EXECUTIVE SUMMARY

PREPARED BY: Kiera Kauffman, Oklahoma State University

SUBJECT: Thermal ecology and multi-scale nest site selection of the scaled quail (*Callipepla squamata*)

ISSUE:

The thermal landscape is increasingly gaining recognition as a critical component of habitat. A growing body of research indicates that several species of ground-nesting bird respond to fine-scale thermal variation on the landscape. For species frequently exposed to extreme air temperatures, the thermal environment near the ground may be particularly important for moderating temperatures of both embryos and the incubating adult. Conservation actions offered by the Natural Resources Conservation Service that alter vegetation, such as prescribed fire and brush control, have been shown to affect the thermal environment and habitat selection of game birds. Scaled quail (*Callipepla squamata*) are a relatively understudied game species that inhabit sparsely vegetated, open landscapes in arid and semiarid climates. To better understand the influence of temperature, vegetation, topography, and management on habitat selection, we investigated nest site selection and nest fate of scaled quail in the core of their distribution at three spatial scales: nest bowl, the area around the nest, and landscape. Additionally, we evaluated habitat selection of adult quail in regard to vegetation, temperature, conservation actions, and anthropogenic features.

USDA-NRCS AGREEMENT NUMBER: 68-3A75-17-477

OBJECTIVES:

- Determine vegetation structure, vegetation composition, and near-ground temperature relative to time since fire.
- Examine scaled quail space use, nest success, brood success, and adult survival relative to vegetation structure, vegetation composition, temperature, topography, and proximity to anthropogenic features.
- Create management recommendations for scaled quail within shinnery oak and mesquite plant communities.

METHODS:

We captured scaled quail at the Sand Ranch Area of Critical Environmental Concern (ACEC) in the early spring of 2018 and 2019 using baited walk-in funnel traps. Each quail received an aluminum leg band and VHF radio-transmitter. 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 three scales: the nest bowl, the area around the nest, and random landscape locations. We collected thermal data using Thermochron ibuttons and assessed visual obstruction, shrub density, vegetation structure, ground cover composition, and local topographic slope. To evaluate factors influencing daily nest survival, we selected 24 variables believed to influence nest fate based on the literature. These were used to create 24 univariate candidate models divided into 6 model groups, and each group was analyzed separately in Program MARK

using an information theoretic approach. Additionally, we investigated breeding season habitat use and survival of brooding and non-brooding adult scaled quail in response to vegetation, temperature, time since fire, and anthropogenic structures. To evaluate factors influencing survival, we used a similar approach to our nest analysis by creating functional groups of univariate models in Program MARK.

RESULTS:

- In 2018 and 2019 we captured and radio-marked 186 scaled quail and detected 48 total nest attempts (including 8 re-nests). We observed 7 hatches (41%) in 2018 and 15 hatches (50%) in 2019. Across both years we monitored a total of 21 broods (6 in 2018 and 15 in 2019), 16 of which survived through early August. Nesting and brooding success were greater in 2019 than in 2018, likely due to increased spring rainfall that year.
- We observed that scaled quail selected nest sites with greater cover of grass and litter, taller vegetation, and less bare ground. This pattern was observed both at the nest bowl and at the area around the nest (within a 10 m radius of the nest bowl).
- Scaled quail nest bowls moderated temperature relative to the ambient temperature. Near-ground temperatures at nest bowls were approximately 5°C cooler on average than those in the area surrounding the nest during the hottest part of the day (1000-1400).
- Although scaled quail tended to select nest sites with particular vegetation and thermal characteristics, none of these factors influenced nest survival. Rather, the most important factors influencing nest survival were proximity to surface water sources and cover of honey mesquite (*Prosopis glandulosa*), with nests having greater daily survival probability closer to these features. Scaled quail showed apparent selection for distances approximately 250-500 m from water sources, but further study is needed to better understand the mechanisms behind this observed relationship.
- Locations used by both brooding and non-brooding adult scaled quail had greater vertical obstruction and a higher density of tall (≥1.5 m) shrubs than the broader landscape. In particular, density of tall mesquite was the primary distinguishing feature of adult quail locations, with non-brooding adult locations having densities almost 20 times greater than those of landscape locations. Both brooding and non-brooding adults showed selection for mesquite cover in general, although selection was weaker for brooding adults than for non-brooding adults.
- The response of scaled quail to time since fire was unclear. This lack of response was likely influenced by the non-random nature of prescribed fire treatments, which targeted habitat for lesser prairie-chickens (*Tympanuchus pallidicinctus*).
- Weather explained more variation in adult and brood survival than any of the other variables we examined. 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.

RECOMMENDATIONS:

- Nest sites selected by scaled quail moderated the thermal environment significantly relative to the surrounding landscape. This may be due in part to the tall vegetation and

increased cover at the nest bowl, although our study cannot confirm the mechanism of nest site selection. Conservation actions should be made with consideration for maintaining diverse vegetation composition and structure to increase the availability of thermal options on the landscape.

- Tall, dense shrubs (> 1 m), specifically mesquite, were heavily used by adult scaled quail, potentially as sources of 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. Conservation actions that suppress 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 conservation goals.
- Our data suggest that proximity to surface water may provide benefits to nesting scaled quail. However, we do not have enough information to recommend the construction of provisional water sources for scaled quail as a means of increasing nest survival. Further study is needed to support these findings and understand the mechanism behind this relationship.

TABLE OF CONTENTS

Chapter Page

I. ROLE OF THE THERMAL ENVIRONMENT IN INFLUENCING SCALED QUAIL NEST SITE SELECTION AND SURVIVAL 1

Abstract 1
Introduction 2
Methods 5
Study site 5
Quail capture and monitoring 6
Thermal and weather data collection 6
Vegetation data collection 7
Statistical analysis 8
Survival analysis 9
Cumulative distribution functions 11
Results 12
Microsite-scale selection 13
Selection at the nest bowl 14
Influence of selection on nest fate 14
Influence of selection on daily nest survival 15
Discussion 16

II. SCALED QUAIL HABITAT USE AND SURVIVAL DURING THE BREEDING SEASON 36

Abstract 36
Introduction 37
Methods 41
Study site 41
Quail capture and monitoring 42
Thermal and weather sampling 43
Vegetation sampling 44
Statistical analysis 46
Survival analysis 47
Results 51
Vegetation use and selection 51
Temperature use 52
Adult and brood survival 53

Chapter Page

Influence of time since fire 54
Discussion 54
Habitat use 55
Adult and brood survival 59
Influence of time since fire 63
Conclusion 65

REFERENCES 90

LIST OF TABLES

Table Page

1.1 Differences in vegetation and topography between scaled quail (*Callipepla squamata*) nest microsites (area within a 10 m radius around the nest bowl) and landscape locations. 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. 23

1.2 Differences in temperature between scaled quail (*Callipepla squamata*) nest microsites (area within a 10 m radius around the nest bowl) and landscape locations. 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). Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. 24

1.3 Differences in vegetation and topography between scaled quail (*Callipepla squamata*) nest bowls and nest microsites (area within a 10 m radius around 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. 25

1.4 Differences in temperature between scaled quail (*Callipepla squamata*) nest bowls and nest microsites (area within a 10 m radius of the nest bowl). 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). Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. 26

1.5 Differences in vegetation and topography between hatched and failed scaled quail (*Callipepla squamata*) nests at both the nest bowl and the nest microsite scales. 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. 27

Table Page

1.6 Differences in temperature between hatched and failed scaled quail (*Callipepla squamata*) nests at both the nest bowl and the nest microsite scales. 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). Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.....28

1.7 Models examining 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.....29

1.8 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.....30

2.1 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. 67

2.2 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. 69

2.3 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) 70

Table Page

2.4 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. 71

2.5 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. 73

2.6 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. 75

2.7 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. 77

2.8 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. 78

2.9 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). 80

LIST OF FIGURES

Figure Page

1.1 Sampling design used for collecting thermal and vegetation data at scaled quail (*Callipepla squamata*) nest locations and landscape locations at Sand Ranch in Chaves County, New Mexico, USA. Each two-dimensional transect consisted of 11 points spaced 2 m apart, with the central point (sample point) placed either in the scaled quail nest bowl (for nest locations) or at a stratified random point (for landscape locations). Transects extended in the direction of a random azimuth and 180° from that azimuth. The extent of the transect at nest locations constituted the "nest microsite."..... 31

1.2 Comparison of temperatures between scaled quail (*Callipepla squamata*) nest microsites (10 m radius around the nest bowl) and the landscape a) across different ambient temperatures and b) across each hour of the day. Temperatures were modeled based on the interactive effects of ambient temperature (°C) and solar radiation (kW per m^2). Thermal data were collected during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA..... 32

1.3 Comparison of temperatures between scaled quail (*Callipepla squamata*) nest bowls and the surrounding nest microsite (2-10 m) a) across different ambient temperatures and b) across each hour of the day. Temperatures were modeled based on the interactive effects of ambient temperature (°C) and solar radiation (kW per m^2). Thermal data were collected during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA..... 33

1.4 Comparison of nest bowl temperatures between hatched and failed scaled quail (*Callipepla squamata*) nests a) across different hours of the day and b) across each hour of the day. Temperatures were modeled based on the interactive effects of ambient temperature (°C) and solar radiation (kW/m^2). Thermal data were collected during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA..... 34

1.5 As distance from the nearest surface water feature or honey mesquite (*Prosopis glandulosa*) increases, the estimated survival probability of scaled quail (*Callipepla squamata*) nests decreases. These data were collected at Sand Ranch in Chaves County, New Mexico, USA during May—July of 2018 and 2019..... 35

Figure Page

1.6 Cumulative distribution function [G(x) – F(x)] describing the distribution of scaled quail (*Callipepla squamata*) nests in relation to a) artificial surface water features and b) honey mesquite (*Prosopis glandulosa*) during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.....36

2.1 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 $p < 0.05$.....81

2.2 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 $p < 0.05$.....82

2.3 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).....83

2.4 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 84

2.5 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) ($n = 71$).....85

Figure Page

2.6 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. 86

2.7 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 $p < 0.05$. 87

2.8 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. 88

2.9 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. 89

CHAPTER I

ROLE OF THE THERMAL ENVIRONMENT IN INFLUENCING SCALED QUAIL NEST SITE SELECTION AND SURVIVAL

Abstract

The important role of temperature in influencing wildlife habitat selection has been increasingly recognized. Temperature is particularly crucial for avian nest sites, which must maintain temperatures suitable for both the incubating adult and embryonic development throughout the incubation period. For species inhabiting arid and semiarid climates, such as the scaled quail (*Callipepla squamata*), thermal conditions may be particularly important for nest survival. Relatively little research has been conducted on nest site selection and fate in scaled quail, although limited data suggests that scaled quail respond to temperature when selecting nest sites. Scaled quail are also known to respond to the presence of surface water and shrub cover on the landscape, two resources which may mitigate heat stress in nesting quail. To better understand the role of the thermal landscape in influencing nest site selection and survival, and to evaluate how landscape cover and resources may provide benefits for nesting quail, we investigated nest site characteristics of scaled quail in southeastern New Mexico. During the breeding seasons of 2018 and 2019, we used radio telemetry to locate nests and monitor nest fate. We recorded temperature and vegetation characteristics at three spatial scales relative to scaled quail nests: nest bowl, nest microsite (within a 10 m radius of the nest bowl), and landscape. We found that nest bowls were cooler than both the nest microsite and the landscape during the hottest part of the day. Nest bowls also had taller vegetation and greater shrub, grass, and litter cover compared to the nest microsite and the landscape. Similarly, the nest microsite had taller vegetation and greater grass and litter cover than the landscape. Despite apparent selection for cooler temperatures and taller vegetation, none of these factors influenced nest survival. Rather, nest survival was positively influenced by landscape features, including proximity to surface water features and honey mesquite (*Prosopis glandulosa*), with survival being highest for nests that were closer to these features. Despite the uncertainty related to potential mechanism for these relationships, our results support the relationship of temperature for the selection of nest sites of ground-nesting birds in semiarid landscapes.

Introduction

Wildlife research has increasingly recognized the role of temperature in defining habitat (Elmore et al. 2017). Like other landscape features such as vegetation, soil, topography, and moisture (Riera et al. 1998, Petrone et al. 2004), temperature exhibits spatial and temporal heterogeneity (Geiger 1965, Suggitt et al. 2011) that is shaped by both biotic and abiotic factors. Even relatively small variations in vegetation, such as cooler temperatures formed by woody shrubs and trees (Tracol et al. 2011, Allred et al. 2013, Rakowski et al. 2018), or the aspect of the ground surface (Bennie et al. 2008, Olson et al. 2014, Hall et al. 2016) can alter solar radiation exposure and create distinct microclimates (Limb et al. 2009, Hovick et al. 2014) that differ markedly from ambient temperature. These microclimates can be highly relevant to habitat selection choices of animals (Suggitt et al. 2011).

Species representing a wide variety of taxa have been shown to respond to the thermal landscape at fine spatial scales (Allred et al. 2013, Angilletta et al. 2009, Blomquist and Hunter 2010, van Beest et al. 2012). These temperatures influence choices that animals make about how to use available resources, which may have important consequences for space use and vital rates. For example, ground surface temperatures were one of the best predictors of chestnut-bellied scaled quail (*Callipepla squamata castanogastris*) space use in South Texas, and scaled quail avoided locations below 24°C above 43°C (Kline et al. 2019). Similarly, exotic Bermudagrass (*Cynodon dactylon*) was found to have higher temperatures than native forbs, and simulations revealed that northern bobwhite (*Colinus virginianus*) chicks foraging in Bermudagrass were likely to reach thermal death earlier than those foraging in native forbs (Martin et al. 2015). This example illustrates how, during certain life stages, thermal environments can have important implications for survival and recruitment of young. The nesting stage is particularly important for some species, as incubation restricts the incubating adult's ability to seek thermal refuge during extreme temperatures. A growing body of literature indicates that nest site selection in ground-

nesting birds is at least partially driven by or correlated with temperature (Hovick et al. 2014, Carroll et al. 2015*a*, Grisham et al. 2016, Carroll et al. 2018, 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 exposed to predation. The incubating adult can mediate the thermal environment through incubation behaviors (White and Kinney 1974, Brown and Downs 2003, Coe et al. 2015, Carroll et al. 2018), 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 and Ghalambor 1999, Martin et al. 2000, Coates and Delehanty 2008). 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, making temperature a critical component of nest site selection.

While the nest microclimate has important implications for survival, there are other ways that ground-nesting birds can moderate both their own body temperatures and those of their eggs. Gular flutter is a method of evaporative cooling used by several ground-nesting species (Guthery et al. 2005, McKechnie et al. 2016). This strategy requires metabolic water, which may be acquired either through food items or free water on the landscape. Increased evaporative cooling due to high nest bowl temperatures may lead to greater water requirements. Provisional surface water structures, such as stock tanks and wildlife drinkers, are commonly constructed for wildlife in arid landscapes (Rosenstock et al. 1999). Despite limited empirical support for benefits, these structures could support metabolic cooling during egg production and incubation by providing a supplementary source of free water, but this needs evaluation.

In arid and semiarid climates, thermal mitigation during egg production and incubation may be even more critical due to extreme weather conditions including high temperatures, high solar radiation, and relatively low moisture conditions. The scaled quail (*Callipepla squamata*) is

a ground-nesting galliform species that occurs in such climates. Scaled quail have experienced population declines since the 1960s (Brennan et al. 1994, Rollins 2000, Pardieck et al. 2019), and there is considerable interest in identifying factors that influence their population dynamics and developing conservation strategies to increase their populations. Despite interest in this species, limited research has been conducted on nest site selection and factors influencing nest fate, with data suggesting that scaled quail select nest sites that moderate temperature relative to the surrounding environment (Carroll et al. 2018). While scaled quail were found to select nest sites that were cooler, successful nests were significantly warmer than failed nests (Carroll et al. 2018). It is unclear from this data as to whether scaled quail select nest sites based on temperature, as temperature may simply be correlated to other factors influencing nest site selection and ultimately nest fate. For example, shrub cover has the potential to provide not only thermal shade for a nest (Carroll et al. 2018), but also physical protection, visual obstruction, and olfactory concealment (Fogarty et al. 2018). Furthermore, because scaled quail habitat use varies substantially across their geographic distribution, along with differences in subspecies and habitat availability (Silvy et al. 2007), the patterns of nest site selection and survival observed in one geographic region may not hold across the entirety of their distribution. More information is needed regarding nesting ecology, including potential relationships with thermal characteristics, to better understand the role of the thermal environment in determining nest site suitability and survival for this species.

To better understand how temperature influences nest site selection and survival of scaled quail, we monitored adult quail and their nests in the geographical core of their distribution. We evaluated both fine-scale nest site characteristics, including vegetation and temperature, as well as proximity of nests to landscape-scale resources that we hypothesized to influence the thermal mitigation ability of incubating adults. Specifically, our objectives were to 1) characterize the thermal environment and vegetation at three spatial scales relative to scaled quail nests: nest

bowl, nest microsite (within 10 m of the nest bowl), and landscape; 2) determine whether thermal differences exist between hatched and failed nests; and 3) examine how nest site characteristics, weather, and landscape features influenced daily nest survival in a semiarid landscape.

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, during 2018 and 2019. The study area was over 23,000 ha and managed cooperatively by the Bureau of Land Management and the New Mexico Department of Game and Fish. Management practices at the site included dormant season (February) prescribed fire, herbicide treatments for honey mesquite (*Prosopis glandulosa*), and cattle grazing. The general topography consisted of undulating sand dunes interspersed with flat expanses of tight soils (Davis et al. 1979). Major soil types included Roswell, Roswell-Jalmar, and Faskin fine sands (NRCS 2017). Together these soils primarily supported vegetation communities dominated by sand shinnery oak (*Quercus havardii*) and honey mesquite. Other prominent woody species included sand sagebrush (*Artemisia filifolia*), four-wing saltbush (*Atriplex canescens*), soapweed yucca (*Yucca glauca*), and broom snakeweed (*Gutierrezia sarothrae*). Common grasses included sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), three-awn (*Aristida* spp.), and sand dropseed (*Sporobolus cryptandrus*). Other prevalent species included western ragweed (*Ambrosia psilostachya*), croton (*Croton* spp.), catclaw sensitive briar (*Acacia greggi*), phlox (*Phlox* sp.), broom groundsel (*Senecio spartioides*), and prickly pear (*Opuntia* spp.; Davis et al. 1979). The climate was semiarid with an average annual precipitation of 39.2 cm and mean annual minimum and maximum 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, with a majority occurring from July through October (Horel et al. 2002). 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 quail using walk-in funnel traps (Stoddard 1931) between mid-February and late April. We fitted captured quail with necklace-style radio transmitters weighing approximately 6-7 grams and 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). We located each radio-marked quail 2-3 times per week by homing within 15-20 m (White and Garrot 1990) of the bird and estimating the azimuth and distance from the observer. We determined a quail to be on nest when it had been located at the same point for three consecutive checks. We calculated the forecasted hatch date for confirmed nests by projecting forward 23 days (Johnsgard 2017) 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, which included evidence of detached membranes and or pipped egg shells.

Thermal and weather data collection

To evaluate the influence of temperature on nest site selection, we collected thermal data at scaled quail nest locations and random landscape locations. We collected thermal data on the day after the hatch was discovered (for hatched nests) or on the forecasted hatch date (for failed nests), and determined landscape locations using a randomly stratified sampling scheme to account for variation in topography and past fire history. At nest and landscape locations, we established 20 m line transects (Figure 1). These transects allowed us to examine the thermal

environment at three scales, which we defined as: the nest bowl (the midpoint of the transect), the nest microsite (the full length of the transect, within a 10 m radius of the nest), and the landscape (random landscape transects). We established the midpoint of each transect at the sample point (the actual nest or the random point). The placement of the transect was determined by a random azimuth, and the transect extended 10 m in the direction of the random azimuth and 10 m in the opposite direction 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 to record temperatures every 15 minutes. iButtons were attached to metal stakes, and the stakes were pushed into the soil until the iButtons occurred at a 10 cm height above the ground surface to approximate temperatures experienced by scaled quail. One iButton was located at the center of the nest bowl or the sample point and then at every 2 m along the transect for a total of 11 iButtons per transect. The point location of each iButton constituted a "point" within the transect, so that each transect consisted of 11 points. We collected temperature data for 48 hours at each transect and 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 data on temperature (°C), solar radiation (W per m^2), relative humidity (%), and precipitation (mm).

Vegetation data collection

Following thermal measurements, we collected vegetation data from the transects. At the center of each sample (i.e., nest or random) point, we estimated vertical obstruction using a Nudds profile board (Nudds 1977) modified for use in a sand shinnery oak community (Guthery et al. 1981). We combined the Nudds strata into three height categories: low (< 4.0 dm), medium (4.0-8.0 dm), and high (> 8.0 dm). We measured the angle of overhead obstruction at each sample point as an index of the three-dimensional structure surrounding the point (Kopp et al. 1998, Harrell and Fuhlendorf 2002). We collected angle measurements in 8 evenly-spaced directions by

affixing a digital level to the Nudd's profile board, 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. The mean of these 8 angles was calculated to determine the angle of obstruction for each sample point. To quantify the density of tall woody vegetation at each point, we used a point-centered quarter method (Cottam and Curtis 1956). In each quarter, we measured the distance to the nearest tall mesquite shrub (≥ 1.5 m tall) and the nearest tall non-mesquite shrub (≥ 1.5 m tall) from the sample point 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.

We also measured vegetation at each point within the transect (11 points per transect, including the sample point). We visually estimated percent cover of 7 functional groups (bare ground, rock, litter, grass, forbs, shrubs, and dead woody vegetation) within a 0.5 m x 0.5 m cover frame centered over each point 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 (cm) and the tallest dead woody vegetation within the frame (cm), and litter depth (cm) at the center of the frame.

Statistical analysis

To evaluate nest site characteristics, we used one-way ANOVA to compare mean differences in vegetation structure and composition. Separate analyses were conducted to compare 1) nest microsites with landscape locations, 2) nest bowls with the surrounding nest microsite, 3) hatched nest microsites with failed nest microsites, and 4) hatched nest bowls with failed nest bowls. Preliminary analysis indicated that individual points within the nest microsite (excepting the nest bowl) were not statistically different from each other in terms of vegetation and thermal variables. Therefore, we combined all non-nest points (≥ 2 m from the nest bowl) within the nest microsite for analysis. We used post-hoc Tukey tests to conduct pairwise comparisons for all analyses, and differences were considered statistically significant at $\alpha = 0.05$ level.

To evaluate thermal conditions at the nest location, we only included those temperatures that were recorded closest to the hour. This allowed us to compare sampled temperatures with hourly ambient temperatures at the same temporal scale. Using the lmer() function in the lme4 package (Bates et al. 2015) in Program R (version 3.6.1, R Core Team 2019), we created generalized linear mixed models to model sampled temperatures at both nest and landscape locations as a function of the interactive effects of ambient temperature and solar radiation, which were recorded hourly by the on-site weather station. We included the "point" as a random effect to account for differences in measurements between individual points within and among locations. We used these models to predict temperatures at all sampled locations, which allowed us to account for both nest locations and landscape locations being sampled on different days. These modeled temperatures were then used to evaluate thermal differences between 1) nest microsites and the landscape, 2) nest bowls and the surrounding microsite, 3) hatched and failed nest microsites, and 4) hatched and failed nest bowls. We conducted all statistical analyses in Program R.

Survival analysis

We examined factors influencing daily nest survival from 24 a priori candidate models using the nest survival model in Program MARK (version 6.2, Cooch and White 2019). Because of relatively small sample sizes we evaluated univariate models, but classified them into six functional groups: vegetation, visual obstruction, microclimate (mean, minimum, and maximum nest bowl temperatures), weather (daily mean ambient temperature, daily mean relative humidity, daily precipitation, and daily maximum solar radiation), temporal variables, and distance to water. We examined the potential for quadratic relationships between landscape variables and nest survival compared to linear effects. We hypothesized each of the variables included in these models to influence daily nest survival based on previous research (Pleasant et al. 2006, Hovick et al. 2014, Fogarty et al. 2017), our analysis of nest site characteristics, or the potential influence of the variables on the thermal environment. We evaluated model support using Akaike Information Criterion adjusted for small sample sizes (AIC_C). We considered models competitive if $\Delta AIC_C < 2$ (Burnham and Anderson 2002), and parameter estimates (β) informative if the 95% confidence intervals excluded 0 ($\beta \neq 0$).

Landscape variables for the survival analysis (distance to water sources and distance to mesquite cover) were determined for each nest in ArcGIS Pro (ESRI 2020). Spatial data were provided by the BLM Roswell Field Office in Roswell, New Mexico. To evaluate the influence of proximity to surface water on nest survival, we used spatial layers representing anthropogenic structures for livestock and wildlife to identify those structures associated with accessible standing water (e.g. livestock troughs, wildlife drinkers, catchments, retention dams). The actual presence of water was temporally variable at some of these structures, particularly during the monsoon season (June—August). These features were extracted and confirmed using a combination of satellite imagery and ground-truthing. Only one natural water feature was present on the study site (Presler Lake, approximately 19 ha in size). We chose to exclude this feature and

focus on artificial water features as we had no nests within 1 km of it. The total density of accessible surface water sources at our site during the study period was 321 ha per water source.

Mesquite density was represented by a 30 m x 30 m raster. This layer was derived from multiband 1 m x 1 m orthophotographs acquired by the National Agriculture Imagery Program (NAIP) during May and June of 2011, which was used to extract individual mesquite locations and classify each pixel into one of 7 discrete canopy cover classes (0 = <1%, 1 = 1-5%, 2 = 5-10%, 3 = 10-15%, 4 = 15-30%, 5 = 30-50%, 6 = >50%). A full description of the derivation of this raster is described by Falkowski et al. (2017). We reclassified pixels with values from 0-2 (0-10%) as "0" to indicate mesquite absence, while pixels with values from 3-6 (>10%) were reclassified as "1" to indicate mesquite presence. We selected 10% as our threshold for mesquite presence because the Arizona scaled quail (*C.s. pallida*) which is the subspecies at our study site, is thought to use grasslands with 10-15% shrub cover (Silvy et al. 2007), and 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 these data to a polygon data format. We created a 20 m buffer around the resulting mesquite presence polygon to account for telemetry error within our 20 m homing radius. We calculated the Euclidean distance from each nest to the nearest water source and to the nearest edge of mesquite cover. These distances were included as individual covariates for the survival analysis in the model groups for vegetation, quadratic vegetation, and distance to water.

Cumulative Distribution Functions

To examine the relationship between landscape variables and nest survival and to identify potential thresholds of site selection/avoidance, we created post-hoc cumulative distribution functions (CDF) on landscape variables that were significant to nest survival. This method has been used to evaluate selection-avoidance-neutral behavior of wildlife relative to continuous

resource variables (Dunkin et al. 2009, Tanner et al. 2015, Londe et al. 2019). These studies describe selection behavior by calculating the difference between the relative cumulative frequency of used locations [$G(x)$] and the cumulative frequency of random locations [$F(x)$] within the same area (i.e., [$G(x) – F(x)$]). This function displays selection/avoidance behavior of organisms, for which a slope > 0 indicates selection, a slope < 0 indicates avoidance, and a slope of approximately 0 indicates a neutral response (Dunkin et al. 2009, Tanner et al. 2015, Londe et al. 2019). We used this methodology to calculate CDFs for both artificial water sources and mesquite cover as preliminary survival analysis indicated they were important. We converted the mesquite cover raster into a point feature class. and generated 3 random points for every mesquite cover point. We also generated 30 random points for every artificial water feature point. These random points were generated within a predefined area of availability, which was formed by a buffered (500 m) minimum convex polygon around the artificial water source locations. A buffer distance of 500 m was chosen to approximate the largest average daily movement of scaled quail during the breeding season (Tanner, unpublished data). We then calculated each CDF for 30 iterations (30 different sets of random points) at 50 m intervals and estimated the average CDF for each feature class (Tanner et al. 2015, Londe et al. 2019).

Results

We captured and radio-marked 186 adult quail during the springs of 2018 and 2019, and 36 of these were censored due to radio collar slips, capture myopathy, etc. prior to the start of the breeding season. Subsequently, we monitored 150 adult scaled quail and located 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%) were successful. Due to logistical constraints, we were unable to sample temperature and vegetation at all 48 nest sites. In total, we measured thermal

and vegetation characteristics from 39 nest locations (22 failed and 17 hatched) and 65 landscape locations.

Microsite-scale selection

At the microsite scale, nest and landscape locations differed in some vegetation characteristics (Table 1). Vertical obstruction at nest microsites was two, three, and three and a half times greater than that of landscape locations for the low, medium, and high height categories, respectively. Nest microsites also had more than twice as much overhead obstruction as landscape locations (Table 1). On average, nest microsites were characterized by greater cover of litter (11.3%) and grass (8.8%), less bare ground (11.3%), and taller live vegetation and dead woody vegetation (both approximately 23.0% taller) than landscape locations. Cover of rock, forbs, shrubs, dead woody vegetation, or litter depth were similar among comparisons. Density of non-mesquite shrubs was twice as high at nest microsites as at landscape locations (Table 1), although density of tall mesquite shrubs was not significantly different. Overall, nest microsites tended to be characterized by greater cover of tall grasses, litter, and higher densities of tall shrubs than landscape locations.

Temperatures at nest microsites generally differed from those at landscape locations. Temperatures were positively related to ambient temperatures at both nest microsites ($\beta = 0.73$; CI = 0.72, 0.74) and landscape locations ($\beta = 0.74$; CI = 0.74, 0.75). Temperatures at nest microsites were warmer than those on the landscape when ambient temperatures exceeded 25°C (Figure 2a, however, these differences were small (<1.0°C) and confidence intervals overlapped. Although the relationship between ambient and sampled temperatures were similar between location types, the patterns of variation in predicted temperature differed across the diel cycle. Specifically, nest microsites were warmer than landscape locations during the morning (06:00—08:00), midday (10:00—14:00), and night (22:00—02:00) (Figure 2b). In contrast, nest

microsites were cooler than landscape locations during the evening (17:00—19:00) (Figure 2b), when ambient temperatures are generally highest.

Selection at the nest bowl

At the nest bowl scale, we found that nest bowls differed from the surrounding nest microsite in both vegetation (Table 2) and temperature. Nest bowls had greater cover of litter (18.6%), grass (32.3%), and shrubs (24.0%) than the surrounding microsite. Nest bowls also had less bare ground (35.7%), taller live vegetation (46.1%), and taller dead woody vegetation (81.0%). Cover of rock, forbs, and litter depth were similar.

Thermal differences were pronounced between the nest bowl and the surrounding nest microsite (Figure 3). The relationship between ambient temperature and sampled temperatures was positive for both the nest bowl ($\beta = 0.58$; CI = 0.55, 0.62) and the nest microsite ($\beta = 0.75$; CI = 0.73, 0.76) (Figure 3a). However, the effect size was smaller for nest bowls than for the nest microsite, indicating that nest bowls warmed more slowly in response to increasing ambient temperature (Figure 3a). Nest bowls remained cooler than nest microsites at ambient temperatures above approximately 23°C, but remained warmer thanat ambient temperatures below 23°C. The relationship between nest bowl and nest microsite temperatures also changed throughout the diel cycle. Nest bowls were cooler than nest microsites during the morning (06:00—08:00), midday (10:00—14:00), and evening (17:00—19:00). At midday when the sun was at its highest angle, nest bowls remained approximately 5°C cooler on average than the surrounding microsite (Figure 3b). Nest bowls moderated temperatures at night (22:00—02:00) by maintaining slightly warmer temperatures (Figure 3b). These differences indicate that nest bowls were located in more stable thermal environments compared to the surrounding environment, as measured by the surrounding nest microsite.

Influence of selection on nest fate

Neither vegetation nor temperature appeared to have an influence on nest fate. Specifically, in terms of vegetation, we did not detect any significant differences in vegetation cover, vegetation structure, or shrub density between hatched and failed nests at either the scale of the nest microsite or the scale of the nest bowl (Table 3). The relationship between ambient temperature and nest bowl/nest microsite temperature was positive for both hatched ($\beta = 0.48$; CI = 0.43, 0.54) and failed ($\beta = 0.68$; CI = 0.63, 0.74) nests. Although the relationship was similar between fates, the slope of the relationship was steeper for failed nests indicating that the effect size was larger. In other words, failed nests warmed more quickly than hatched nests with increasing ambient temperature (Figure 4b). Hatched and failed nests did not differ in temperature at any time of day, 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 4a).

Influence of selection on daily nest survival

There was considerable model uncertainty with 9 models having ΔAICc <4 and accounting for cumulative w_i of 67%. Nest survival was estimated at 39.1% for a 23-day incubation period from the best model. There was little evidence for any within or between year temporal pattern to nest survival (ΔAICc >4). Daily nest survival was best explained by proximity to landscape features and less by fine-scale vegetation or temperature (Table 4). The two competing models (ΔAICc <2) that were best supported were linear distance to water sources and linear distance to mesquite. The probability of nest survival decreased with increasing distance to water sources ($\beta = -0.0011 \pm 0.0005$) and mesquite ($\beta = -0.000652 \pm 0.00035$; Figure 5).

Based on the slopes of our CDFs, scaled quail nests showed a general neutral relationship to water for approximately 300 m and then possible selection to 450 m (Figure 6a). Nesting quail

avoided close proximity to mesquite cover (Figure 6b), with strong avoidance observed within 100 m of the nest. However, past 100 m, the slope shifts, suggesting that while nesting quail show avoidance of mesquite cover within 100 m of the nest, they tend to be in areas of the landscape that have more mesquite cover.

Discussion

In arid and semi-arid climates, nesting birds must make decisions about how to balance their energy budgets in order to mitigate thermal extremes and increase the chances of survival for them and their offspring. Our findings add to the growing body of evidence that the thermal environment at the nest bowl may have an important role in mitigating thermal stress for incubating adults and, subsequently, their eggs. We found that scaled quail placed their nest bowls in locations that provided cooler temperatures than the surrounding microsite when ambient temperatures were high, moderating temperatures by almost 5°C during the hottest part of the day. These nest bowls were characterized by taller vegetation as well as more vegetation cover and litter. The sharp thermal and vegetation contrasts observed over such a short distance demonstrate fine-scale nest site selection that may have provided critical protection for both the adults and young relative to thermal stress and/or predator avoidance. Previous studies of other ground-nesting species have similarly shown that nests moderate temperature relative to the surrounding environment (Carroll et al. 2015*a*, Hovick et al. 2014, Grisham et al. 2016, Raynor et al. 2018). Choosing nest sites that moderate temperature may reduce the energy required for thermoregulation by incubating adults (Lyon and Montgomerie 1987, Giuliano et al. 1998) and allow them to take longer, less frequent foraging bouts, which may reduce the risk of detection by predators (Thomson et al. 1998, DuRant et al. 2012).

These moderate microclimates were likely influenced in part by vegetation characteristics, as we found that nest bowls had more and taller vegetation than nest microsites. Several studies have suggested that shrub cover can be an important source of thermal cover for wildlife (Patten et al. 2005, Carroll et al. 2015*a*, Raynor et al. 2018). Shrubs provide a source of overhead shading that intercepts solar radiation and may also decrease temperatures beneath the canopy through evapotranspiration and/or air movement (Geiger 1965). In the South Texas Plains, ground surface temperatures were observed to decrease with increasing vertical obstruction, and these cooler temperatures simultaneously increased the probability of use by non-nesting adult scaled quail (Kline et al. 2019).

Temperatures at nest microsites exceeded the threshold for hyperthermia in avian embryos (Webb 1987, Guthery et al. 2005). However, these high temperatures were unlikely to be biologically relevant for nesting quail, as they spend the majority of their time on the nest bowl (which was much cooler) to incubate the eggs. Even during foraging off-bouts adults typically avoid the nest area due to the risk of attracting visually-oriented predators (Burhans 2000, Bures and Pavel 2003).

While nest site characteristics are important in shaping nest microclimate, adult behavior also contributes to the temperatures experienced by developing embryos. Adult quail have been known to actively monitor and adjust egg temperatures throughout incubation. The presence of an incubating parent aids in optimizing egg incubation temperature when ambient temperatures fluctuate (Brown and Downs 2003, Coe et al. 2015, Carroll et al. 2018). Of course, there are limits to what an incubating adult can tolerate, and at some point, a threshold would be crossed causing the adult to abandon the nest or to seek thermal refuge for a period of time. Additionally, adults must periodically feed and defecate off the nest. The timing and duration of these off-bouts may be influenced by the thermal environment of the nest. Previous work indicates that scaled quail time their off-bouts between 06:00-08:00 and 17:00-19:00 coinciding with periods when

ambient temperatures most approximated incubation temperatures (Carroll et al. 2018). Our results suggest that temperatures at hatched nest bowls tended to be moderated relative to failed nest bowls during these off-bout periods. Specifically, the locations of successful nests were slightly warmer before the presumed timing of the morning off-bout (03:00-06:00) and slightly cooler after the presumed timing of the afternoon off-bout (19:00-22:00). This pattern may be biologically relevant as changes in incubation temperature of < 1°C have been shown to reduce hatchability and alter the duration of incubation in gallinaceous birds (French 2000, Belnap et al. 2019).

The majority of failed nests in our study showed evidence of depredation, and although thermal stress can increase depredation risk indirectly (Londoño et al. 2008, Lyon and Montgomerie 1987, Martin and Ghalambor 1999, Martin et al. 2000), there are other factors that may also increase vulnerability of the nest such as visual or olfactory detectability (Fogarty et al. 2017). While we cannot confirm the cause of failure for each nest, it is clear from our data that scaled quail chose nest bowls with distinctly cooler microclimates. Despite evidence for nest site selection both at the nest bowl and the nest microsite, the variables that best explained nest survival were found at broader scales. This finding supports those of similar studies on ground-nesting species. Smith et al. (2019) found that fine-scale vegetation characteristics at greater sage grouse (*Centrocercus urophasianus*) nests had no relationship with nest fate, and that sage grouse were able to find successful nest sites within a variety of habitat patches across their range. Other studies have described similar results for vegetation, but found that temperature was an important factor in nest success (Hovick et al. 2014, Carroll et al. 2015*a*, Carroll et al. 2018, Raynor et al. 2018). In all of these studies, except for Carroll et al. (2018) on scaled quail, cooler temperatures were associated with successful nests. Temperature did not influence nest fate in our study despite apparent selection for cooler locations. It is possible that the climatic conditions that occurred during the two years of our study (with a limited sample size of nests) may not have

been conditions under which thermal selection influenced nest success in this population. In fact, in 2019, total precipitation was above average and minimum temperatures were below average during the breeding season (February—August; PRISM Climate Group 2019). These wetter, cooler conditions could have facilitated vegetation growth and increased thermal options on the landscape, reducing the impact of ambient temperatures on hatchability. Furthermore, 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 low precipitation or high temperatures. Such conditions, even if infrequent, could nevertheless exert selection pressure over time (Brown and Brown 2000). It is also possible that scaled quail are selecting for other fine-scale features that are merely correlated with temperature, and that temperature is not a selection cue and/or is not driving nest fate. However, given the consistent findings from other similar studies, this seems less likely.

At broader scales, we found that daily nest survival probability decreased as distance from water increased. CDF analysis suggested an initial neutral relationship with nest site selection and distance from surface water out to about 250 m and then apparent selection to nearly 500 m. Previous research has provided limited support for water developments for quail, with data suggesting that scaled quail habitat selection was related to surface water features, yet providing little evidence to suggest that those sources provided a fitness benefit (Campbell 1960, Tanner et al. 2015). Similarly, lesser prairie-chickens (*Tympanuchus pallidicinctus*) selected for nest locations in close proximity to stock tanks in the sand shinnery oak prairie of Texas (Grisham et al. 2014). Although this study did not find evidence for a relationship with nest fate, they did photo-document over 1200 visits to stock tanks, the majority of which occurred between April and June when hens would have been forming, laying, and incubating eggs (Grisham et al. 2014). Similarly, scaled quail in the sand shinnery oak prairie may use surface water during the

breeding season to supplement their resources for egg production, or to mitigate the effects of thermally stressful nest microclimates. Scaled quail have been observed to increase food consumption under conditions of water deprivation, a behavior which is suspected to increase water retention and create metabolic water (Giuliano et al. 1998). Increasing food and water intake may facilitate metabolic cooling when the nest microclimate becomes too warm. Lab studies have demonstrated that both northern bobwhite and scaled quail can survive on the metabolic water obtained from food alone (Giuliano et al. 1998, Guthery and Koerth 1992). If food were limited, particularly food high in water content such as insects, free standing water may be important. These data should be interpreted with caution, however, due to the variable presence of water associated with ephemeral rains and water structure disrepair at our study site. Further investigation using a before-after-control-impact design could illuminate the importance of surface water for nesting quail and assess whether provisional water may play a role in mitigating heat stress during the breeding season.

We also found that the further mesquite cover was from a nest, the less likely it would successfully hatch. The CDF analysis indicated an initial avoidance within 100 m and then selection up to 1000 m. These data suggest that scaled quail may select patches with lower mesquite cover for nesting, but generally occur in landscapes with higher levels of mesquite. While shrubs can provide a source of thermal cover and overhead concealment as our data found, dense patches of taller mesquite shrubs may provide perches for aerial predators (Hagen et al. 2004). Overall, our data indicate that nest bowls are placed in locations with taller cover (including shrubs), but the nest microsite generally has less shrub cover. Heterogeneity of vegetation structure is likely important in habitat selection for nesting quail and this is likely at least partially due to thermal mitigation.

Our findings contribute to the growing body of literature related to the role of temperature for avian nest sites, particularly in semiarid landscapes. Shrub cover appears to be an

important component of fine-scale nest site selection, possibly contributing both overhead concealment and shading. Although the implications for nest fate are unclear, our results suggest that large-scale shrub removal may affect the availability of preferred nesting substrate for scaled quail, yet heterogeneity in vegetation cover, with patches of less dense shrub cover, may be important. Structurally diverse vegetation mosaics provide a wide range of cover options for nesting scaled quail. Although our results suggest that proximity to artificial surface water may provide advantages for nesting quail, there is not enough evidence to recommend the construction of wildlife water developments for scaled quail management at this time. Until such evidence is available, we recommend that managers in semiarid rangelands prioritize diversification of vegetation structure and composition to increase the availability of suitable nesting cover that includes thermal considerations.

Table 1. Differences in vegetation and topography between scaled quail (*Callipepla squamata*) nest microsites (area within a 10 m radius around the nest bowl) and landscape locations. 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 microsite		Landscape			
	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**
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 microsites (area within a 10 m radius around the nest bowl) and landscape locations. 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). Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

	Nest microsite		Landscape			
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 nest microsites (area within a 10 m radius around 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		Nest microsite			
	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**

Table 4. Differences in temperature between scaled quail (*Callipepla squamata*) nest bowls and nest microsites (area within a 10 m radius of the nest bowl). 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). Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA

	Nest bowl		Nest microsite			
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 nest bowl and the nest microsite scales. 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*
Nest microsite	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
	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
Nest bowl	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

Table 6. Differences in temperature between hatched and failed scaled quail (*Callipepla squamata*) nests at both the nest bowl and the nest microsite scales. 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). Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA

		Hatched		Failed			
	Time period	Mean	SE	Mean	SE	F	*p*
Nest microsite	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
Nest bowl	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 examining 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

Model	K	ΔAICc	W_i
Distance to water source (m)	2	0.000	0.217
Distance to mesquite cover (m)	2	1.286	0.114
Distance to mesquite cover^2 (m)	3	2.316	0.068
Null	1	2.503	0.062
Shrub cover^2: transect (%)	3	2.800	0.054
Linear time trend	2	3.093	0.046
Daily mean relative humidity (%)	2	3.611	0.036
Daily mean ambient temperature (°C)	2	3.628	0.035
Overhead angle of obstruction (°)	2	3.661	0.035
Year	2	4.071	0.028
Vertical cover low: 0-4 dm (%)	2	4.143	0.027
Shrub cover^2: nest bowl (%)	3	4.148	0.027
Shrub cover: transect (%)	2	4.259	0.026
Mean nest bowl temperature (°C)	2	4.433	0.024
Minimum nest bowl temperature (°C)	2	4.440	0.024
Vertical cover medium: 5-8 dm (%)	2	4.479	0.023
Vertical cover high: 9-12 dm (%)	2	4.489	0.023
Maximum nest bowl temperature (°C)	2	4.494	0.023
Daily precipitation (mm)	2	4.499	0.023
Daily maximum solar radiation (W/m^2)	2	4.500	0.023
Quadratic time trend	2	5.085	0.017
Vegetation height: nest bowl (mm)	2	5.109	0.017
Shrub cover: nest bowl (%)	2	5.365	0.015
Vegetation height ^{2}: nest bowl (mm)	3	5.883	0.011

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

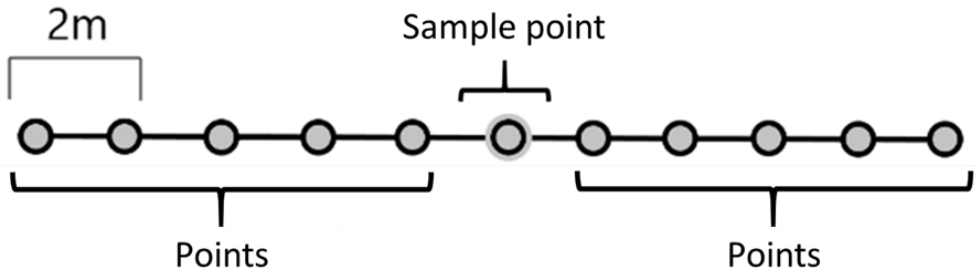

Figure 1. Sampling design used for collecting thermal and vegetation data at scaled quail (*Callipepla squamata*) nest locations and landscape locations at Sand Ranch in Chaves County, New Mexico, USA. Each two-dimensional transect consisted of 11 points spaced 2 m apart, with the central point (sample point) placed either in the scaled quail nest bowl (for nest locations) or at a stratified random point (for landscape locations). Transects extended in the direction of a random azimuth and 180° from that azimuth. The extent of the transect at nest locations constituted the "nest microsite."

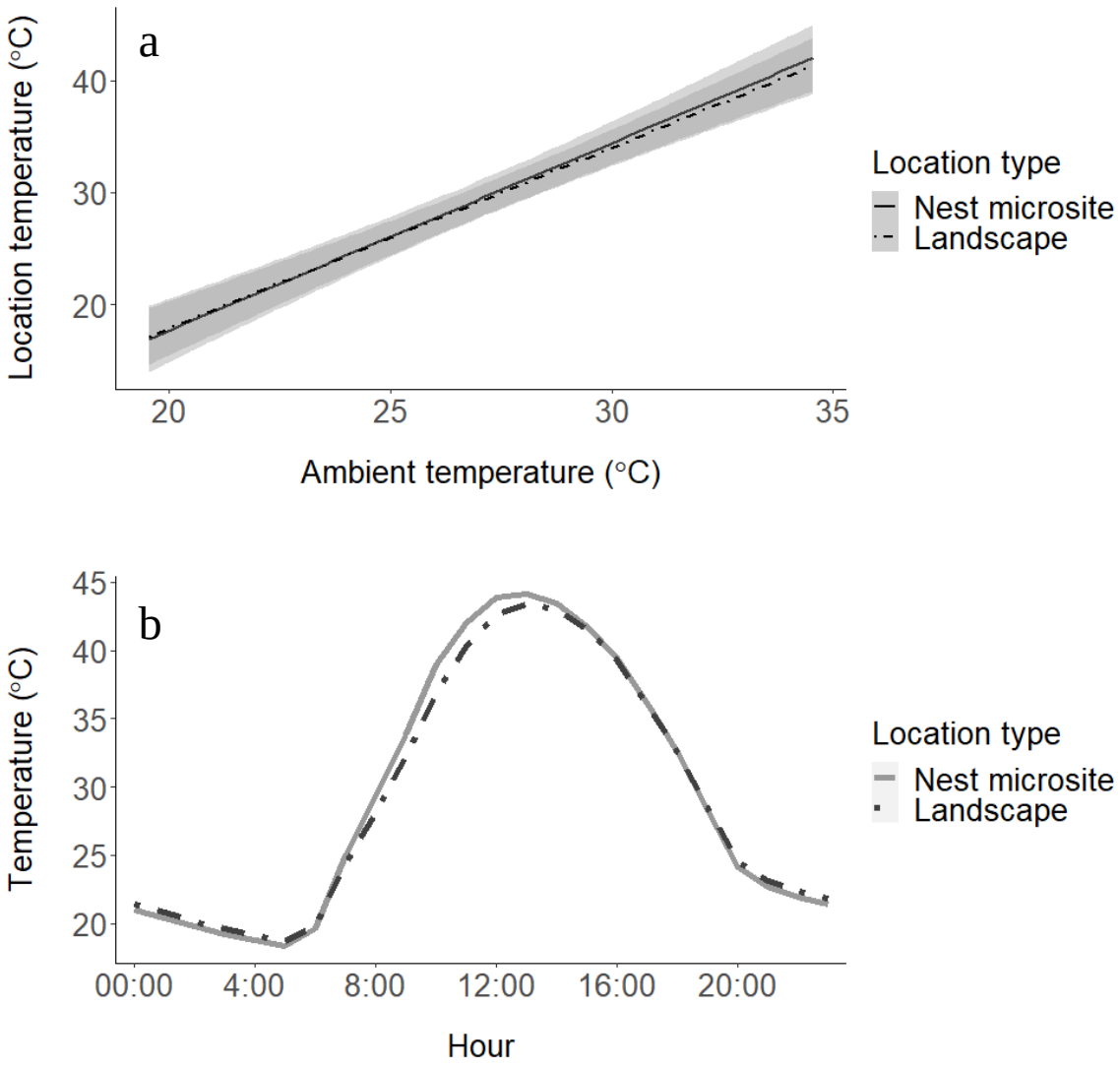

Figure 2. Comparison of temperatures between scaled quail (*Callipepla squamata*) nest microsites (10 m radius around the nest bowl) and the landscape a) across different ambient temperatures and b) across each hour of the day. Temperatures were modeled based on the interactive effects of ambient temperature (°C) and solar radiation (kW per m^2). Thermal data were collected during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

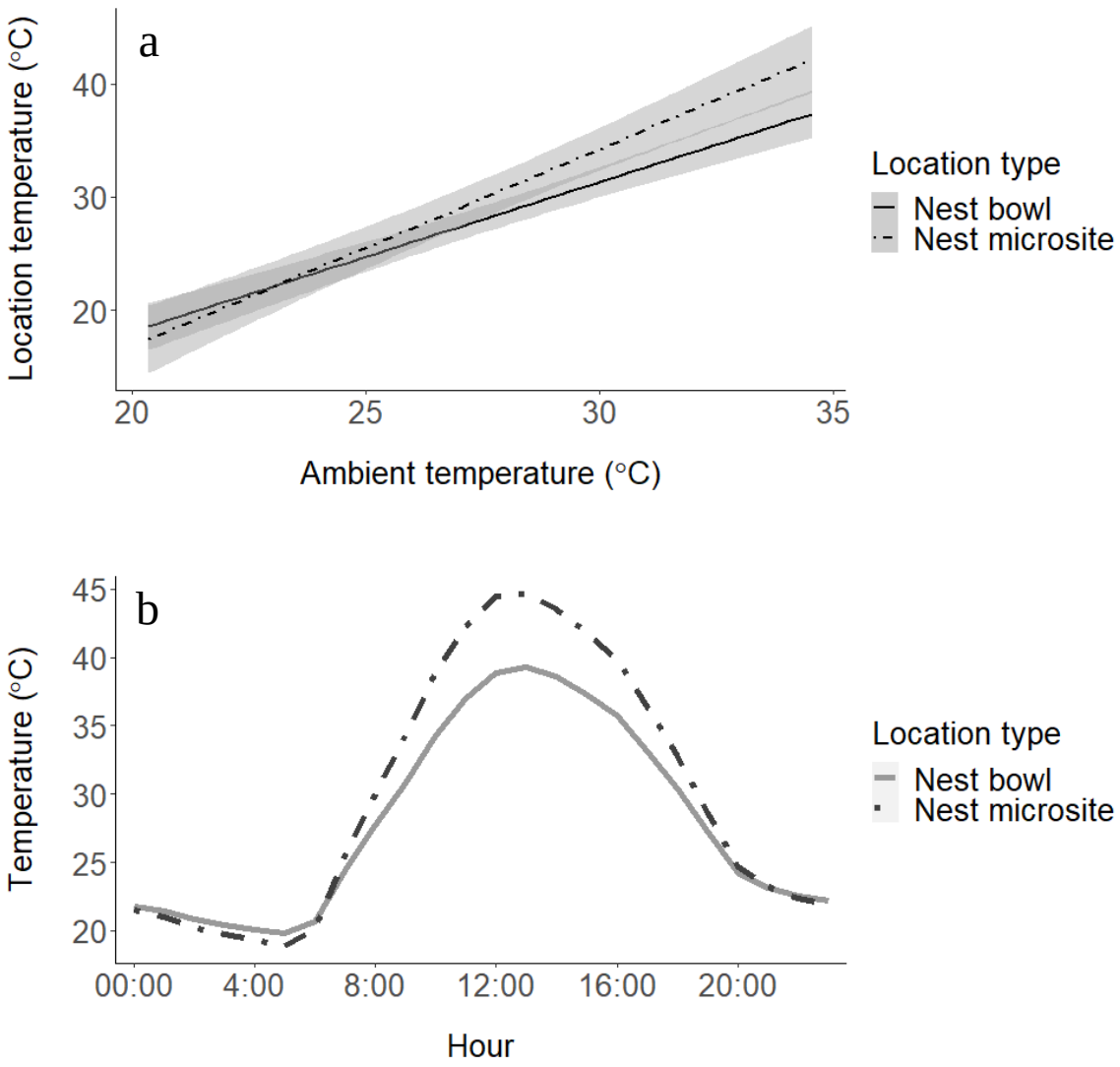

Figure 3. Comparison of temperatures between scaled quail (*Callipepla squamata*) nest bowls and the surrounding nest microsite (2-10 m) a) across different ambient temperatures and b) across each hour of the day. Temperatures were modeled based on the interactive effects of ambient temperature (°C) and solar radiation (kW per m^2). Thermal data were collected during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

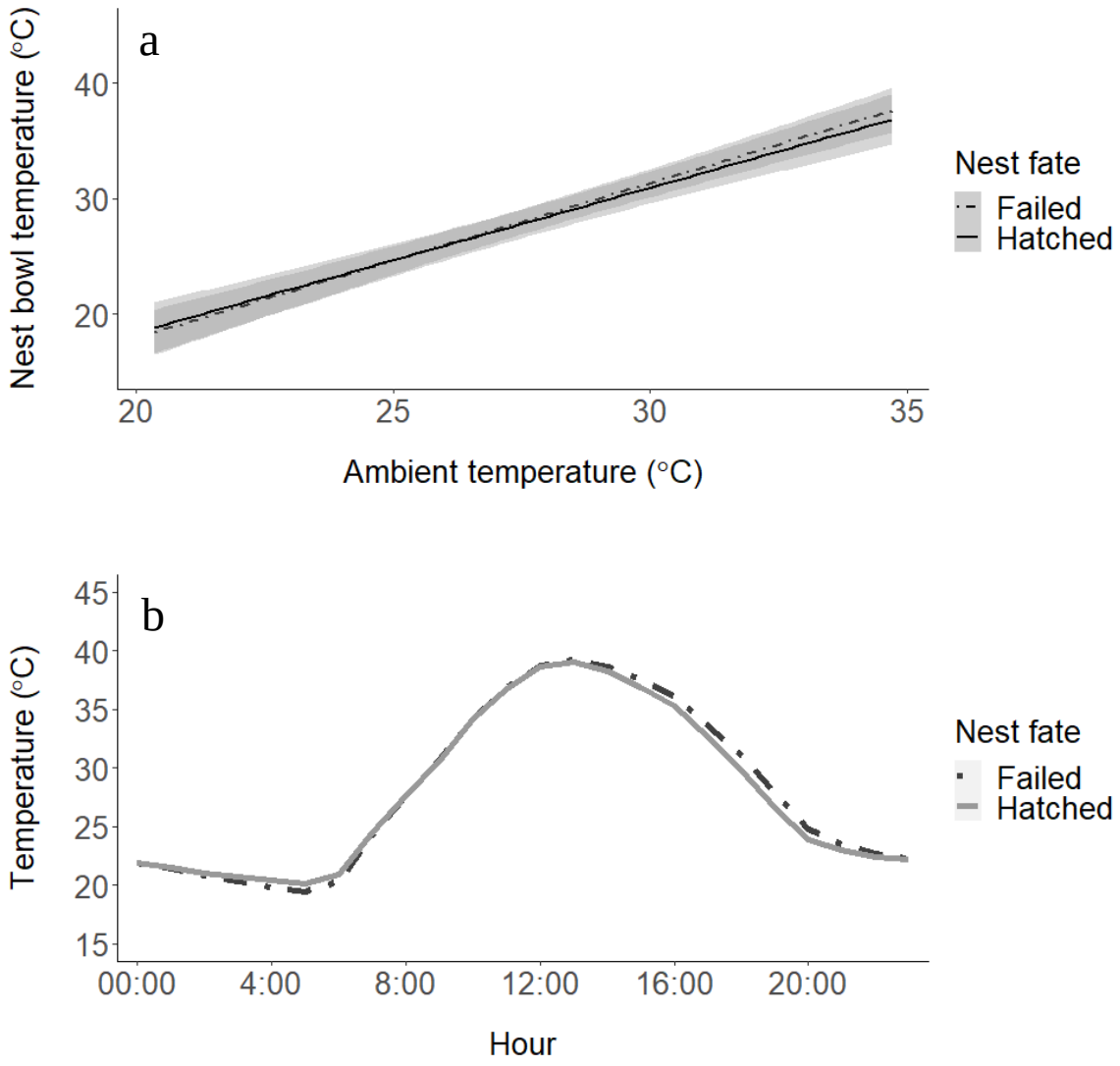

Figure 4. Comparison of nest bowl temperatures between hatched and failed scaled quail (*Callipepla squamata*) nests a) across different hours of the day and b) across each hour of the day. Temperatures were modeled based on the interactive effects of ambient temperature (°C) and solar radiation (kW/m^2). Thermal data were collected during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA.

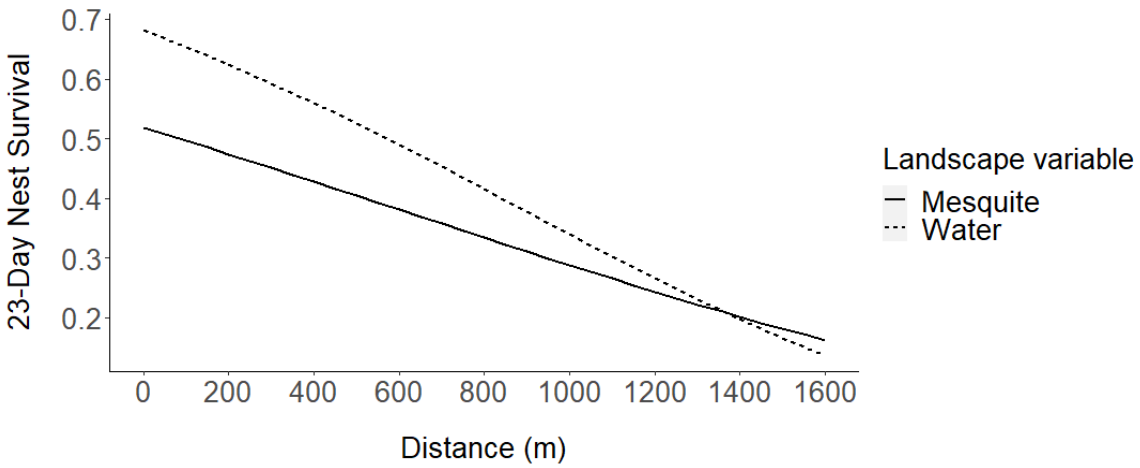

Figure 5. As distance from the nearest surface water feature or honey mesquite (*Prosopis glandulosa*) increases, the estimated survival probability of scaled quail (*Callipepla squamata*) nests decreases. These data were collected at Sand Ranch in Chaves County, New Mexico, USA during May—July of 2018 and 2019.

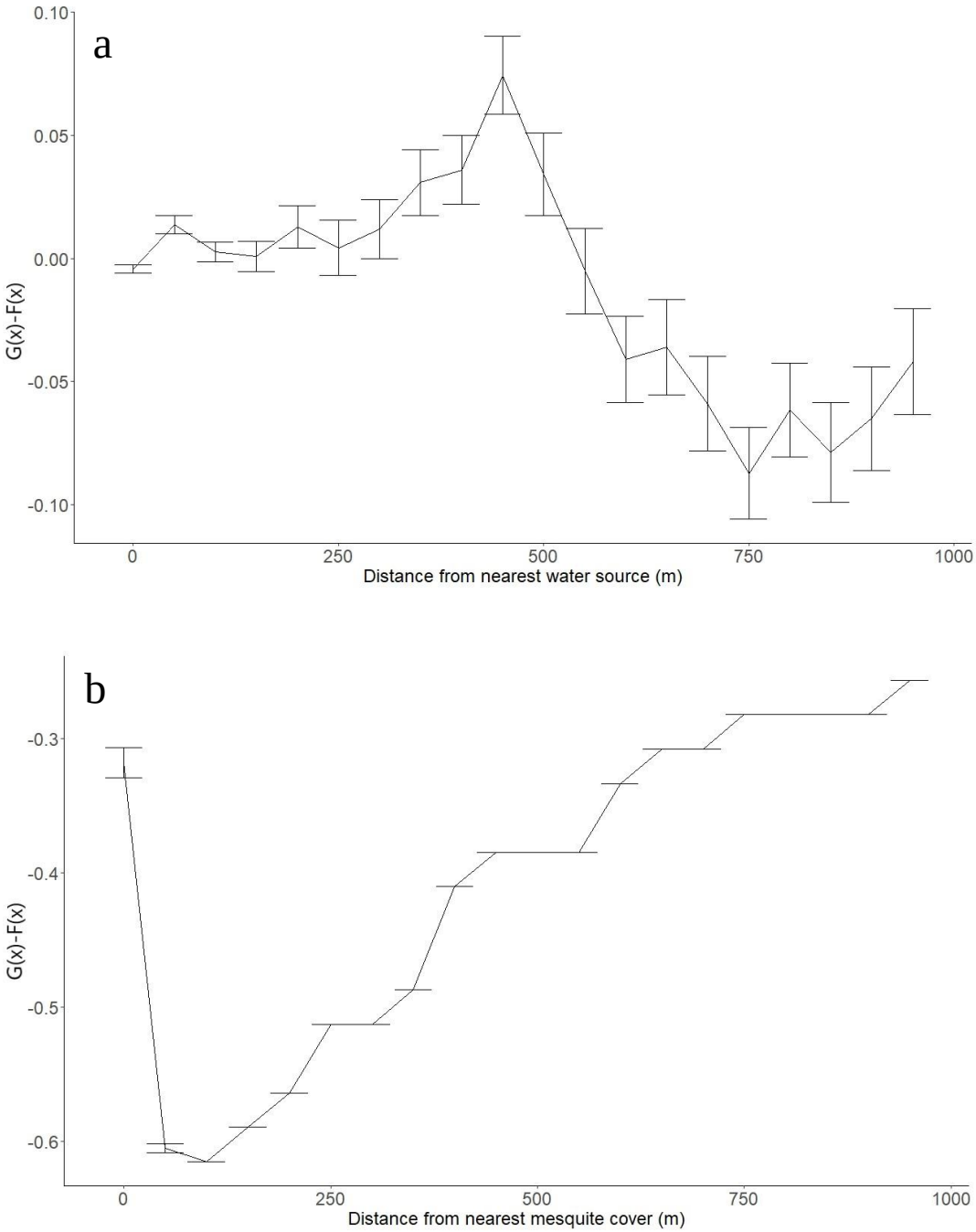

Figure 6. Cumulative distribution function [G(x) – F(x)] describing the distribution of scaled quail (*Callipepla squamata*) nests in relation to a) artificial surface water features and b) honey mesquite (*Prosopis glandulosa*) during May—July of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, 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 targeted habitat for lesser prairie-chickens (*Tympanuchus pallidicinctus*). 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 et al. 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 21 broods (*n* = 6 in 2018 and *n* = 15 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 ($D_{Brooding} = 0.71$, $D_{Non\text{-}brooding} = 0.64$) and the post-treatment mesquite layer ($D_{Brooding} = 0.56$, $D_{Non\text{-}brooding} = 0.48$) (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 ($\Delta AIC_C = 0.56$).

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**	-

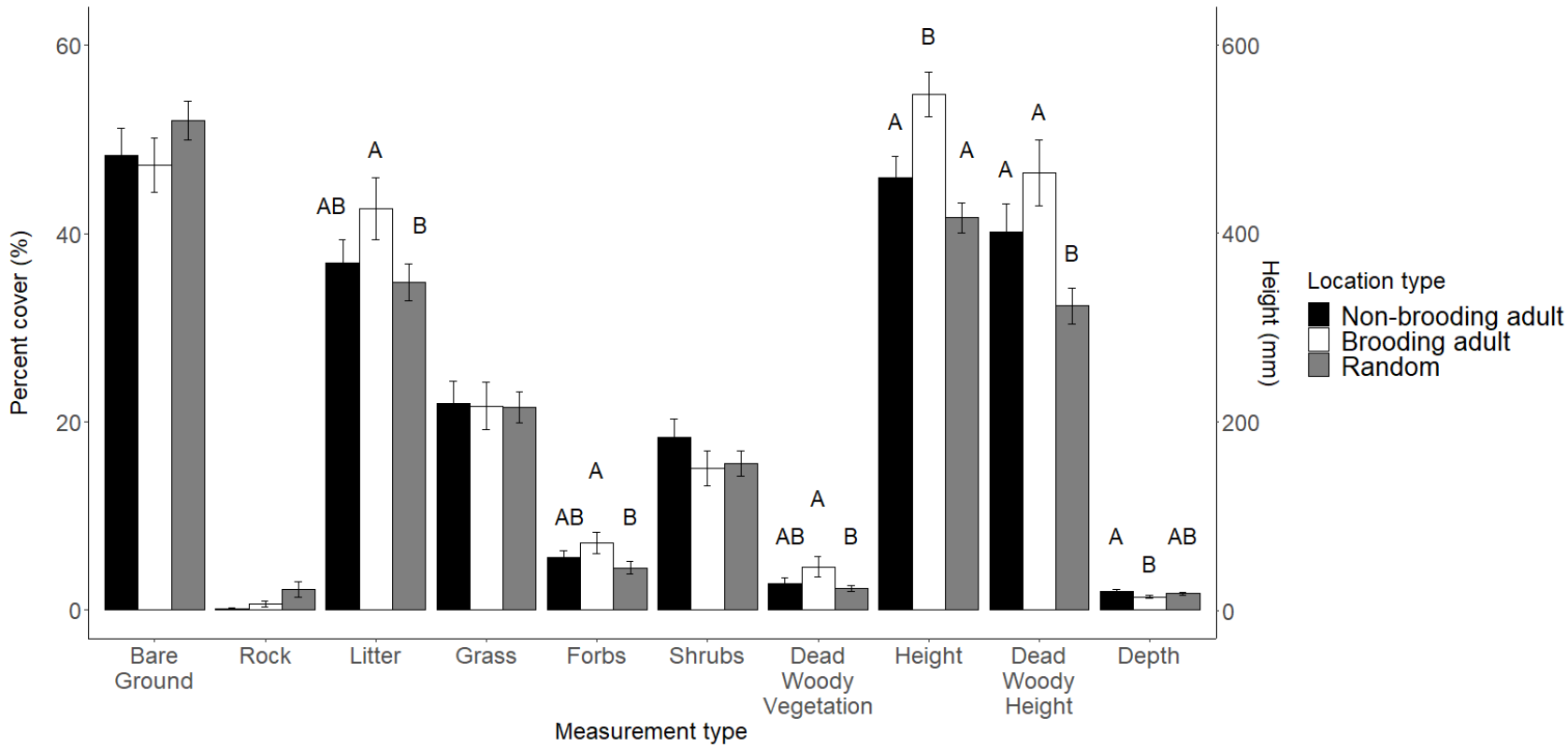

Figure 1. Mean vegetation cover and structure (along with standard errors) at locations used by non-brooding adult scaled quail (*Callipepla squamata*), locations used by brooding scaled quail, and random locations. Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves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

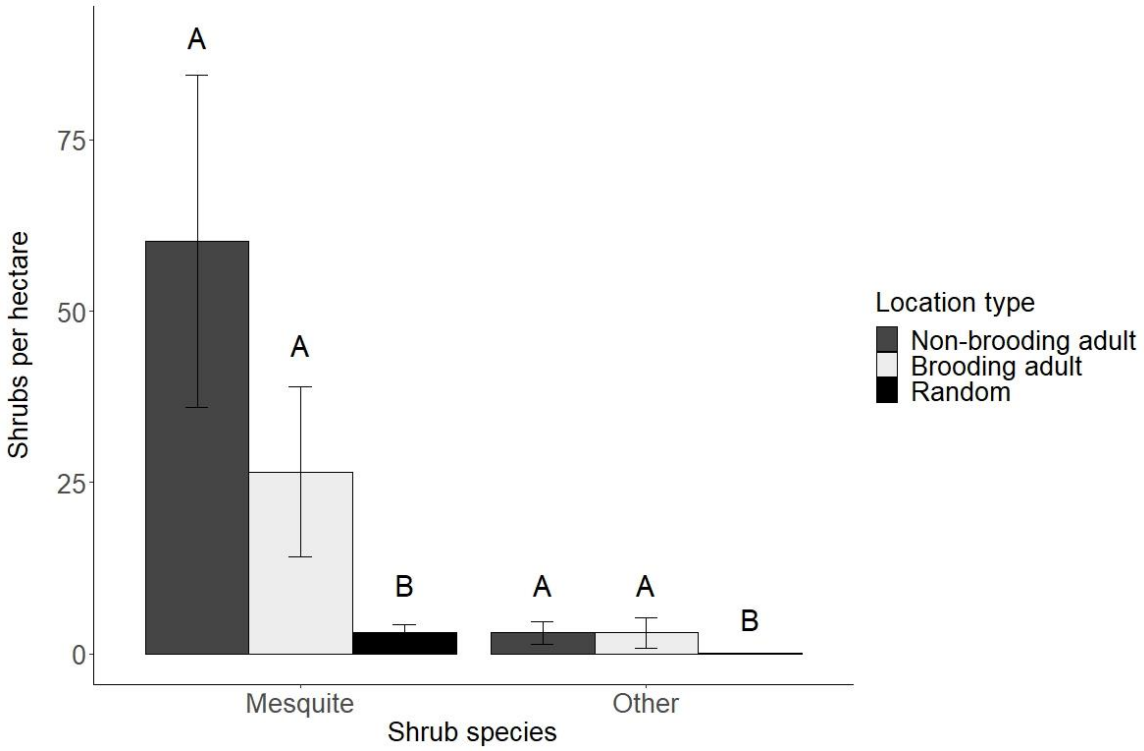

Figure 2. Mean density of tall (> 1.5 m) shrubs at locations used by non-brooding adult scaled quail (*Callipepla squamata*), locations used by brooding scaled quail, and random locations. Data were collected in 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Different letters indicate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

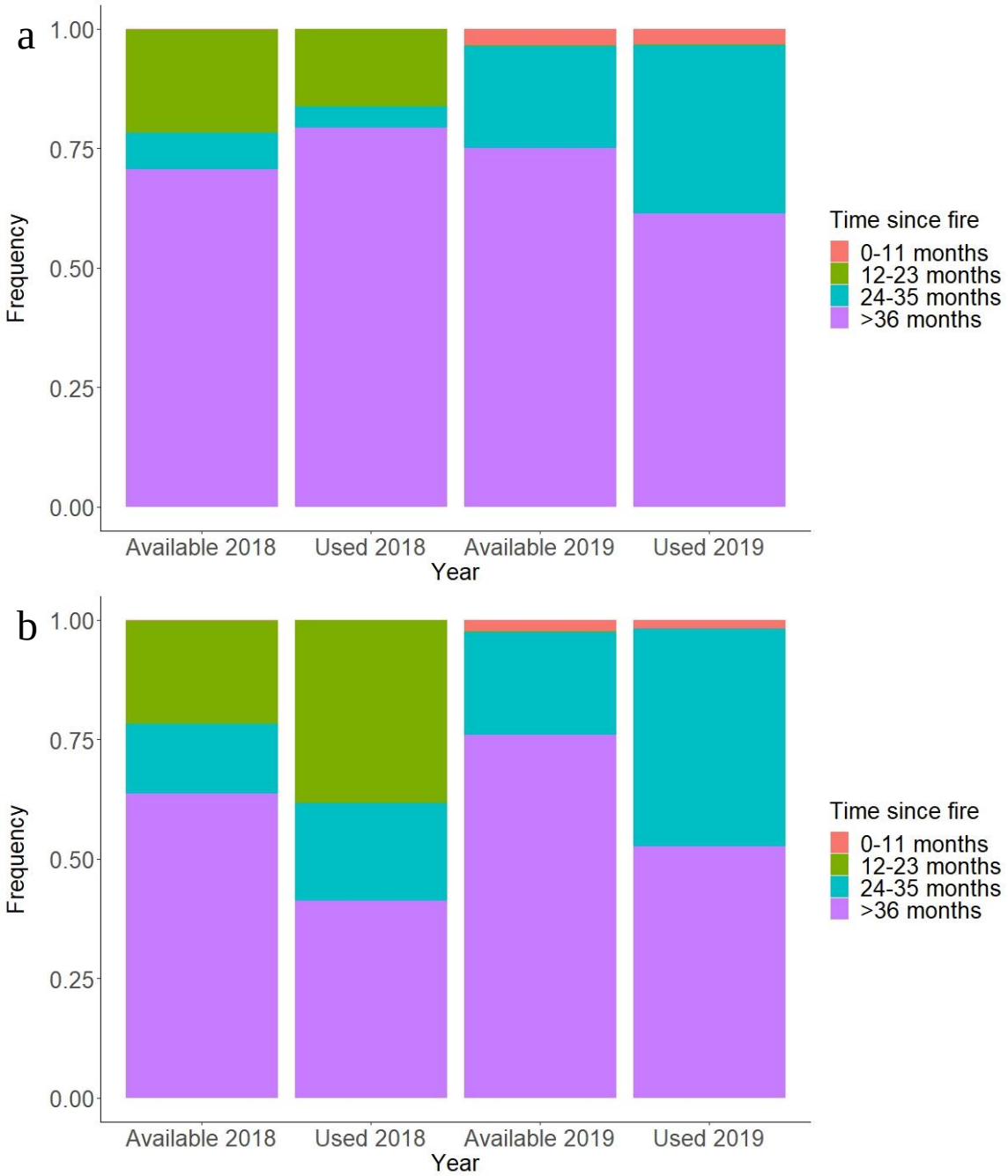

Figure 3. Use of different time since fire (TSF) by a) adult scaled quail (*Callipepla squamata*) (both brooding and non-brooding) and b) scaled quail broods at Sand Ranch in Chaves County, New Mexico, USA. Data are shown for the breeding season of 2018 (February—July) and the breeding season of 2019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

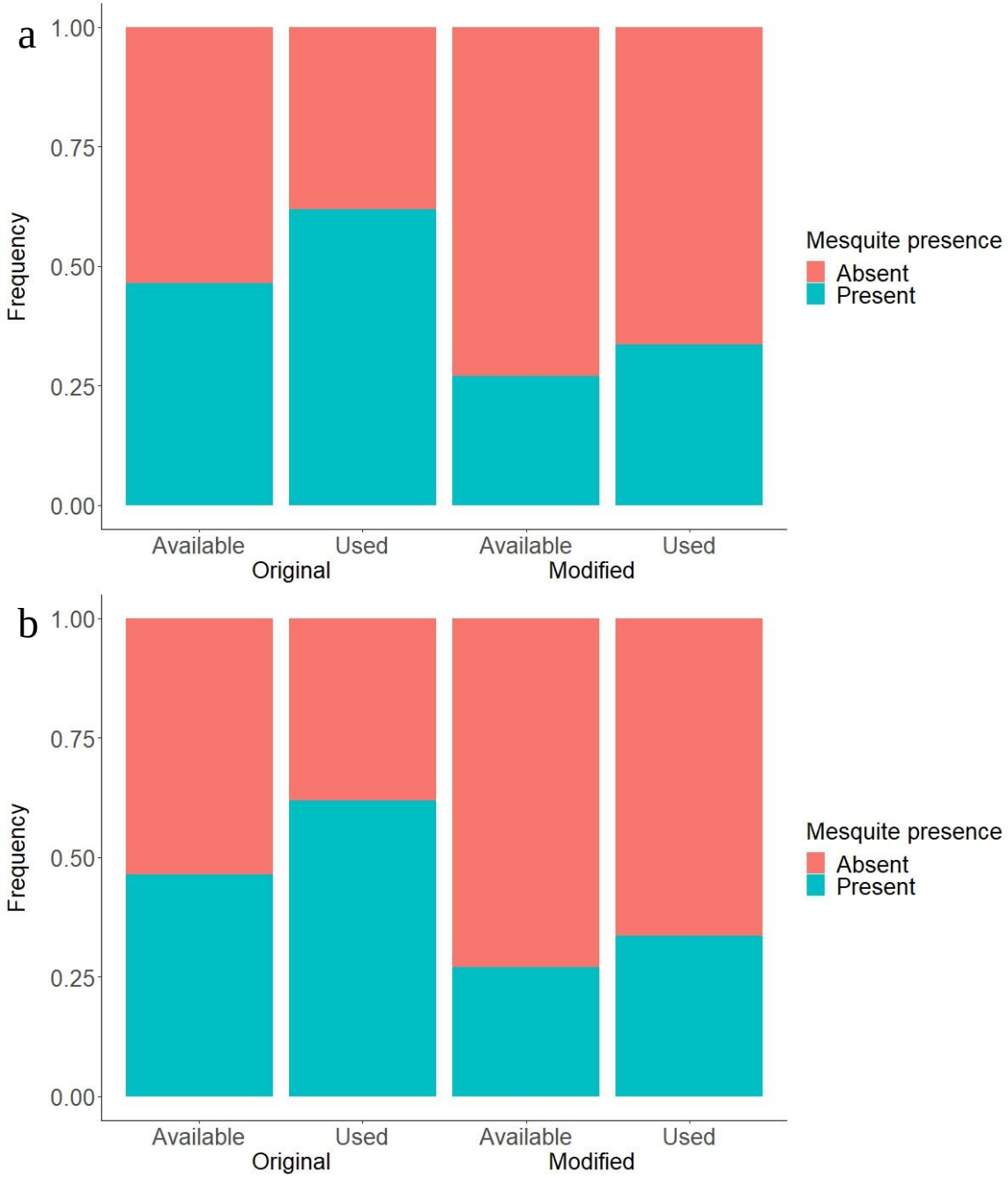

Figure 4. Use of different mesquite cover by a) adult scaled quail (*Callipepla squamata*) (both brooding and non-brooding) and b) scaled quail broods. Data were collected during the breeding seasons of 2018 and 2019 at Sand Ranch in Chaves County, New Mexico, USA. Data are presented for two datasets: 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.

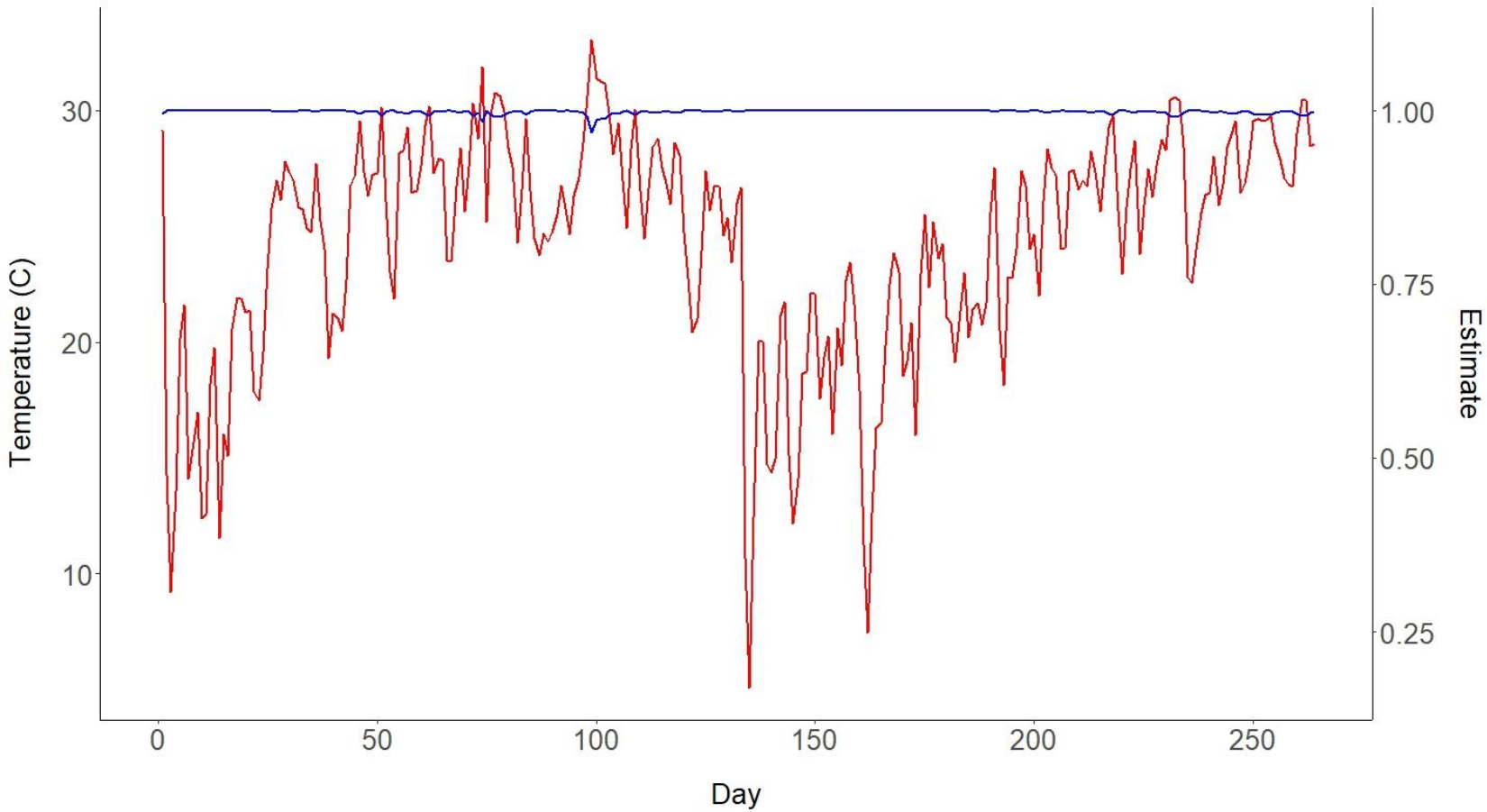

Figure 5. Influence of average daily temperature on estimated daily survival rate (DSR) of scaled quail (*Callipepla squamata*) (both brooding and non-brooding) at Sand Ranch in Chaves County, New Mexico, USA. Data were collected during the breeding seasons of 2018 (days 0 to 132) and 2019 (days 133 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).

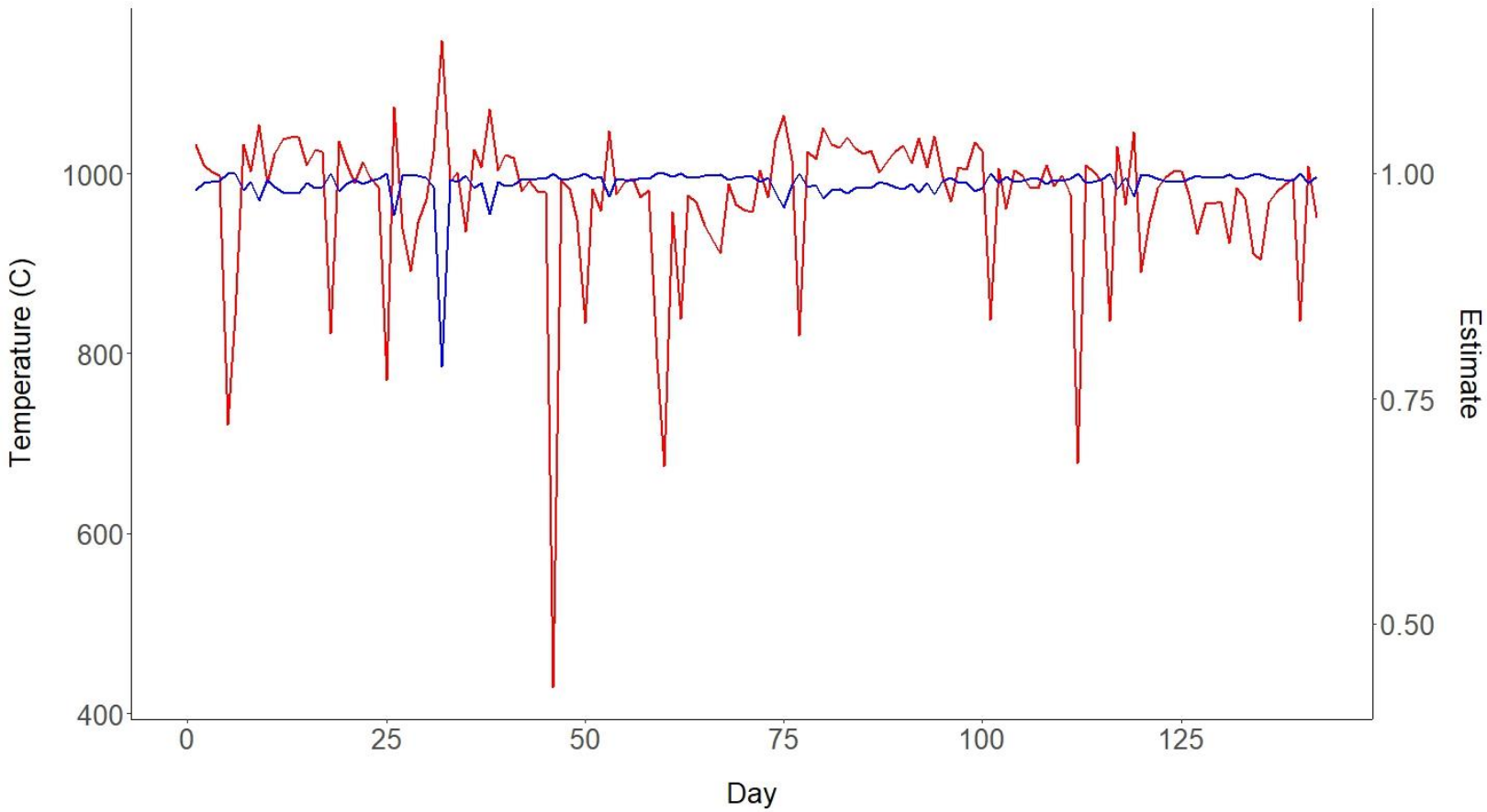

Figure 6. Influence of maximum daily solar radiation on estimated daily survival rate (DSR) of scaled quail (*Callipepla squamata*) broods at Sand Ranch in Chaves County, New Mexico, USA. Data were collected during the breeding seasons of 2018 (days 0 to 132) and 2019 (days 133 to 264). The red line 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.

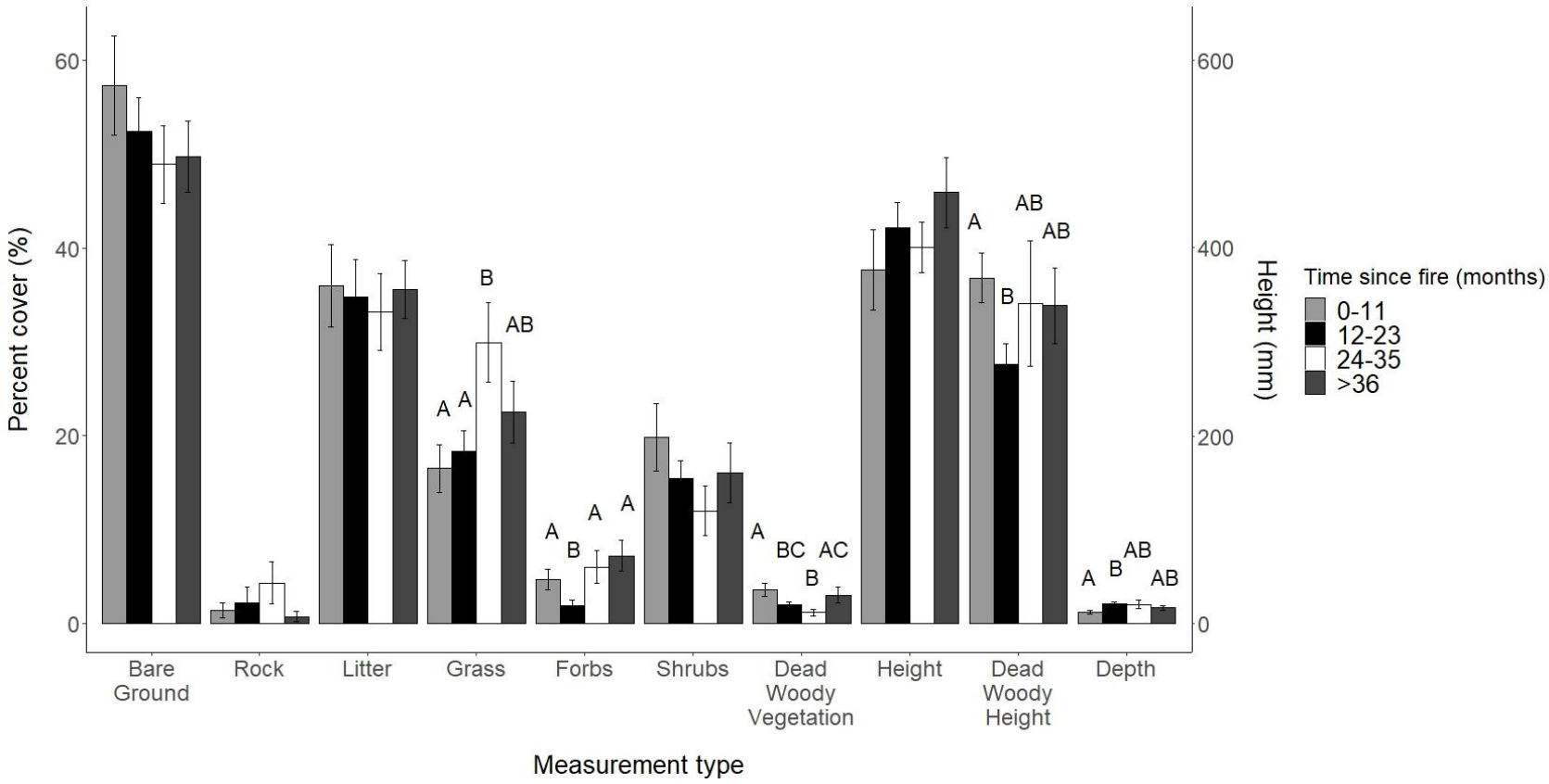

Figure 7. Mean vegetation cover and structure (along with standard errors) across different times since fire (TSF) at Sand Ranch in Chaves County, New Mexico, USA. Data were collected in May—July of 2018 and 2019. Different letters indicate statistical significance at $p < 0.05$.

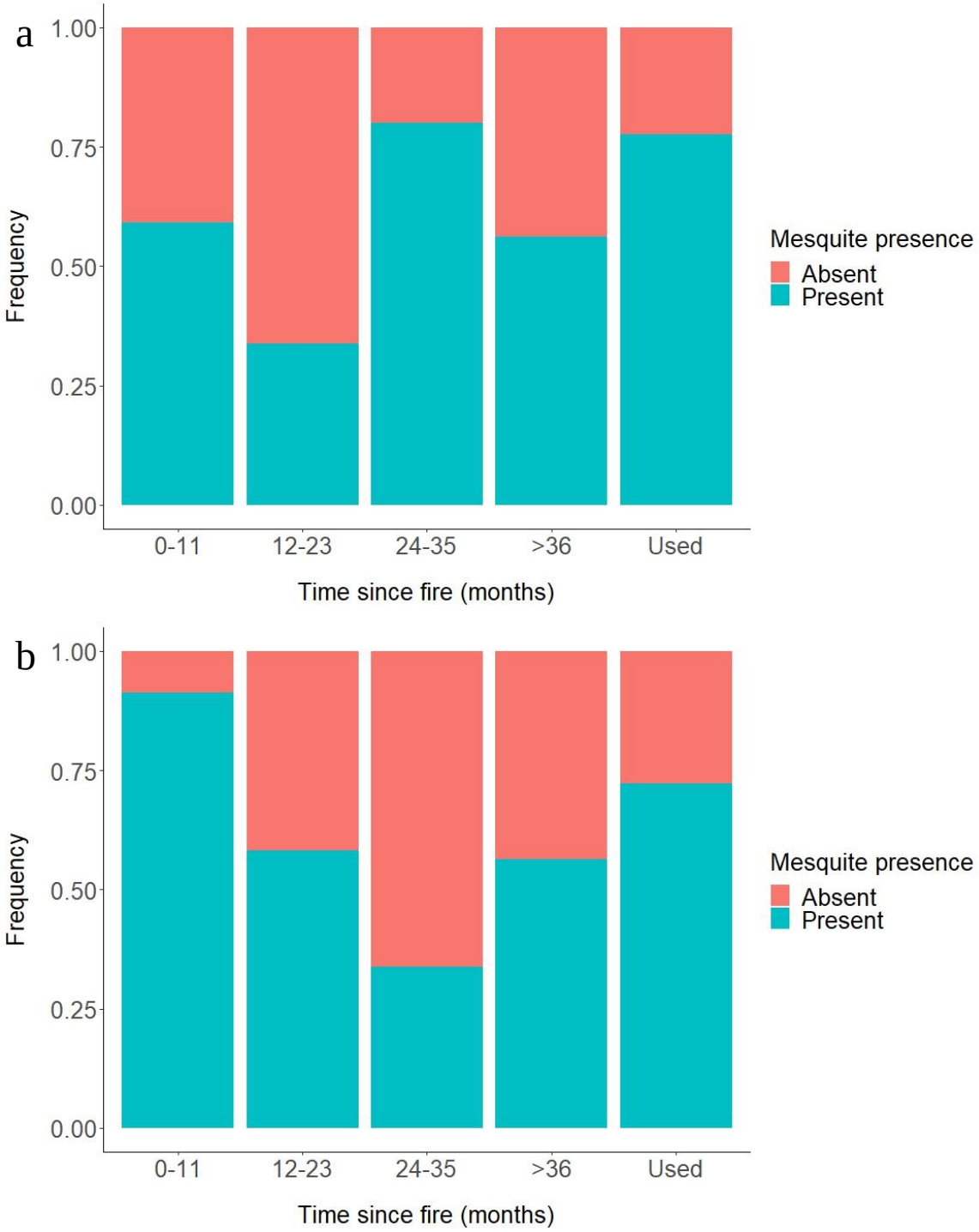

Figure 8. Availability of mesquite cover within each time since fire (TSF) category in a) 2018 and b) 2019 at Sand Ranch in Chaves County, New Mexico, USA. The frequency of all adult quail locations (brooding and non-brooding) in mesquite cover is included for reference. Frequency of mesquite in each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

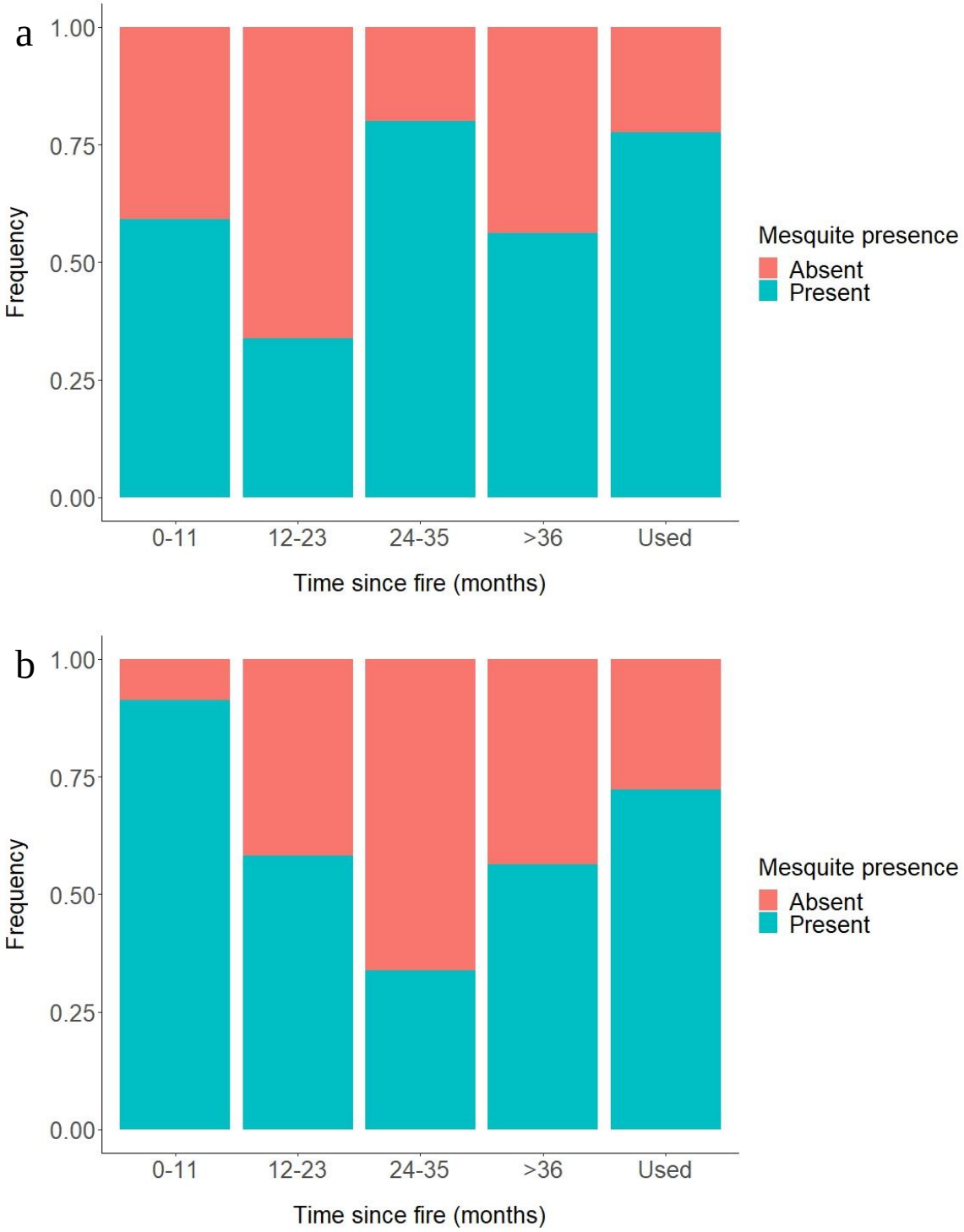

Figure 9. Availability of mesquite cover within each time since fire (TSF) category in a) 2018 and b) 2019 at Sand Ranch in Chaves County, New Mexico, USA. The frequency of all adult quail locations (brooding and non-brooding) in mesquite cover is included for reference. Frequency of mesquite in each 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.

REFERENCES

Aebischer, N.J., P.A. Robinson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Allred, B.W., S.D. Fuhlendorf, T.J. Hovick, R.D. Elmore, D.M. Engle, and A. Joern. 2013. Conservation implications of native and introduced ungulates in a changing climate. Global Change Biology 19:1875-1883.

Angilletta Jr., M.J., M.W. Sears, and R.M. Pringle. 2009. Spatial dynamics of nesting behavior: Lizards shift microhabitats to construct nests with beneficial thermal properties. Ecology 90:2933-2939.

Ansley, R.J., M. Mirik, C.B. Heaton, and X.B. Wu. 2013. Woody cover and grass production in a mesquite savanna: geospatial relationships and precipitation. Rangeland Ecology and Management 66:621-633.

Ansley, R.J., W.E. Pinchak, W.R. Teague, B.A. Kramp, D.L. Jones, and P.W. Jacoby. 2004. Long-term grass yields following chemical control of honey mesquite. Rangeland Ecology and Management 57:49-57.

Bakken, G.S. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist 32:194-216.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Behny, A.C., C.W. Boal, H.A. Whitlaw, and D.R. Lucia. 2012. Raptor community composition in the Texas Southern High Plains lesser prairie-chicken range. Wildlife Society Bulletin 36:291-296.

Belnap, S.C., J.P. Currea, and R. Lickliter. 2019. Prenatal incubation temperature affects neonatal precocial birds' locomotor behavior. Physiology & Behavior 206:51-58.

Bennie, J., B. Huntley, A. Wiltshire, M.O. Hill, and R. Baxter. 2008. Slope, aspect, and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. Ecological Modelling 216:47-59.

Bestelmeyer, B.T., D.P.C. Peters, S.R. Archer, D.M. Browning, G.S. Okin, R.L. Schooley, and N.P. Webb. 2018. The grassland-shrubland regime shift in the southwestern United States: misconceptions and their implications for management. BioScience 68:678-690.

Blomquist, S.M, and M.L. Hunter. 2010. A multi-scale assessment of amphibian habitat selection: Wood frog response to timber harvesting. Ecoscience 17:251-264.

Borchelt, P., and R.K. Ringer. 1973. Temperature regulation development in bobwhite quail (*Colinus virginianus*). Poultry Science 52:793-798.

Boyd, C.S., and T.G. Bidwell. 2001. Influence of prescribed fire on lesser prairie-chicken habitat in shinnery oak communities in western Oklahoma. Wildlife Society Bulletin 29:938-947.

Brennan, L.A. 1994. Broad-scale population declines in four species of North American quail: an examination of possible causes. Sustainable ecological systems: implementing an ecological approach to land management. USDA Forest Service General Technical Report RM-247:44-50.

Bridges, A.S., M.J. Peterson, N.J. Silvy, F.E. Smeins, and X.B. Wu. 2001. Differential influence of weather on regional quail abundance in Texas. The Journal of Wildlife Management 65:10-18.

Bristow, K.D., and R.A. Ockenfels. 2006. Fall and winter habitat use by scaled quail in southeastern Arizona. Rangeland Ecology and Management 59:308-313.

Brown, C.R., and M.B. Brown. 2000. Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). Behavioral Ecology and Sociobiology 47:339-345

Brown, M., and C.T. Downs. 2003. The role of shading behaviour in the thermoregulation of breeding crowned plovers (*Vanellus coronatus*). Journal of Thermal Biology 28:51-58.

Bures, S. and V. Pavel. 2003. Do birds behave in order to avoid disclosing their nest site? Bird Study 50:73-77.

Burhans, D.E. 2000. Avoiding the nest: responses of field sparrows to the threat of nest predation. The Auk 117:803-806.

Burnham, K.P, and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Cable, D.R. 1967. Fire effects on semidesert grasses and shrubs. Rangeland Ecology and Management/Journal of Range Management Archives 20:170-176.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519.

Campbell, H.C. 1960. An evaluation of gallinaceous guzzlers for quail in New Mexico. The Journal of Wildlife Management 24:21-26.

Campbell, H., and B.K. Harris. 1965. Mass population dispersal and long-distance movements in scaled quail. The Journal of Wildlife Management 29:801-805.

Campbell, H. 1968. Seasonal precipitation and scaled quail in eastern New Mexico. The Journal of Wildlife Management 32:641-644.

Campbell, H., D.K. Martin, P.E. Ferkovich, and B.K. Harris. 1973. Effects of hunting and some other environmental factors on scaled quail in New Mexico. Wildlife Monographs 34:3-49.

Campbell, R.E., M.B. Baker, Jr., P.F. Ffolliott, F.R. Larson, and C.C. Avery. 1977. Wildfire effects on a ponderosa pine ecosystem: an Arizona case study. Research Paper RM-191. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Carroll, J.M., C.A. Davis, R.D. Elmore, and S.D. Fuhlendorf. 2015*a*. A ground-nesting galliform's response to thermal heterogeneity: implications for ground-dwelling birds. PLoS ONE 10(11):e0143676.

Carroll, J.M., C.A. Davis, R.D. Elmore, S.D. Fuhlendorf, and E.T. Thacker. 2015*b*. Thermal patterns constrain diurnal behavior of a ground-dwelling bird. Ecosphere 6:1-15.

Carroll, J.M., C.A. Davis, R.D. Elmore, and S.D. Fuhlendorf. 2017*a*. Response of northern bobwhite movements to management-driven disturbance in a shrub-dominated ecosystem. Rangeland Ecology and Management 70:175-182.

Carroll, J.M., T.J. Hovick, C.A. Davis, R.D. Elmore, and S.D. Fuhlendorf. 2017*b*. Reproductive plasticity and landscape heterogeneity benefit a ground-nesting bird in a fire-prone ecosystem. Ecological Applications 27:2234-2244.

Carroll, R.L., C.A. Davis, S.D. Fuhlendorf, R.D. Elmore, S.E. DuRant, and J.M. Carroll. 2018. Avian parental behavior and nest success influenced by temperature fluctuations. Journal of Thermal Biology 74:140-148.

Coates, P.S. and D.J. Delehanty. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. The Condor 110:627-638.

Coe, B.H., M.L. Beck, S.Y. Chin, C.M.B. Jachowski, and W.A. Hopkins. 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. Journal of Avian Biology 46:385-394.

Coffman, J.M., B.T. Bestelmeyer, J.F. Kelly, T.F. Wright, and R.L. Schooley. 2014. Restoration practices have positive effects on breeding bird species of concern in the Chihuahuan Desert. Restoration Ecology 22:336-344.

Conway, C.J., and T.E. Martin. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54:670-685.

Cooch, E.G., and G.C. White. 2019. Program MARK: a gentle introduction. 19th ed. Retrieved 17 September 2019 from http://www.phidot.org/software/mark/docs/book/.

Cottam, G., and J.T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

Daubenmire, R. 1959. Canopy coverage method of vegetation analysis. Northwest Science 33:43-64.

Davis, C.A., T.Z. Riley, R.A. Smith, H.R. Suminski, and M.J. Wisdom. 1979. Habitat evaluation of lesser prairie-chickens in eastern Chaves County, New Mexico. New Mexico State University Agricultural Experiment Station, Las Cruces, New Mexico, USA.

Dinsmore, S.J., G.C. White, and F.L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476-3488.

Doxon, E.D., and J.P. Carroll. 2010. Feeding ecology of ring-necked pheasant and northern bobwhite chicks in Conservation Reserve Program fields. Journal of Wildlife Management 74:249-256.

Du, W.G., S.J. Yan, and X. Ji. 2000. Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, *Eumeces elegans*. Journal of Thermal Biology 25:197-202.

Dunkin, S.W., F.S. Guthery, S.J. DeMaso, A.D. Peoples, and E.S. Parry. 2009. Influence of anthropogenic structures on northern bobwhite space use in western Oklahoma. Journal of Wildilfe Management 73:253-259.

Duquette, C.A., C.A. Davis, S.D. Fuhlendorf, and R.D. Elmore. 2019. Northern bobwhite (*Colinus virginianus*) space use minimally affected by oil and gas development. Rangeland Ecology and Management 72:484-491.

DuRant, S.E., W.A. Hopkins, A.F. Wilson, and G.R. Hepp. 2012. Incubation temperature affects the metabolic cost of thermoregulation in a young precocial bird. Functional Ecology 26:416-422.

Elmore, R.D., J.M. Carroll, E.P. Tanner, T.J. Hovick, B.A. Grisham, S.D. Fuhlendorf, and S.K. Windels. 2017. Implications of the thermal environment for terrestrial wildlife management. Wildlife Society Bulletin 41:183-193.

ESRI 2020. ArcGIS Pro: version 2.5.0. Redlands, CA: Environmental Systems Research Institute.

Falkowski, M.J., J.S. Evans, D.E. Naugle, C.A. Hagen, S.A. Carleton, J.D. Maestas, A.H. Khalyani, A.J. Poznanovic, and A.J. Lawrence. 2017. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecololgy and Management 70:15-24.

Fogarty, D.T., R.D. Elmore, S.D. Fuhlendorf, and S.R. Loss. 2017. Influence of olfactory and visual cover on nest site selection and nest success for grassland-nesting birds. Ecology and Evolution 7:6247-6258.

Fogarty, D.T., R.D. Elmore, S.D. Fuhlendorf, and S.R. Loss. 2018. Variation and drivers of airflow patterns associated with olfactory concealment and habitat selection. Ecology 99:289-299.

French, N.A. 2000. Effects of short periods of high incubation temperature on hatchability and incidence of embryo pathology of turkey eggs. British Poultry Science 41:377-382.

Fulbright, T.E., H.N. Kline, D.B. Wester, E.D. Grahmann, F. Hernandez, L.A. Brennan, and M.W. Hehman. 2019. Non-native grasses reduce scaled quail habitat. The Journal of Wildlife Management 83(7): 1581-1591.

Geiger, R. 1965. The climate near the ground. Harvard University Press, Cambridge Massachusetts, USA.

Germano, D.J., R. Hungerford, and S.C. Martin. 1983. Responses of selected wildlife species to the removal of mesquite from desert grassland. Journal of Range Management 36:309-311.

Ghalambor, C.K., and T.E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494-497.

Gibbens, R.P. C.H. Herbel, H.L. Morton, W.C. Lindemann, J.A. Ryder-White, D.B. Richman, E.W. Huddleston, W.H. Conley, C.A. Davis, J.A. Reitzel, D.M. Anderson, and A. Guiao. 1986. Some impacts of 2, 4, 5-T on a mesquite duneland ecosystem in southeastern New Mexico: a synthesis. Rangeland Ecology and Management/Journal of Range Management Archives 39:320-326.

Giuliano, W.M., and R.S. Lutz. 1993. Quail and rain: what’s the relationship? National Quail Symposium Proceedings 3:64-68.

Giuliano, W.M., R. Patiño, and R.S. Lutz. 1998. Comparative reproductive and physiological responses of northern bobwhite and scale quail to water deprivation. Comparative Biochemistry and Physiology 119:781-786.

Goldstein, D.L. 1984. The thermal environment and its constraint on activity of desert quail in summer. The Auk 101:542-550.

Goodwin, J.G., Jr., and C.R. Hungerford. 1977. Habitat use by native Gambel's and scaled quail and released masked bobwhite quail in southern Arizona. Research Paper RM-197. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Grisham, B.A., P.K. Borsdorf, C.W. Boal, and K.K. Boydston. 2014. Nesting ecology and nest survival of lesser prairie-chickens on the Southern High Plains of Texas. Journal of Wildlife Management 78:857-866.

Grisham, B.A., A.J. Godar, C.W. Boal, and D.A. Haukos. 2016. Interactive effects between nest microclimate and nest vegetation structure confirm microclimate thresholds for lesser prairie-chicken nest survival. The Condor 118:728-746.

Guthery F.S., T.B. Doerr, and M.A. Taylor. 1981. Use of a profile board in sand shinnery oak communities. Journal of Range Management 34:157-158.

Guthery, F.S. 1986. Beef, brush and bobwhites: quail management in cattle country. Golden Banner Press, Corpus Christi, Texas, USA.

Guthery, F.S. and N.E. Koerth. 1992. Substandard water intake and inhibition of bobwhite reproduction during drought. Journal of Wildlife Management 56:760-768.

Guthery, F.S., N.M. King, W.P. Kuvlesky, Jr., S. DeStefano, S.A. Gall, and N.J. Silvy. 2001. Comparative habitat use by three quails in desert grassland. The Journal of Wildlife Management 65:850-860.

Guthery, F.S., A.R. Rybak, S.D. Fuhlendorf, T.L. Hiller, S.G. Smith, W.H. Puckett, Jr., and R.A. Baker. 2005. Aspects of the thermal ecology of bobwhites in north Texas. Wildlife Monographs 159:1-36.

Hagen, C.A., B.E. Jamison, K.M. Giesen, and T.Z. Riley. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. The Wildlife Society Bulletin 32:69-82.

Hall, L.E., A.D. Chalfoun, E.A. Beever, and A.E. Loosen. 2016. Microrefuges and the occurrence of thermal specialists: implications for wildlife persistence amidst changing temperatures. Climate Change Responses 3:1-12.

Harrell, W.C., and S.D. Fuhlendorf. 2002. Evaluation of habitat structural measures in a shrubland community. Journal of Range Management 55:488-493.

Henderson, C.W. 1971. Comparative temperature and moisture responses in Gambel's and scaled quail. The Condor 73:430-436.

Hiller, T.L., and F.S. Guthery. 2005. Microclimate versus predation risk in roost and covert selection by bobwhites. Journal of Wildlife Management 69:140-149.

Hollister, E.B., C.W. Schadt, A.V. Palumbo, R.J. Ansley, and T.W. Boutton. 2010. Structural and functional diversity of soil bacterial and fungal communities following woody plant encroachment in the southern Great Plains. Soil Biology and Biochemistry 42:1816-1824.

Horel, J., M. Splitt, L. Dunn, J. Pechmann, B. White, C. Ciliberti, S. Lazarus, J. Slemmer, D. Zaff, and J. Burks. 2002. MesoWest: cooperative mesonets in the western United States. Bulletin of the American Meteorological Society 83:211-226.

Hovick, T.J., R.D. Elmore, B.W. Allred, S.D. Fuhlendorf, and D.K. Dahlgren. 2014. Landscapes as a moderator of thermal extremes: a case study from an imperiled grouse. Ecosphere 5:1-12.

Hurst, G.A. 1972. Insects and bobwhite quail brood Habitat Management. National Quail Symposium Proceedings 1:13.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413-417.

Johnsgard, P.A. 2017. The North American Quails, Partridges, and Pheasants. Zea E-Books. 58. Retrieved 23 October 2017 at http://digitalcommons.unl.edu/zeabook/58.

Kline, H.N., T.E. Fulbright, E.D. Grahmann, F. Hernandez, D.B. Wester, L.A. Brennan, and M.W. Hehman. 2019. Temperature influences resource use by chestnut-bellied scaled quail. Ecosphere 10:1-16.

Kopp, S.D., F.S. Guthery, N.D. Forrester, and W.E. Cohen. 1998. Habitat selection modeling for northern bobwhites on subtropical rangeland. The Journal of Wildlife Management 62:884-895.

Limb, R.F., S.D. Fuhlendorf, and D.E. Townsend. 2009. Heterogeneity of thermal extremes: driven by disturbance or inherent in the landscape. Environmental Management 43:100-106.

Londe, D.W., S.D. Fuhlendorf, R.D. Elmore, C.A. Davis, and J. Rutledge. 2019. Female greater prairie-chicken response to energy development and rangeland management. Ecosphere 10:1-21.

Londoño, G.A., D.J. Levey, and S.K. Robinson. 2008. Effects of temperature and food on incubation behavior of the northern mockingbird, *Mimus polyglottos*. Animal Behavior 76:669-677.

Long, A.M., W.E. Jensen, and R.S. Matlack. 2012. Effects of prescribed burning on avian nest survival in the southern Great Plains. The Journal of Wildlife Management 76:899-906.

Lusk, J.J., F.S. Guthery, S.A. Cox, S.J. DeMaso, and A.D. Peoples. 2005. Survival and growth of northern bobwhite chicks in western Oklahoma. The American Midland Naturalist 153:389-395.

Lusk, J.J., F.S. Guthery, R.R. George, M.J. Peterson, and S.J. DeMaso. 2002. Relative abundance of bobwhites in relation to weather and land use. The Journal of Wildlife Management 66(4):1040-1051.

Lyon, B.E., and R.D. Montgomerie. 1987. Ecological correlates of incubation feeding: a comparative study of high arctic finches. Ecology 68:713-722.

Martin, J.A., J.K. Burkhart, R.E. Thackston, and J.P. Carroll. 2015. Exotic grass alters micro-climate and mobility for northern bobwhite chicks. The Wildlife Society Bulletin 39:834-839.

Martin, T.E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London B 267:2287-2293.

Martin, T.E., and C.K. Ghalambor. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? The American Naturalist 153:131-139.

McKechnie, A.E., B. Smit, M.C. Whitfield, M.J. Noakes, W.A. Talbot, M. Garcia, A.R. Gerson, and B.O. Wolf. 2016. Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal desert specialist, Burchell's sandgrouse (*Pterocles burchelli*). Journal of Experimental Biology 219:2137-2144.

Monasmith, T.J., S. Demarais, J.J. Root, and C.M. Britton. 2010. Short-term fire effects on small mammal populations and vegetation of the northern Chihuahuan Desert. International Journal of Ecology 2010:1-9.

Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Retrieved 31 December 2017 at https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx.

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113-117.

Olson, B., S.K. Windels, M. Fulton, and R. Moen. 2014. Fine-scale temperature patterns in the southern boreal forest: implications for the cold-adapted moose. Alces 50:105-120.

Pardieck, K.L., D.J. Ziolkowski Jr., M. Lutmerding, V. Aponte and M-A.R. Hudson. 2019. North American Breeding Bird Survey Dataset 1966 - 2018, version 2018.0. U.S. Geological

Survey, Patuxent Wildlife Research Center. Retrieved 10 April 2020 at https://doi.org/10.5066/P9HE8XYJ.

Patten, M.A., D.H. Wolfe, E. Shochat, and S.K. Sherrod. 2005. Effects of microhabitat and microclimate selection on adult survivorship of the lesser prairie-chicken. Journal of Wildlife Management 69:1270-1278.

Peterson, R.S., and C.S. Boyd. 1998. Ecology and management of sand shinnery oak communities: a literature review. RMRS GTR-16. United States Department of Agriculture, Forest Service, Rocky Mountain Experiment Station, Fort Collins, Colorado, USA.

Petrone, R.M., J.S. Price, S.K. Carey, and J.M. Waddington. 2004. Statistical characterization of the spatial variability of soil moisture in a cutover peatland. Hydrological Processes 18:41-52.

Pleasant, G.D., C.B. Dabbert, and R.B. Mitchell. 2006. Ecology and survival of scaled quail in the southern high plains of Texas. The Journal of Wildlife Management 70:632-640.

PRISM Climate Group. 2019. 30-year normals. Oregon State University. Retrieved 22 November 2019 from http://www.prism.oregonstate.edu.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rakowski, A.E., R.D. Elmore, C.A. Davis, S.D. Fuhlendorf, and J.M. Carroll. 2018. Thermal refuge affects space use and movement of a large-bodied galliform. Journal of Thermal Biology 80: 37-44.

Raynor, E.J., L.A. Powell, and W.H. Schacht. 2018. Present and future thermal environments available to sharp-tailed grouse in an intact grassland. PLoS ONE 13(2): e0191233.

Reid, R.R., C.E. Grue, and N.J. Silvy. 1993. Habitat requirements of breeding scaled quail in Texas. National Quail Symposium Proceedings 3:1-6.

Reyna, K.S. 2019. Acute exposure to hyperthermic oscillating temperatures during pre-incubation influences northern bobwhite development, hatching, and survival. PLoS ONE 14(7): e0219368.

Rho, P., X.B. Wu, F.E. Smeins, N.J. Silvy, and M.J. Peterson. 2015. Regional land cover patterns, changes and potential relationships with scaled quail (*Callipepla squamata*) abundance. Journal of Ecology and the Environment 38:185-193.

Rich, P.M., W.A. Hetrick, and S.C. Saving. 1995. Modeling topographic influences on solar radiation: a manual for the SOLARFLUX model. No. LA-12989-M. Los Alamos National Lab, New Mexico, USA.

Rich, P.M., G.S. Hughes, and F.J. Barnes. 1993. Using GIS to reconstruct canopy architecture and model ecological processes in pinyon-juniper woodlands. Proceedings of the Thirteenth Annual ESRI User Converence 2:435-445.

Riera, J.L., J.J. Magnuson, J.R. Vande Castle, and M.D. MacKenzie. 1998. Analysis of large-scale spatial heterogeneity in vegetation indices among North American landscapes. Ecosystems 1:268-282.

Rollins, D. 2000. Status, ecology and management of scaled quail in West Texas. Proceedings of the National Quail Symposium 4:165-172.

Rollins, D., B.D. Taylor, T.D. Sparks, T.E. Wadell, and G. Richards. 2006. Species visitation at quail feeders and guzzlers in southern New Mexico. National Quail Symposium Proceedings 6:210-219.

Roseberry, J.L., and W.D. Klimstra. 1984. Population ecology of the bobwhite. Southern Illinois University Press, Carbondale, Illinois, USA.

Rosenstock, S.S., W.B. Ballard, and J.C. Devos, Jr. 1999. Viewpoints: benefits and impacts of wildlife water developments. Journal of Range Management 52:302-311.

Saiwana, L., J.L. Holechek, A. Tembo, R. Valdez, and M. Cardenas. 1998. Scaled quail use of different seral stages in the Chihuahuan Desert. The Journal of Wildlife Management 62:550-556.

Schemnitz, S.D. 1961. Ecology of the scaled quail in the Oklahoma Panhandle. The Wildlife Society: Wildlife Monographs 8:3-47.

Schemnitz, S.D. 1964. Comparative ecology of bobwhite and scaled quail in the Oklahoma panhandle. The American Midland Naturalist 71:429-433.

Silvy, N.J., D. Rollins, and S.W. Whisenant. 2007. Scaled Quail ecology and life history. In L.A. Brennan, editor, Texas quails: ecology and management. Texas A&M University Press, College Station, Texas, USA.

Smith, J.T., B.W. Allred, C.S. Boyd, J.C. Carlson, K.W. Davies, C.A. Hagen, D.E. Naugle, A.C. Olsen, and J.D. Tack. 2019. Are sage-grouse fine-scale specialists or shrub-steppe generalists? Journal of Wildlife Management 84:759-774.

Stoddard, H.L. 1931. The bobwhite quail: its habits, preservation and increase. Charles Scribner and Sons, New York, New York, USA.

Stormer, F.A. 1981. Characteristics of scaled quail loafing coverts in northwest Texas. Research Note RM-395. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Suggitt, A.J., P.K. Gillingham, J.K. Hill, B. Huntley, W.E. Kunin, D.B. Roy, and C.D. Thomas. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos 120:1-8.

Tanner, E.P., R.D. Elmore, S.D. Fuhlendorf, C.A. Davis, E.T. Thacker, and D.K. Dahlgren. 2015. Behavioral responses at distribution extremes: how artificial surface water can affect quail movement patterns. Rangeland Ecology and Management 68:476-484.

Tanner, E.P., R.D. Elmore, C.A. Davis, S.D. Fuhlendorf, D.K. Dahlgren, E.T. Thacker, and J.P. Orange. 2016. Does the presence of oil and gas infrastructure potentially increase risk of harvest in northern bobwhite? Wildlife Biology 22:294-304.

Tanner, E.P., R.D. Elmore, S.D. Fuhlendorf, C.A. Davis, D.K. Dahlgren, and J.P. Orange. 2017. Extreme climatic events constrain space use and survival of a ground-nesting bird. Global Change Biology 23:1832-1846.

Tanner, E.P., J.P. Orange, C.A. Davis, R.D. Elmore, and S.D. Fuhlendorf. 2019. Behavioral modifications lead to disparate demographic consequences in two sympatric species. Ecology and Evolution 00:1-17.

Tiedemann, A.R., and J.O. Klemmedson. 1973. Effect of mesquite on physical and chemical properties of the soil. Rangeland Ecology and Management/Journal of Range Management Archives 26:27-29.

Tiedemann, A.R., and J.O. Klemmedson. 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. Rangeland Ecology and Management/Journal of Range Management Archives 30:361-367.

Thomson, D.L., P. Monaghan, and R.W. Furness. 1998. The demands of incubation and avian clutch size. Biological Reviews 73:293-304.

Tracol, Y., J.R. Gutiérrez, and F.A. Squeo. 2011. Plant area index and microclimate underneath shrub species from a Chilean semiarid community. Journal of Arid Environments 75:1-6.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197-215.

Van Beest, F., B.F.A. Van Moorter, and J.M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84:723-735.

Wallmo, O.C. 1956. Ecology of scaled quail in West Texas. Texas Game and Fish Commission, 1-134.

Webb, D.R. 1987. Thermal tolerance of avian embryos: a review. The Condor 89:874-898.

White, G.C., and R.A. Garrot. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, Inc., San Diego, California, USA.

White, F.N., and J.L. Kinney. 1974. Avian incubation. Science 186:107-115.

Wilson, M.H., and J.A. Crawford. 1987. Habitat selection by Texas bobwhites and chestnut-bellied scaled quail in south Texas. The Journal of Wildlife Management 51:575-582.

Wolf, B. 2000. Global warming and avian occupancy of hot deserts; a physiological and behavioral perspective. Revista Chilena de Historia Natural 73:395-400.

United States Census Bureau. 2019. TECHNICAL DOCUMENTATION: 2019 TIGER/Line Shapefiles. Retrieved 31 March 2020 at http://proximityone.com/tiger/TGRSHP2019_TechDoc.pdf.

Young, V.A., F.R. Anderwald, and W.G. McCully. 1947. Brush problems on Texas ranges. Texas Agricultural Experiment Station, Miscellaneous Publication 21:1-19.