.023	0.010
	Proportion in mesquite cover (pre-treatment)	1.648	0.226	2	-0.007	-0.030	0.016

Table 5. Models explaining the effects of landscape features, weather, and other factors on daily survival probability of non-brooding adult scaled quail (*Callipepla squamata*) in Chaves County, New Mexico, USA, during the breeding seasons of 2018 and 2019. Survival was analyzed at both the location scale and the home range scale. Significant relationships ($\beta_1 \neq 0$) are indicated in bold.

Group	Model	ΔAICc	w	k	B_1	LCI	UCI
Individual	Null	0.000	0.535	1	-	-	-
	Age	1.443	0.260	2	0.568	-0.930	2.066
	Sex	1.913	0.205	2	-0.230	-1.728	1.269
Temporal	Null	0.000	0.406	1	-	-	-
	Year	0.759	0.278	2	-1.069	-3.187	1.049
	Linear time	1.775	0.167	2	-0.002	-0.010	0.006
	Quadratic time	1.994	0.150	2	- <0.001	- <0.001	<0.001
Weather	Average daily temperature	0.000	0.998	2	**-0.771**	**-1.264**	**-0.279**
	Null	14.694	<0.001	1	-	-	-
	Daily variation in temperature	15.126	<0.001	2	0.382	-0.192	0.957
	Daily precipitation	16.426	<0.001	2	0.105	-0.669	0.878
	Average daily humidity	16.507	<0.001	2	-0.011	-0.061	0.039
	Maximum daily solar radiation	16.532	<0.001	2	-0.003	-0.019	0.013
Time since fire: Location scale	>36 months since fire	0.000	0.379	2	-5.356	-13.896	3.183
	12-23 months since fire	0.127	0.356	2	365.857	-224202.960	224934.670
	Null	2.747	0.096	1	-	-	-
	24-35 months since fire	2.779	0.094	2	4.191	-5.606	13.989
	Distance to edge of burn	4.524	0.039	2	- <0.001	- <0.001	<0.001
	0-11 months since fire	4.748	0.035	2	-0.037	-9.438	9.363
Time since fire: Home range scale	>36 months since fire	0.000	0.321	2	-0.036	-0.088	0.015
	12-23 months since fire	0.266	0.281	2	0.082	-0.084	0.248
	Null	1.369	0.162	1	-	-	-
	24-35 months since fire	2.431	0.095	2	0.021	-0.033	0.075
	Distance to edge of burn	3.039	0.070	2	- <0.001	- <0.001	<0.001
	0-11 months since fire	3.039	0.070	2	-0.028	-0.116	0.059
All range structures:	Null	0.000	0.251	1	-	-	-
	Distance to oil and gas wells	0.046	0.246	2	- <0.001	-0.001	<0.001

	Distance to all roads	0.515	0.194	2	-0.002	-0.004	<0.001
	Distance to range structures	1.623	0.112	2	- <0.001	-0.002	0.001
	Distance to highway	1.775	0.103	2	<0.001	- <0.001	<0.001
	Distance to water sources only	1.966	0.094	2	<0.001	-0.002	0.002
All range structures: Home range scale	Null	0.000	0.352	1	-	-	-
	Distance to all roads	0.920	0.222	2	-0.002	-0.004	0.001
	Distance to highway	1.767	0.145	2	<0.001	- <0.001	<0.001
	Distance to range structures	1.786	0.144	2	- <0.001	-0.003	0.002
	Distance to water sources only	1.892	0.137	2	<0.001	-0.002	0.002
Oil and gas: Home range scale	Wells per hectare in home range	0.000	0.383	2	117.697	-77.091	312.484
	Total wells in home range	0.617	0.281	2	0.596	-0.294	1.487
	Distance to oil and gas wells	1.976	0.143	2	- <0.001	-0.002	<0.001
	Null	2.056	0.137	1	-	-	-
	Home range area	3.842	0.056	2	- <0.001	-0.001	<0.001
Mesquite: Location scale	Null	0.000	0.515	1	-	-	-
	Proportion in mesquite cover (pre-treatment)	1.111	0.296	2	1.164	-1.157	3.485
	Proportion in mesquite cover (post-treatment)	2.002	0.189	2	0.010	-1.894	1.915
Mesquite: Home range scale	Null	0.000	0.575	1	-	-	-
	Proportion in mesquite cover (pre-treatment)	1.988	0.213	2	0.002	-0.024	0.028
	Proportion in mesquite cover (post-treatment)	2.001	0.212	2	<0.001	-0.020	0.020

Table 6. Models explaining the effects of landscape features, weather, and other factors on daily survival probability of brooding adult scaled quail (*Callipepla squamata*) in Chaves County, New Mexico, USA, during the breeding seasons of 2018 and 2019. Survival was analyzed at both the location scale and the home range scale. Significant relationships ($\beta_1 \neq 0$) are indicated in bold.

Group	Model	ΔAICc	w	k	B_1	LCI	UCI
Individual	Null	0.000	0.558	1	-	-	-
	Sex	1.780	0.229	2	0.674	-2.099	3.447
	Age	1.920	0.213	2	0.408	-2.365	3.180
Temporal	Linear time	0.000	0.477	2	-0.096	-0.231	0.038
	Quadratic time	0.048	0.466	2	- <0.001	- <0.001	<0.001
	Null	5.255	0.034	1	-	-	-
	Year	6.101	0.023	2	35.933	-296469.630	296541.490
Weather	Daily precipitation	0.000	0.315	2	**-0.119**	**-0.215**	**-0.023**
	Null	0.852	0.206	1	-	-	-
	Daily variation in temperature	1.162	0.176	2	0.731	-0.328	1.791
	Average daily humidity	1.757	0.131	2	-0.069	-0.205	0.066
	Average daily temperature	2.365	0.096	2	-0.128	-0.529	0.272
	Maximum daily solar radiation	2.830	0.076	2	-0.001	-0.017	0.015
Time since fire: Location scale	≥36 months since fire	0.000	0.367	2	**-337.911**	**-337.911**	**-337.911**
	24-35 months since fire	1.247	0.197	2	40.000	-1191.696	1271.696
	Null	1.295	0.192	1	-	-	-
	12-23 months since fire	2.894	0.086	2	15.878	-6598.244	6629.999
	0-11 months since fire	3.071	0.079	2	40.000	-392.463	472.463
	Distance to edge of burn	3.087	0.078	2	<0.001	-0.001	0.002
Time since fire: Home range scale	≥36 months since fire	0.000	0.319	2	-0.080	-0.330	0.170
	Null	0.770	0.217	1	-	-	-
	24-35 months since fire	1.048	0.189	2	0.059	-0.132	0.250
	12-23 months since fire	2.369	0.098	2	0.189	-99.430	99.807
	0-11 months since fire	2.506	0.091	2	1.126	-67.651	69.903
	Distance to edge of burn	2.591	0.087	2	<0.001	-0.001	0.002
All range structures: Location scale	Distance to highway	0.000	0.619	2	-0.002	-0.005	0.002
	Distance to water sources only	2.809	0.152	2	0.007	-0.003	0.017
	Distance to range structures	4.172	0.077	2	0.008	-0.005	0.020

	Distance to all roads	4.417	0.068	2	0.013	-0.011	0.037
	Null	5.374	0.042	1	-	-	-
	Distance to oil and gas wells	5.412	0.041	2	0.003	-0.003	0.008
All range structures: Home range scale	Distance to highway	0.000	0.832	2	-0.001	-0.004	0.001
	Null	5.205	0.062	1	-	-	-
	Distance to water sources only	5.930	0.043	2	0.003	-0.003	0.009
	Distance to all roads	6.118	0.039	2	0.005	-0.006	0.015
	Distance to range structures	7.044	0.025	2	0.001	-0.005	0.007
Oil and gas: Home range scale	Null	0.000	0.313	1	-	-	-
	Total wells in home range	0.541	0.239	2	1.667	-4.111	7.444
	Distance to oil and gas wells	1.311	0.163	2	0.001	-0.002	0.004
	Wells per hectare in home range	1.385	0.157	2	40.000	-166.114	246.114
	Home range area	1.783	0.128	2	-0.001	-0.005	0.003
Mesquite: Location scale	Proportion in mesquite cover (post-treatment)	0.000	0.495	2	**-332.790**	**-332.790**	**-332.790**
	Proportion in mesquite cover (pre-treatment)	0.507	0.384	2	-23.063	-113.541	67.415
	Null	2.808	0.122	1	-	-	-
Mesquite: Home range scale	Proportion in mesquite cover (post-treatment)	0.000	0.414	2	-0.030	-0.077	0.017
	Null	0.388	0.341	1	-	-	-
	Proportion in mesquite cover (pre-treatment)	1.047	0.245	2	-0.032	-0.096	0.032

Table 7. Models explaining the effects of landscape features, weather, and other factors on daily survival probability of scaled quail (*Callipepla squamata*) broods (n = 22) in Chaves County, New Mexico, USA, during the breeding seasons of 2018 and 2019. Survival was analyzed at the location scale only. Significant relationships ($\beta_1 \neq 0$) are indicated in bold.

Group	Model	ΔAICc	w	K	B_1	UCI	LCI
Individual	Null	0.000	0.516	1	-	-	-
	Sex	1.223	0.280	2	**-14.849**	**-14.849**	**-14.849**
	Age	1.857	0.204	2	0.363	-1.435	2.161
Temporal	Linear time	0.000	0.363	2	0.023	-0.005	0.051
	Null	0.564	0.273	1	-	-	-
	Quadratic time	0.865	0.235	2	<0.001	- <0.001	<0.001
	Year	2.071	0.129	2	-0.676	-2.477	1.125
Weather	Null	0.000	0.246	1	-	-	-
	Maximum daily solar radiation	0.177	0.225	2	**-0.023**	**-0.046**	**- <0.001**
	Daily precipitation	0.307	0.211	2	74.100	-460873.550	461021.750
	Average daily temperature	1.518	0.115	2	0.168	-0.287	0.622
	Daily variation in temperature	1.595	0.111	2	-0.379	-1.579	0.820
	Average daily humidity	1.937	0.093	2	0.013	-0.081	0.108
Time since fire	Null	0.000	0.390	1	-	-	-
	12-23 months since fire	0.732	0.271	2	36.180	-211026.780	211099.140
	0-11 months since fire	1.396	0.194	2	40.000	-540.721	620.721
	≥36 months since fire	1.981	0.145	2	0.190	-1.791	2.170
All range structures	Null	0.000	0.429	1	-	-	-
	Distance to range structures	1.202	0.235	2	-0.001	-0.004	0.001
	Distance to water sources only	1.785	0.176	2	- <0.001	-0.003	0.002
	Distance to oil and gas wells	1.971	0.160	2	<0.001	-0.001	0.001
Roads	Null	0.000	0.500	1	-	-	-
	Distance to all roads	0.905	0.318	2	0.002	-0.002	0.005
	Distance to highway	2.015	0.182	2	- <0.001	- <0.001	<0.001
Mesquite	Null	0.000	0.387	1	-	-	-
	Distance to edge of burn	0.943	0.241	2	<0.001	- <0.001	0.002
	Proportion in mesquite cover (pre-treatment)	1.223	0.210	2	1.088	-1.286	3.463
	Proportion in mesquite cover (post-treatment)	1.734	0.162	2	-0.514	-2.384	1.357

Table 8. Mean differences in vegetation structure and composition (along with standard errors) between different times since fire (TSF) categories at Sand Ranch in Chaves County, New Mexico, USA. Data were collected in May—July of 2018 and 2019. Significant differences ($p < 0.05$) are indicated in bold.

Variable	TSF	Mean	SE	0-11	12-23	24-35
Bare ground cover (%)	0-11	57.35	5.27	-		
	12-23	52.50	3.53	0.436	-	
	24-35	48.92	4.16	0.203	0.519	-
	≥36	49.77	3.77	0.233	0.617	0.880
Rock cover (%)	0-11	1.36	0.82	-		
	12-23	2.18	1.72	0.746	-	
	24-35	4.30	2.25	0.263	0.449	-
	≥36	0.73	0.50	0.496	0.528	0.134
Litter cover (%)	0-11	36.00	4.43	-		
	12-23	34.84	3.92	0.855	-	
	24-35	33.18	4.07	0.640	0.779	-
	≥36	35.62	3.09	0.942	0.891	0.638
Grass cover (%)	0-11	16.50	2.58	-		
	12-23	18.30	2.20	0.618	-	
	24-35	29.95	4.24	**0.011**	**0.007**	-
	≥36	22.55	3.27	0.156	0.263	0.171
Forb cover (%)	0-11	4.68	1.09	-		
	12-23	1.89	0.53	**0.010**	-	
	24-35	6.02	1.72	0.536	**0.006**	-
	≥36	7.21	1.67	0.222	**<0.001**	0.620
Shrub cover (%)	0-11	19.85	3.57	-		
	12-23	15.42	1.97	0.237	-	
	24-35	12.00	2.66	0.072	0.295	-
	≥36	16.06	3.22	0.429	0.858	0.329
Dead woody vegetation cover (%)	0-11	3.58	0.71	-		
	12-23	2.00	0.30	**0.016**	-	
	24-35	1.14	0.32	**0.001**	0.060	-
	≥36	2.99	0.86	0.602	0.196	**0.043**
Vegetation height (mm)	0-11	37.70	4.29	-		
	12-23	42.19	2.65	0.351	-	
	24-35	40.04	2.69	0.630	0.589	-
	≥36	45.94	3.78	0.148	0.406	0.199
Dead woody vegetation height (mm)	0-11	36.81	2.65	-		
	12-23	27.62	2.22	**0.009**	-	
	24-35	34.07	6.70	0.695	0.262	-
	≥36	33.87	4.04	0.551	0.142	0.979
Litter depth (mm)	0-11	1.14	0.19	-		
	12-23	2.05	0.23	**0.010**	-	
	24-35	2.01	0.46	0.107	0.923	-
	≥36	1.64	0.28	0.151	0.267	0.499
Overhead obstruction (°)	0-11	30.18	3.13	-		
	12-23	42.63	2.69	**0.005**	-	
	24-35	29.92	2.59	0.949	**0.001**	-
	≥36	37.81	4.16	0.154	0.308	0.103
Vertical cover low: 0-4 dm (%)	0-11	39.32	7.96	-		
	12-23	49.19	4.54	0.247	-	

	24-35	37.50	4.79	0.838	0.090	-
	≥36	53.70	5.98	0.144	0.552	**0.033**
Vertical cover medium: 5-8 dm (%)	0-11	10.89	5.38	-		
	12-23	5.83	1.47	0.239	-	
	24-35	4.50	1.96	0.225	0.581	-
	≥36	12.31	3.57	0.823	**0.049**	**0.047**
Vertical cover high: 9-12 dm (%)	0-11	1.61	1.50	-		
	12-23	0.81	0.36	0.489	-	
	24-35	0.54	0.50	0.460	0.658	-
	≥36	0.29	0.21	0.363	0.311	0.657
Tall mesquite (shrubs per ha)	0-11	2.32	1.11	-		
	12-23	0.72	0.42	0.101	-	
	24-35	7.51	5.21	0.381	0.099	-
	≥36	2.85	1.00	0.718	**0.022**	0.396
Other tall shrubs (shrubs per ha)	0-11	0.00	0.00	-		
	12-23	0.05	0.05	0.483	-	
	24-35	0.12	0.08	0.214	0.508	-
	≥36	0.24	0.19	0.250	0.253	0.553

Table 9. Differences in temperature across times since fire (TSF) at Sand Ranch in Chaves County, New Mexico, USA. Data were collected from May—July in 2018 and 2019. Significant differences ($p < 0.05$) are indicated in bold. We evaluated thermal differences for 5 time periods: full (all hours), morning (06:00-08:00), midday (10:00-14:00), evening (17:00-19:00), and night (22:00-02:00).

Time period	Time since fire (months)	Mean	SE	0-11	12-23	24-35	≥36
Morning	0-11	21.00	0.28	-			
	12-23	22.90	0.20	**<0.001**	-		
	24-35	22.30	0.29	**0.002**	0.115	-	
	≥36	21.00	0.30	0.913	**<0.001**	**<0.001**	-
Midday	0-11	38.80	0.41	-			
	12-23	40.30	0.30	**0.005**	-		
	24-35	42.60	0.26	**<0.001**	**<0.001**	-	
	≥36	38.60	0.39	0.603	**0.002**	**<0.001**	-
Evening	0-11	38.30	0.49	-			
	12-23	39.30	0.35	0.077	-		
	24-35	41.40	0.39	**<0.001**	**<0.001**	-	
	≥36	37.00	0.41	**0.046**	**<0.001**	**<0.001**	-
Night	0-11	18.60	0.28	-			
	12-23	21.20	0.20	**<0.001**	-		
	24-35	21.00	0.25	**<0.001**	0.709	-	
	≥36	18.70	0.27	0.835	**<0.001**	**<0.001**	-

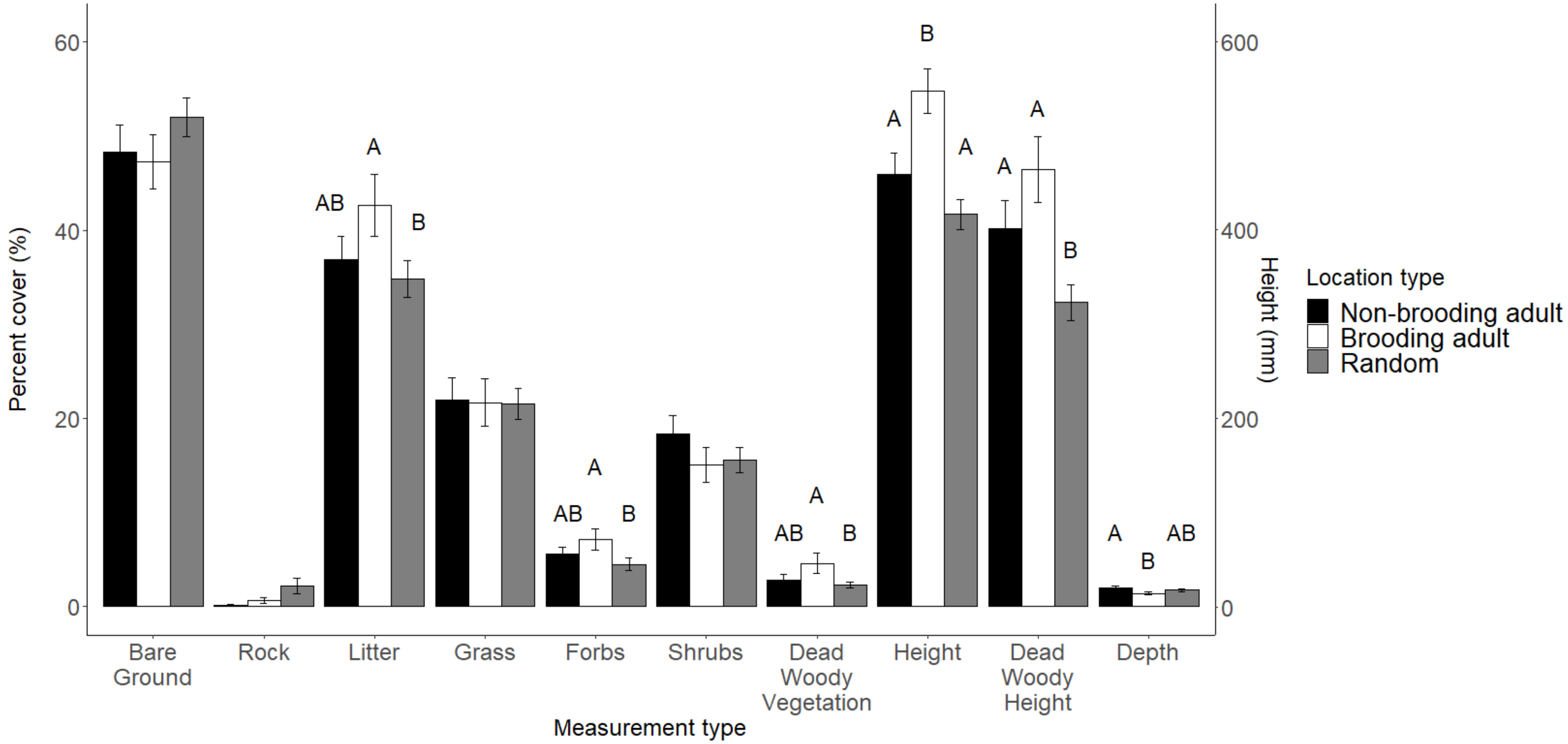

Figure 1. Mean vegetation cover and structure (along with standard errors) at locations used by non-brooding adult scaled quail (*Callipepla squamata*), locations used by brooding scaled quail, and random locations. Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Different letters indicate statistical significance at $p < 0.05$.

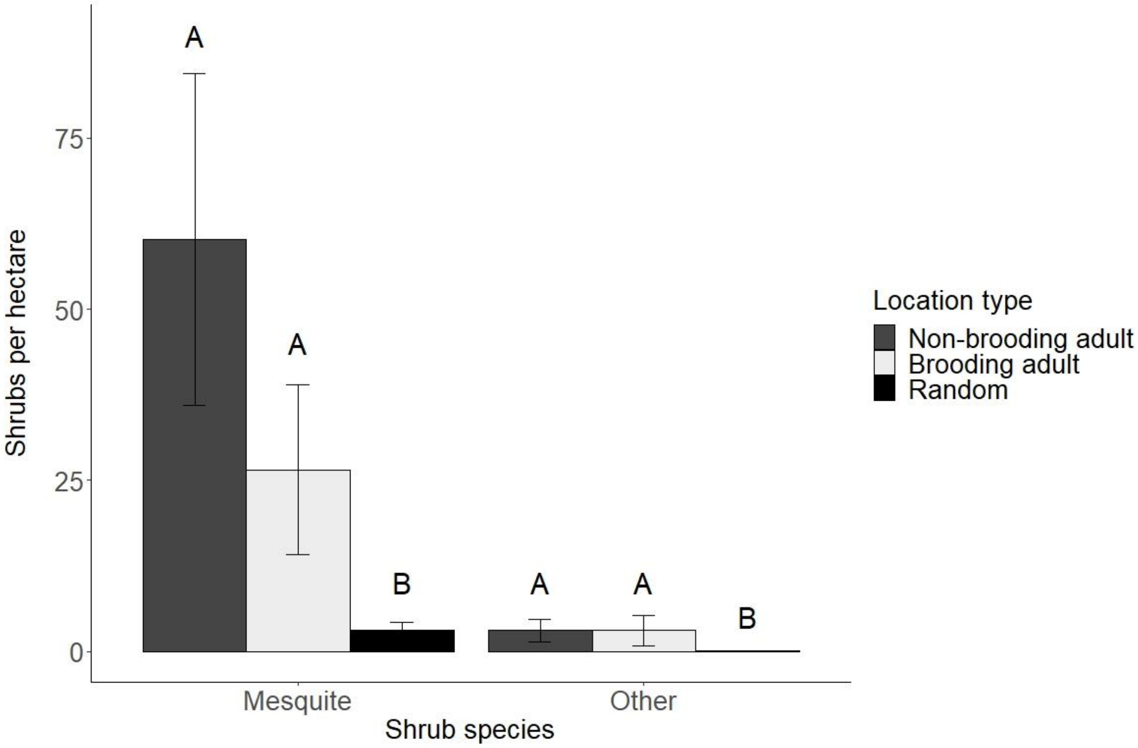

Figure 2. Mean density of tall (> 1.5 m) shrubs at locations used by non-brooding adult scaled quail (*Callipepla squamata*), locations used by brooding scaled quail, and random locations. Data were collected in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Different letters indicate statistical significance at $p < 0.05$.

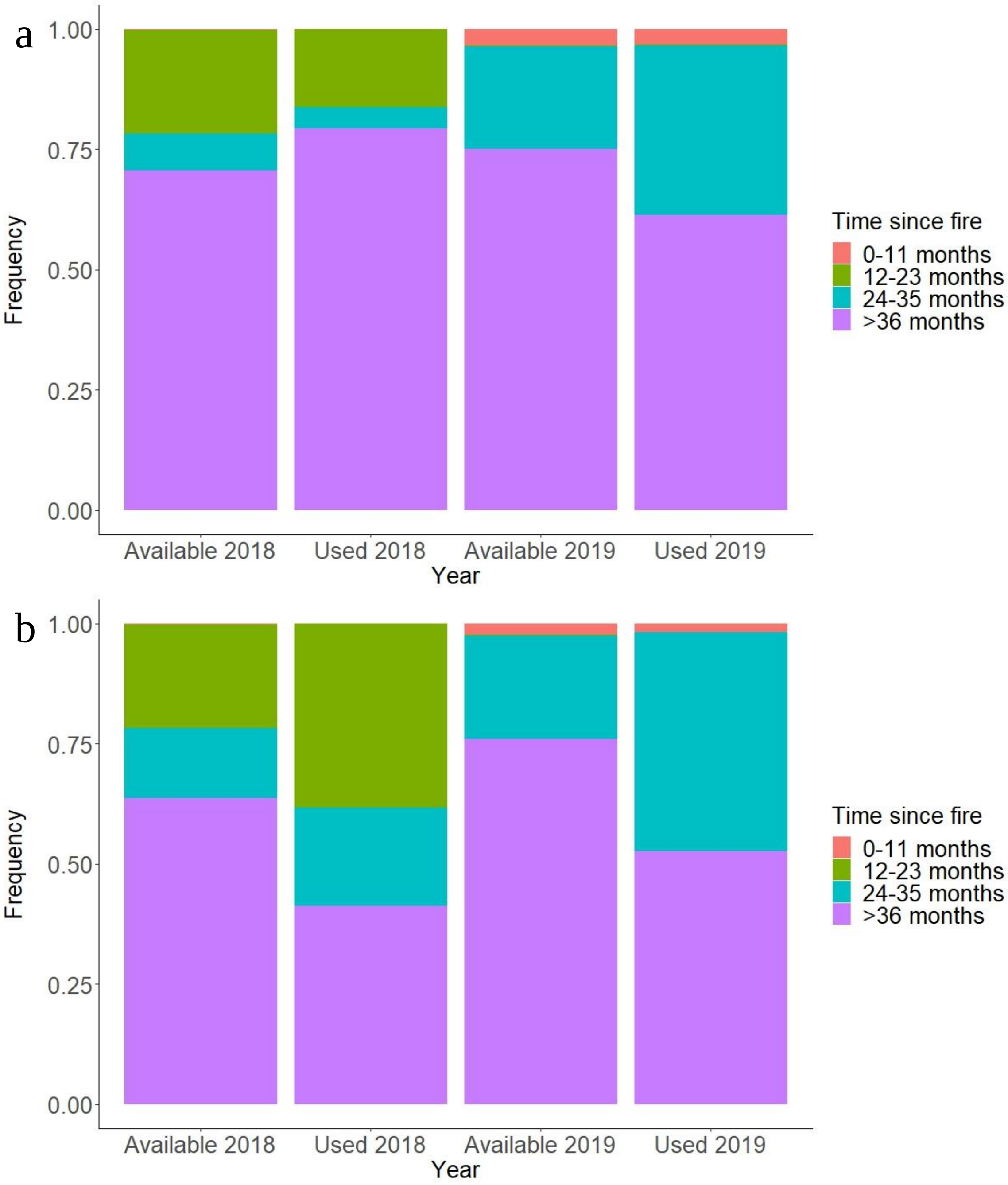

Figure 3. Use of different time since fire (TSF) by a) adult scaled quail (*Callipepla squamata*) (both brooding and non-brooding) and b) scaled quail broods at Sand Ranch in Chaves County, New Mexico, USA. Data are shown for the breeding season of 2018 (February—July) and the breeding season of 2019 (February—August).

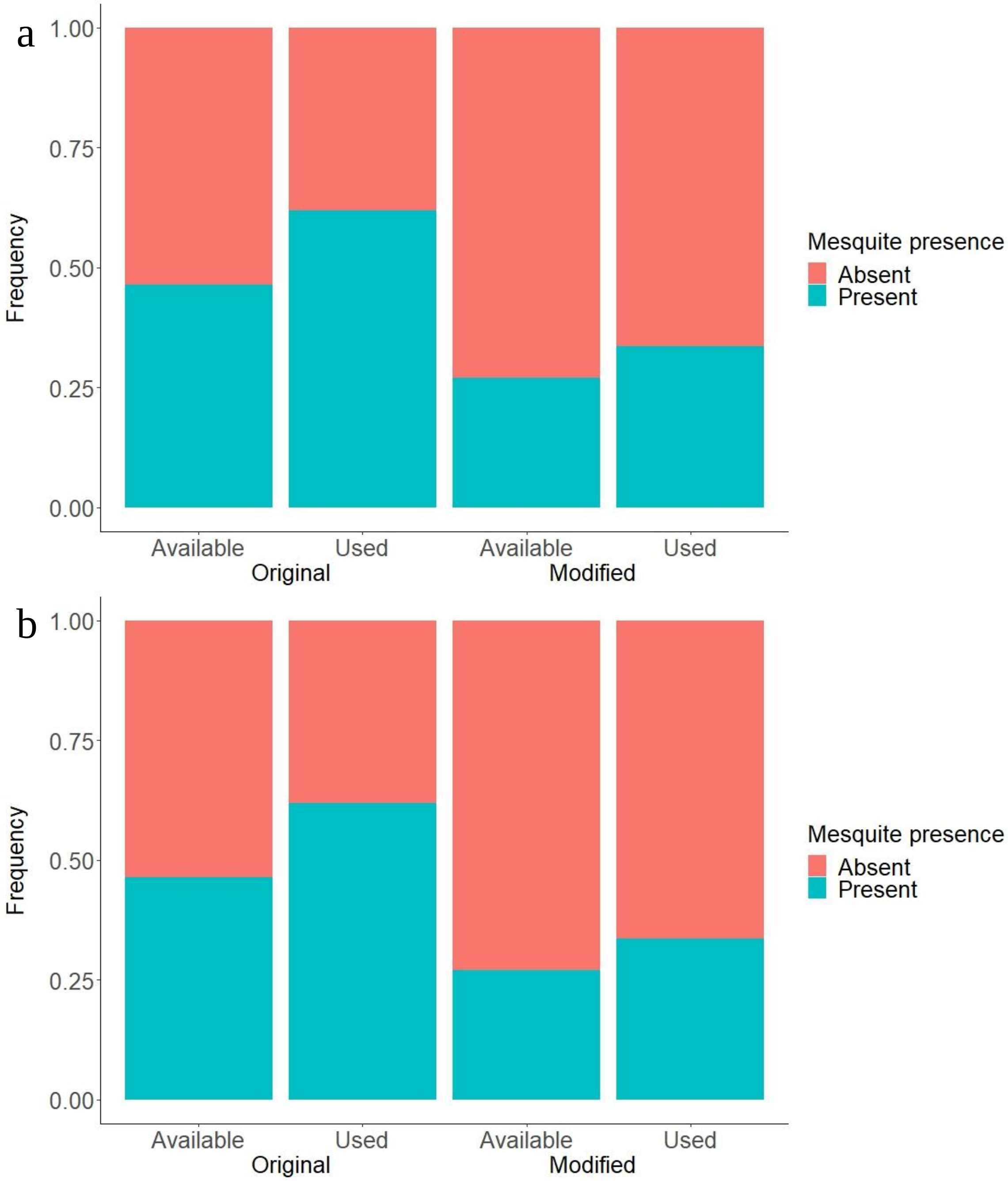

Figure 4. Use of different mesquite cover by a) adult scaled quail (*Callipepla squamata*) (both brooding and non-brooding) and b) scaled quail broods. Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Data are presented for two datasets: the mesquite presence data provided by the Bureau of Land Management (BLM) from 2011 (labeled "Original"), and a modified mesquite dataset in which all mesquite treatments since 2011 were removed from the original BLM dataset (labeled "Modified") to estimate current mesquite presence.

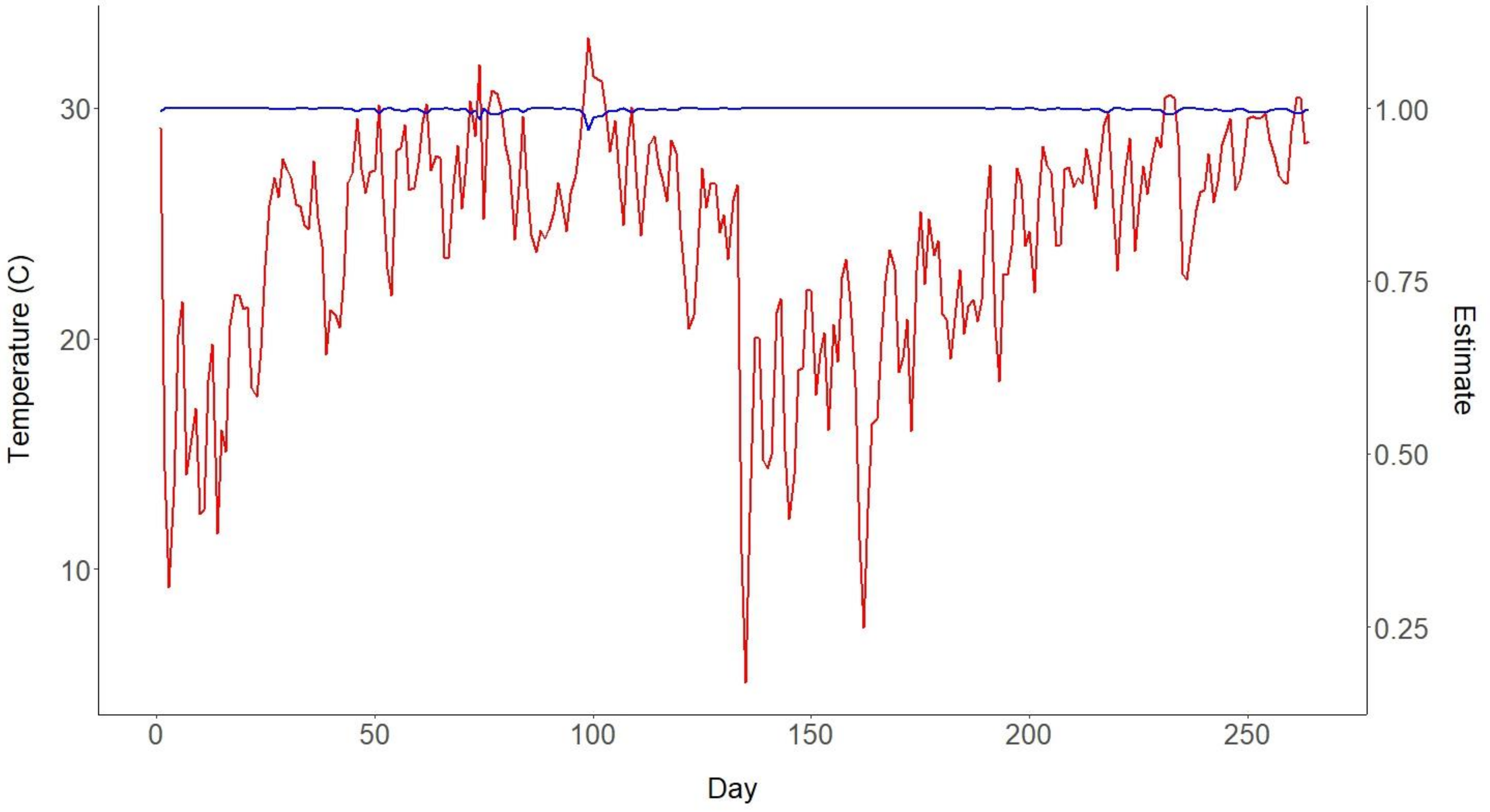

Figure 5. Influence of average daily temperature on estimated daily survival rate (DSR) of scaled quail (*Callipepla squamata*) (both brooding and non-brooding) at Sand Ranch in Chaves County, New Mexico, USA. Data were collected during the breeding seasons of 2018 (days 0 to 132) and 2019 (days 133 to 264). The red line describes average daily temperature (°C) and the blue line describes changes in estimated DSR of adult scaled quail (both brooding and non-brooding combined) (*n* = 71).

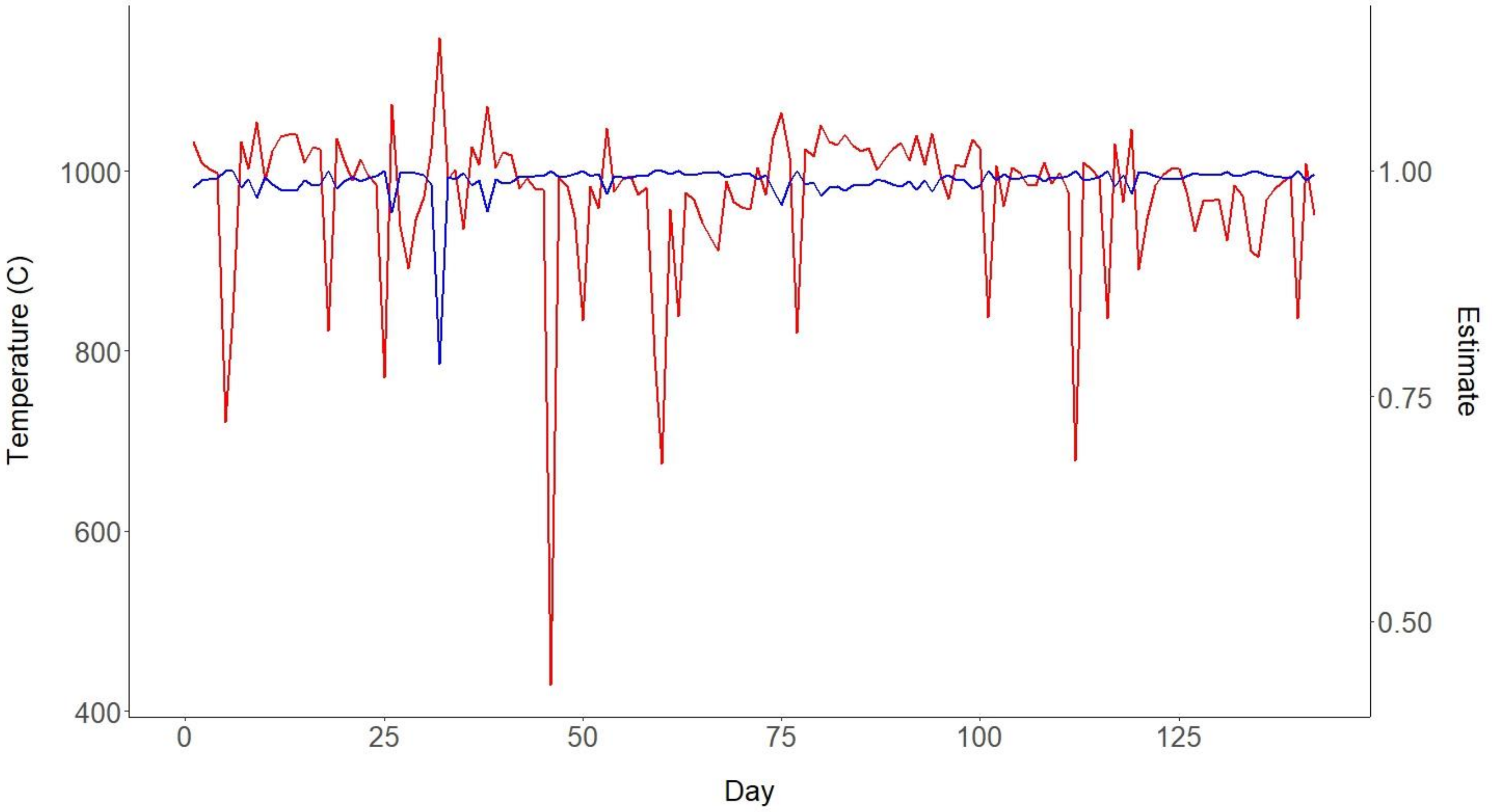

Figure 6. Influence of maximum daily solar radiation on estimated daily survival rate (DSR) of scaled quail (*Callipepla squamata*) broods at Sand Ranch in Chaves County, New Mexico, USA. Data were collected during the breeding seasons of 2018 (days 0 to 132) and 2019 (days 133 to 264). The red line describes maximum solar radiation (W/m^2) and the blue line describes estimated DSR of broods (n = 22). We considered a brood successful if at least one chick was still present with the brooding adult 20 days after hatch.

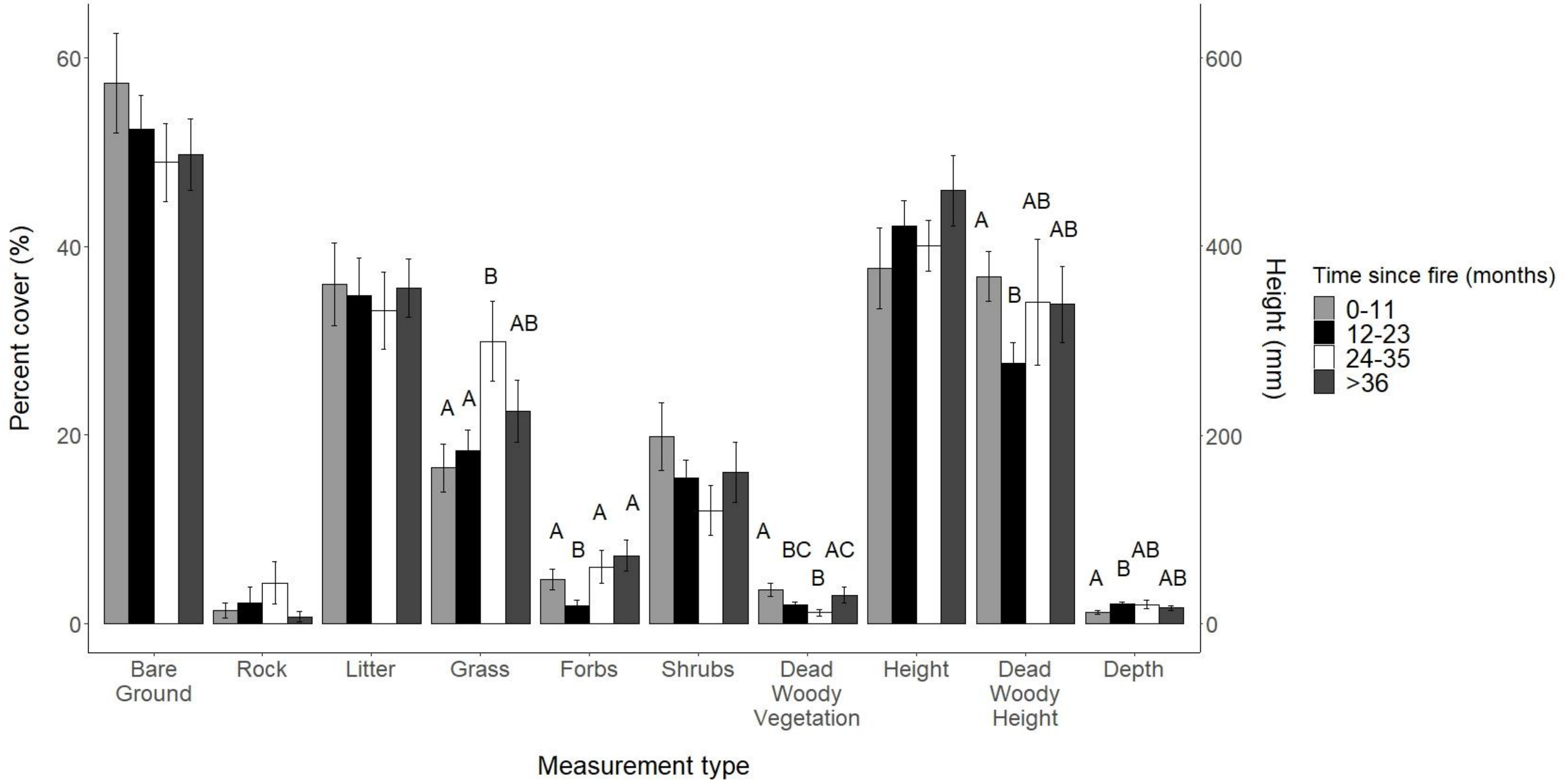

Figure 7. Mean vegetation cover and structure (along with standard errors) across different times since fire (TSF) at Sand Ranch in Chaves County, New Mexico, USA. Data were collected in May—July of 2018 and 2019. Different letters indicate statistical significance at $p < 0.05$.

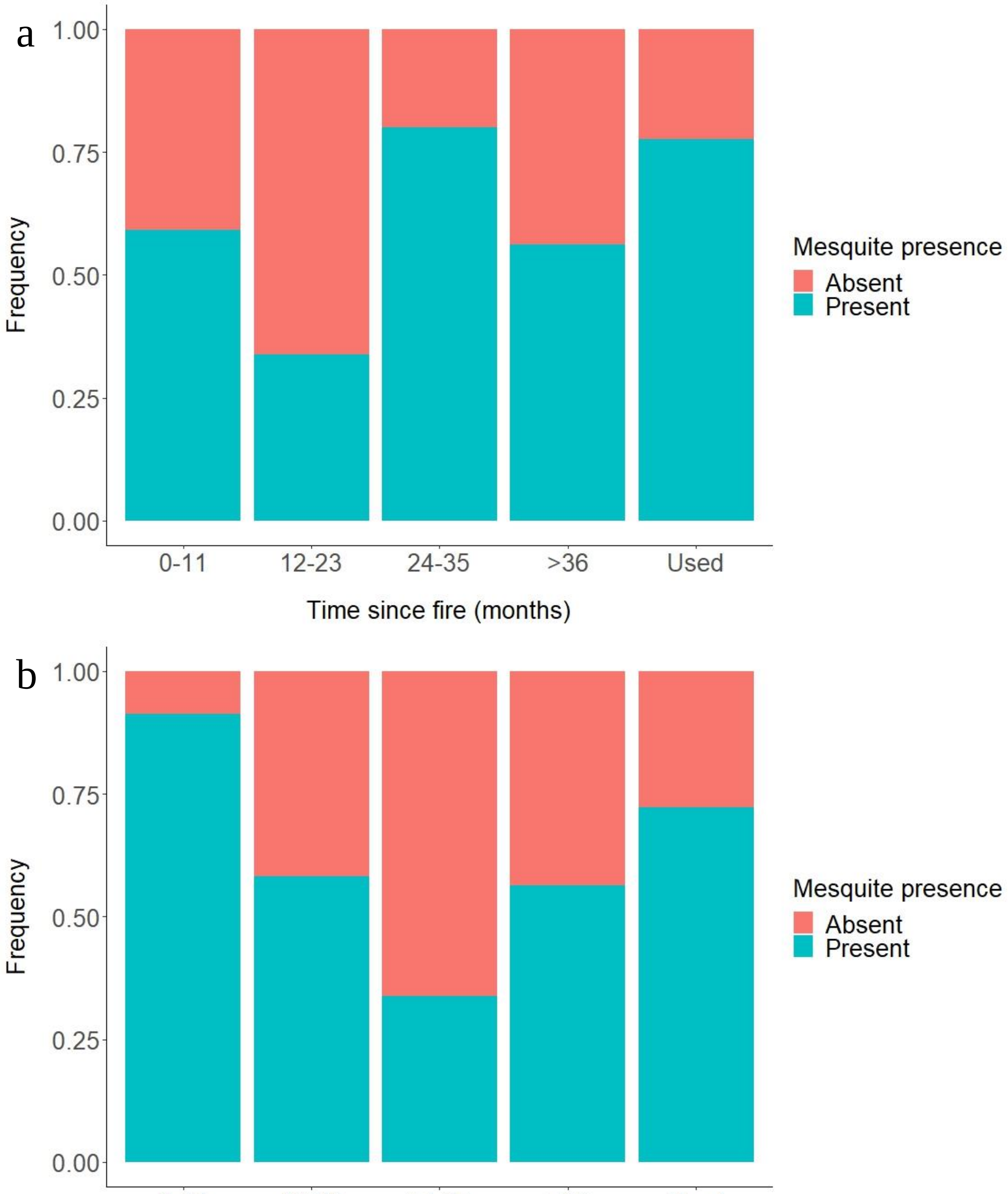

Figure 8. Availability of mesquite cover within each time since fire (TSF) category in a) 2018 and b) 2019 at Sand Ranch in Chaves County, New Mexico, USA. The frequency of all adult quail locations (brooding and non-brooding) in mesquite cover is included for reference. Frequency of mesquite in each TSF was determined using mesquite presence data provided by the Bureau of Land Management (BLM) from 2011.

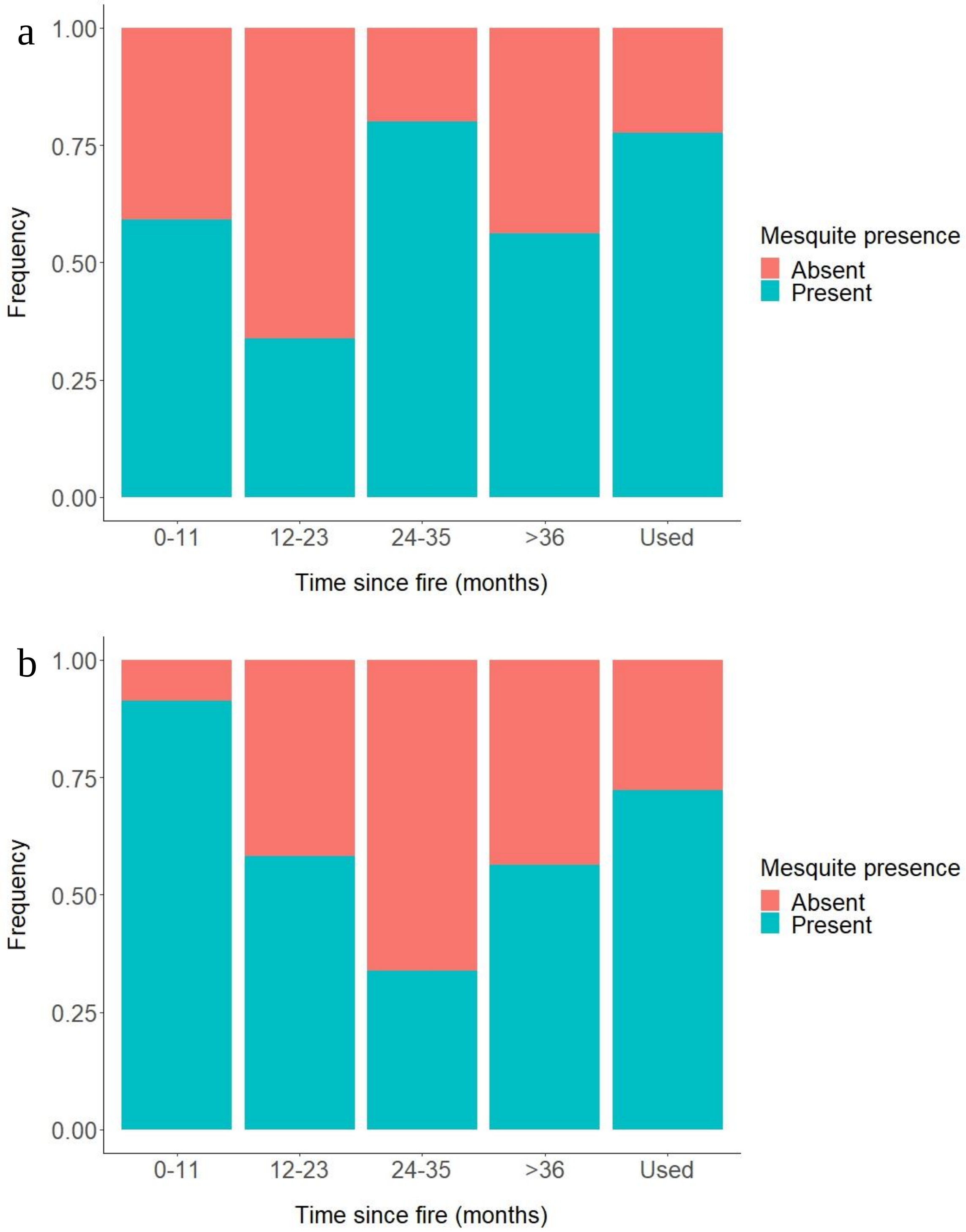

Figure 9. Availability of mesquite cover within each time since fire (TSF) category in a) 2018 and b) 2019 at Sand Ranch in Chaves County, New Mexico, USA. The frequency of all adult quail locations (brooding and non-brooding) in mesquite cover is included for reference. Frequency of mesquite in each TSF was determined using a modified mesquite dataset, in which all mesquite treatments since 2011 were removed from the original dataset provided by the Bureau of Land Management (BLM) from 2011 to estimate current mesquite presence.

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