THE ROLE THAT CLIMATE VARIABILITY AND LANDSCAPE HETEROGENEITY HAVE ON THE MOVEMENT ECOLOGY OF NORTHERN BOBWHITE

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Abstract: Movement is a fundamental characteristic of life influencing survival and population connectivity. Therefore, understanding how animals move is critical to their conservation in a changing world. Animal behavior is influenced by many different factors including diel and seasonal rhythms, climate variability, and changes on the landscape. Furthermore, climate change is predicted to increase the intensity and frequency of climate extremes, threatening biodiversity and altering ecosystems. Understanding how animals use move in response climate extremes will be critical for understanding how to maintain animal populations into the future. Sedentary species are predicted to be more negatively impacted by climate extremes because they require predictable resources. Limitations in technology has prevented researchers from understanding how these factors influence the movement of many small species (<14 kg) including Northern Bobwhite (*Colinus virginianus*; hereafter bobwhite). We investigated how the movement ecology of bobwhite, a small sedentary declining galliform, is influenced by diel and seasonal rhythms, climate extremes, and changes on the landscape at a fine temporal scale. We collected global positioning system data on Northern Bobwhite across western Oklahoma during 2019–2020. We acquired meteorological and vegetation data from the Oklahoma Mesonet, rangeland analysis platform, and calculated normalized difference vegetation index from Pléiades imagery. We used a generalized linear-mixed or a linear-mixed modeling approach to analyze our data. Our findings suggest that diel and seasonal rhythms shaped bobwhite movement. Bobwhite were most sedentary during winter. The daily bimodal movement pattern exhibited by bobwhite may reflect behavioral tradeoffs aimed at increasing survival. The interaction between multiple climate variables influences this species' movement patterns. Bobwhite movement appeared most limited during extreme cold or heat in conjunction with solar radiation. Our findings suggest that bobwhite use habitat differently during different climate extremes reinforcing the need to manage habitat that allows species like bobwhite to tolerate a wide range of climate extremes. In addition, different climate extremes alter how changes on the landscape influence the movement of some animals. Our study stresses the need to manage for landscape heterogeneity to allow animals to tolerate climate extremes by increasing their realized thermal niche on the landscape.

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CHAPTER I

UNDERSTANDING HOW DIEL AND SEASONAL RHYTHMS AFFECT THE MOVEMENTS OF A SMALL NON-MIGRATORY BIRD

ABSTRACT

Diel and seasonal rhythms affect an animal's environment and life history. Understanding how these rhythms influence movement increases our knowledge on how animals adjust to changing resources, environmental conditions, and risk to their survival. To better understand how diel and seasonal rhythms affect animals, we evaluated movements of Northern Bobwhite (*Colinus virginianus*); hereafter, bobwhite. Because bobwhite are a small non-migratory species that must cope with daily and seasonal changes in their environment year-around, they are a model species to study how diel and seasonal rhythms influence animal movement of a non-migratory species. Global positioning system data from transmitters attached to bobwhite at four wildlife management sites across Oklahoma were collected during 2019–2021. We parsed the diel data as daytime (7:00–19:00 Central Daylight Savings Time [CDT]) and nighttime (19:00–7:00 CDT), and diurnal (sunrise–sunset) and nocturnal (sunset–sunrise) as well as by astronomical season. We calculated three movement metrics: net displacement (Euclidean distance from the starting fix to the ending fix of a path which encompasses consecutive relocations in a time series of geographic fixes), cumulative distance (sum of all Euclidean distances between each consecutive fix along the path), and hourly movement. We modeled the data using a generalized linear mixed-modeling approach. Across season, model predictions showed that net displacement was highest during spring, and daytime cumulative distance slowly increased as the year progressed. Bobwhite had two movement peaks during the diurnal period, one during 9:00–10:00 and the other during 17:00–20:00 depending on the season. Despite being diurnal, bobwhite occasionally made nocturnal movements, likely in response to a disturbance by a predator, inclement weather, or energetic demands. Movement peaks during the diurnal period may reflect changes in behavior in response to energy requirements, predator risk, and changes in air temperature. Life history events likely cause seasonal differences in movement. This study furthers our understanding on how animals move daily and seasonally suggesting the importance of analyzing movement across the entire year because animals move differently across the day and year.

INTRODUCTION

Animal movement can alter ecological processes such as nutrient and energy flow and ultimately trophic dynamics of ecosystems (Holyoak et al. 2005, Nathan et al. 2008, Earl and Zollner 2014). Moreover, animal movement significantly influences the spatial and temporal distribution of animals across landscapes leading to gene flow (Clobert et al. 2001) and distribution shifts in populations (Knowlton and Graham 2010, Earl et al. 2016). Two major factors that influence the movements of organisms are diel and seasonal rhythms (a strong, regular, repeated pattern), which can alter an animal’s environment and life history (Zavalaga et al. 2011, Owen-Smith and Goodall 2014, Lenz et al. 2015, Komal et al. 2017, Ellington et al. 2020). Diel and seasonal rhythms have been shown to influence the foraging patterns of animals (Zavalaga et al. 2011, Lenz et al. 2015). For example, foraging competition, changes in resources, thermal constraints and rates of digestive passage caused by diel and seasonal rhythms have been found to alter the movements of some animals (Zavalaga et al. 2011, Owen-Smith and Goodall 2014, Lenz et al. 2015, McMillan et al. 2021). Furthermore, environmental changes (i.e., lower temperatures, snowfall) driven by seasonal rhythms influence the diel and seasonal movements of some animals, allowing individuals to avoid predation, and exposure to harsh winters as well as to take advantage of available resources (Somveille et al. 2015, Komal et al. 2017, Ellington et al. 2020). Other factors vary with these rhythms including daylight, age of animal, and hormone levels further stating the importance of studying movement pattern broadly across these rhythms (Myers et al. 2006). Lastly, conspecific individuals at different sites can move differently in response to seasonal rhythms (McMillan et al. 2021). For example, bison (*Bison bison*) at two sites moved differently during the fall, which McMillan et al. (2021) suggested was related to topographical differences between the sites. These examples indicate how diel and seasonal rhythms can influence the movement patterns of animals, thus revealing how animals respond to changing resources, environmental conditions, and risks to their survival (Owen-Smith and Goodall 2014).

Historically, very high frequency (VHF) telemetry technology was commonly used to collect movement data, but this technology required researchers to be present in the field to track an animal, limiting the amount of data collected and potentially influencing animal behavior (Caganacci et al. 2010). Furthermore, our ability to collect movement data at fine-temporal scales was limited by VHF telemetry. Given the technological advancements in telemetry and accessibility of global positioning system (GPS) technology, scientists and managers are now able to better understand movement patterns at fine-temporal scales (Cagnacci et al. 2010, McMillan et al. 2021). In fact, GPS technology has significantly increased our understanding on how diel and seasonal rhythms affect movements of large mammals and large birds (Cagnacci et al. 2010, Zavalaga et al. 2011, Owen-Smith and Goodall 2014, McMillan et al. 2021). Despite this, little is known how diel and seasonal rhythms affect the movement of smaller animals (<14 kg), partly because of technological constraints (e.g., size and weight limits for using telemetry; Cagnacci et al. 2010). Because of these technological constraints, many previous movement studies involving smaller animals typically entailed obtaining only a few daily locations of individuals that were often restricted to diurnal periods and or during the breeding season (Culik et al. 1998, Carroll et al. 2015, Laarman et al. 2018). Because movement plays an important role in an animal’s life (Nathan et al. 2008), it is also important we understand how animals move throughout the day as well as across all seasons. Such information increases our understanding on how animals respond to environmental change. Because smaller animals often perceive their environment and energetic needs at different spatial scales than larger animals (McNab 1963, Wiens 1989), smaller animals may respond to diel and seasonal rhythms differently, potentially creating differences in how smaller and larger (e.g., ungulates) animals move across landscapes. With GPS technology rapidly becoming smaller and more accessible as a tool for studying the movements of smaller animals (Cagnacci et al. 2010), an opportunity exists to study the movement ecology of these animals across diel and seasonal rhythms at much finer temporal and spatial scales.

The Northern Bobwhite (*Colinus virginianus,* hereafter bobwhite) is a small non-migratory North American galliform that has experienced distribution-wide population declines (Brennan et al. 2020). Bobwhite are a relatively sedentary species throughout their lifetime, typically living within 1 km of their natal site; however, some individuals occasionally undergo long-distance movements moving as far as 12.4 km over several days (Townsend et al. 2003, Lohr et al. 2011, Brennen et al. 2020). This contrast in behavior offers an opportunity to use bobwhite as a model species to better understand how the movement ecology of a non-migratory bird is influenced by diel and seasonal rhythms. More specifically, it allows us to explore broad movement patterns of a predominantly sedentary species throughout its annual cycle and potentially apply such knowledge to the management and conservation of landscapes that promotes the connectivity of sub-populations of small non-migratory species. Interestingly, because most research on bobwhite has focused on diurnal movements little information is available on their nocturnal movements except that disruption of roosts can cause movement (Brennan et al. 2020). Seasonal variation in the daily movement of bobwhite has been reported (Cohen et al. 2020), but it is currently unknown whether bobwhite at different sites move similarly or differently to seasonal rhythms. Therefore, our objective was to better understand how diel and seasonal rhythms shape the movements of a small terrestrial non-migratory bird by analyzing net displacement, cumulative distance, and hourly movement across diel and seasonal rhythms. Furthermore, we sought to determine if differences in site altered how bobwhite moved in response to diel and seasonal rhythms.

We hypothesized that during the day, bobwhite would exhibit a bimodal hourly movement pattern across all seasons. Such movement patterns have been reported in some ungulates and Wild Turkey (*Meleagris gallopavo*; Bourgoin et al. 2011, Owen-Smith and Goodall 2014, Rakowski et al. 2019), and bobwhites have been shown to exhibit such patterns at least during the breeding season (Carroll et al. 2015). Given the relationship between seasonal rhythms and life histories of animals (i.e., timing of different life history events), we would expect bobwhite movements to be altered by seasonal rhythms. In fact, recent studies on other animals have shown movement patterns are related to seasonal rhythms (Lenz et al. 2015, McMillan et al. 2021).

METHODS

Study Areas

GPS data were collected at the following wildlife management areas (WMA) across Oklahoma, USA: Cross Timbers (33.964043, -97.366169), Packsaddle (35.895249, -99.717387), Sandy Sanders (35.071182, -99.837630), and Beaver River (36.832998, -100.608260). Vegetation communities at each WMA include post oak (*Quercus stellate*), blackjack oak (*Quercus marilandica*) forest and tallgrass prairie at Cross Timbers; mixed-grass prairie and shinnery oak-grassland at Packsaddle; mesquite-grassland and pinion-juniper woodland at Sandy Sanders; and shortgrass prairie and sandsage-grassland at Beaver River (Tyrl et al. 2008). Elevation ranged between 258 and 746 m across WMAs with Packsaddle having the highest elevation and Cross Timbers having the lowest. Average annual rainfall at these sites varies from 559 to 956 mm with Cross Timbers experiencing the highest annual rainfall and Beaver River experiencing the lowest (Tyrl et al. 2008, US Climate Data 2020). Average annual minimum temperature ranges from 5.0 to 11.7 ^{o}C, while average maximum annual temperature ranges from 20.6 to 23.3 ^{o}C (US Climate Data 2020). Across the site the hottest air temperatures occur at Sandy Sanders, while the coldest temperatures occur at Beaver River (US Climate Data 2020).

Data Collection

During 2019–2020, we captured male and female bobwhite for GPS attachment year-around using Stoddard walk-in funnel traps (Stoddard 1931, Smith et al. 1981) baited with a mixture of cracked corn (*Zea mays*) and milo (*Sorghum bicolor*) at each WMA. Traps were checked several times during the day. We fitted each bobwhite with a 7.2-g, solar-powered GPS transmitter (Lotek, Wareham, United Kingdom; average location accuracy <15 m) attached by a backpack-style harness made from 4.76-mm tubular Teflon® ribbon. If we trapped a covey, we only fitted a maximum of four individuals from that covey with transmitters, which allowed us to maintain an adequate number individuals within a covey while maximizing the number of coveys with marked individuals as much as possible. Because mortality rate in bobwhite is high (Brennan et al. 2020) and battery life was variable among GPS transmitters there was little overlap in quail location data among individuals from the same covey, thereby reducing pseudo-replication concerns of placing transmitters on individuals from the same covey. Transmitters were only attached to bobwhite weighing $\geq$ 150 g to ensure a transmitter weight $\leq$ 5% of the bird's body weight (Bridge et al. 2011). Each GPS transmitter was scheduled to collect 18 hourly fixes per day between 05:00–22:00 Central Daylight Savings Time (CDT), however, due to satellites being unavailable or transmitter battery level being low, we averaged 13 hourly fixes per day. We did not collect location data between the hours of 22:00–5:00 to conserve battery. We excluded the first day of data collection from each bird to allow it to acclimate to the GPS transmitter. To account for GPS error, we removed all GPS fixes that were marked as "fail" or "corrected" during data retrieval via satellite, based on <4 acquired satellites, or with an indicated dilution of precision > 3.9. Average GPS error was confirmed to be < 15 m under relevant field conditions after these corrections (K. Andersson, Oklahoma State University, unpublished data). We removed any duplicate fixes with the same timestamp. We used data from bobwhite monitored between January 2019 and January 2021. We did not eliminate any limited or repeated movement paths from birds presumed to be nesting because we were interested in understanding the natural variance of movement across changes in diel and seasonal rhythms and removing such paths would not reflect all potential movements that occur through the annual cycle of a bobwhite. Capturing and handling protocols were approved by Oklahoma State University Animal Care and Use Committee (ACUP AG-18-7).

Data Analysis

Net Displacement and Cumulative Distance. We used the R package "amt" to calculate net displacement (Euclidean distance from the starting fix to the ending fix of a path that includes consecutive relocations in a time series of geographic fixes) and cumulative distance (sum of all Euclidean distances between each consecutive fix along the path; Chiaverano et al. 2014, Seidel et al 2018, Signer et al. 2019, R Core Team 2021) from GPS data. We separated the data into two 12-hour periods for each individual labeled daytime and nighttime using the functions *track_resample,* and *filter_min_n_burst*. We defined 7:00–19:00 (CDT) as daytime and 19:00–7:00 (CDT) as nighttime. We determined that 7:00 and 19:00 were the mean annual sunrise and sunset times in Oklahoma. Because sunrise and sunset times change based on season, we recognize that this method did not eliminate all daylight from the nighttime portion and vice versa, depending on the season; however, this approach created a standardized method to compare net displacement and cumulative distance across the year. Further, this approach provides better consistency in temporal scale across each diel period, which allows for a standardized assessment of how diel rhythms influence movement, particularly net displacement (Seidel et al. 2018). Because we did not collect location data between 22:00 and 5:00 (CDT), we collected more consecutive hour fixes during daytime (13 fixes) than nighttime (7 fixes). Because paths that did not have 13 consecutive hourly fixes during the daytime and 7 consecutive hourly fixes during the nighttime were excluded from the dataset, all paths used in the analyses spanned an entire daytime and nighttime period.

We used the R package “amt” (animal movement tools) to calculate net displacement and cumulative distance. Specifically, we calculated squared net displacement using the function *nsd* and then converted this value to net displacement by obtaining its square root, allowing for simpler interpretation of the data (Signer et al. 2019, R Core Team 2021). We calculated cumulative distance using the function *cum_dist* (Signer et al. 2019, R Core Team 2021). We separated the data across four seasons using pre-determined calendar dates that separated each season based on astronomical changes. For 2019, winter, spring, summer, and fall ended on March 19, June 20, September 22, and December 20, respectively, while for 2020, the seasons ended on March 18, June 19, September 21, and December 20, respectively.

To analyze our data, we used gamma distributed generalized linear mixed-models with a log link using the R package “lme4” (Bates et al. 2015, R Core Team 2021) to model how differences in diel and seasonal rhythms and site alter the net displacement and cumulative distance of bobwhite relative to 12-hour paths. Because the number of consecutive fixes differed between daytime and nighttime, we did not model daytime and nighttime cumulative distance together. All 0 m net displacements were removed from the analysis because of challenges with model convergence. Within each model, we included id as a random intercept to account for individual variation, potential pseudo-replication, and uneven sampling among individuals (Gillies et al. 2006). We removed any individuals that had less than 10 hourly movements because of data constraints when fitting a random effect structure within our models. For development and testing of our models, we used an *a priori* approach to determine the most appropriate models given our data (Burnham et al. 2011). Data constraints prevented us from developing models with interactions. We quantified which model best supported the data by using Akaike Information Criterion using the R package “bbmle” (Bolker and R Core Team 2021). Models were considered competitive if a model had a Δ AICc < 2.0 (Burnham and Anderson 2002).

Hourly Movement. To understand how bobwhite change their hourly movement across an 18-hour period (i.e., 5:00–22:00 CDT) we used the R package “amt” to analyze hourly movement (Signer et al. 2019, R Core Team 2021). We used the functions *track_resample*, *filter_min_n_burst,* and *steps_by_burst* to resample our entire dataset into a continuous series of 1-hour movements across each individual to calculate hourly movement (Signer et al. 2019, R Core Team 2021). We used the function *time_of_day*, which takes into account seasonal sunrise and sunset changes, to categorize hourly movements into two diel periods: diurnal and nocturnal (Signer et al. 2019, R Core Team 2021). For hourly movement, we defined sunrise to sunset as diurnal and sunset to sunrise as nocturnal. An hourly movement was considered nocturnal when both the starting and ending fix of an hourly movement occurred during the nocturnal period otherwise it was considered diurnal. Similar to net displacement and cumulative distance, we separated the data into four seasons using the same pre-determined calendar dates that separate each season based on astronomical changes.

To analyze hourly movement, we used gamma distributed generalized linear mixed models with log link functions using the R package "lme4" (Bates et al. 2015, R Core Team 2021) to model how diel and seasonal rhythms and site and their interactions alter the hourly movement of bobwhite. Within each model, we included id as a random intercept to account for individual variation, potential pseudo-replication, and uneven sampling among individuals (Gillies et al. 2006). We removed any individuals that had less than 10 hourly movements because of data constraints when fitting a random effect structure within our models. All 0 m movements were removed from the analysis because of challenges with model convergence. Our approach to model development and testing hourly movement was similar to our approach to model development and testing net displacement and cumulative distance. In addition, we calculated mean hourly movement and standard error across each specific hour and day and graphically presented the data.

RESULTS

Net Displacement and Cumulative Distance

We analyzed 848 12-hour paths from 27 bobwhite during 2019–2020, with 72% of the movements from Packsaddle (n = 615), 14% from Cross Timbers (n = 119), 11% from Beaver River (n = 91), and 3% from Sandy Sanders (n = 23). Mean ± SE net displacement was 148.5 m ± 4.3 and ranged from 1.1–1,248.4 m. Only 2% (*n* = 13) of net displacements were ≥ 500 m, confirming the sedentary nature of this species (Figure 1.1). Observed mean net displacement was variable across the sites (Table 1.1). Throughout the year, mean net displacement was longest during the spring and shortest during the summer. Bobwhite exhibited longer net displacement during the daytime than the nighttime; however, > 1,000 m net displacements occurred during the daytime and nighttime (Daytime: $\bar{x}$ = 176.9 m ± 7.5, range = 1.8–1,248.4 m; Nighttime: $\bar{x}$ = 129.5 m ± 4.9, range = 1.1–1,100.2 m). During the daytime, mean ± SE cumulative distance was 593.6 m ± 19.8 with cumulative distance ranging from 35.8–2,519.5 m. Forty-nine percent (*n* = 165) of 12-hour paths had a daytime cumulative distance ≥ 500 m. At nighttime, mean ± SE cumulative distance was 207.3 m ± 7.2 with cumulative distance ranging between 2.8–1,354.1 m. Only 4% (*n* = 22) of 12-hour paths during the nighttime had a cumulative distance ≥500 m. Observed mean cumulative distance during the daytime and nighttime was variable across the sites. During the daytime, observed mean cumulative distance across seasons was highest during the fall and lowest during the winter; however, mean nighttime cumulative distance was longest during the spring and shortest during the fall (Table 1.2).

Net Displacement Modeling. We investigated 8 different models to better understand how diel and seasonal rhythms and site differences influence bobwhite net displacement relative to a 12-hour path. The model that best described the data was an additive model that included season, diel period, and site (Table 1.3). Two models (season + diel period; diel period) were competitive to the best-fit model suggesting that site may not be an important predictor of net displacement. According to the best-fit model, net displacement was longest during spring, but similar across the year, while net displacement was similar across each site (Figure 1.2). The model indicated that bobwhite exhibit longer net displacement during daytime than nighttime (Figure 1.2).

Cumulative Distance Modeling. We evaluated 4 different models to determine how seasonal rhythms and site alter bobwhite cumulative distance relative to a 12-hour path during daytime and nighttime. During the daytime, season and site best described the data (Table 1.3). One model (season) was competitive to the best-fit model; suggesting that season maybe more important than site at predicting daytime cumulative distance. According to the best-fit model, cumulative distance increased during daytime as the year progressed, while cumulative distance across site was variable (Figure 1.3). At nighttime, season and site best described the data (Table 1.3). The best-fit model suggested that nighttime cumulative distance was highest during the spring and summer and variable across sites (Figure 1.3).

Hourly Movement

We analyzed 45,600 hourly movements of 288 bobwhite during 2019–2021. Forty-five percent of the movements were from Packsaddle (n = 20,409), 29% from

Beaver River (n = 13,286), 17.5% from Cross Timbers (n = 7,988), and 8.5% from Sandy Sanders (n = 3,917). Mean ± SE hourly movement was 50.6 m ± 0.4 and ranged from between 0.4–1,882.5 m. Only 0.4% of hourly movements were $\geq$ 500 m (Figure 1.4). Observed mean hourly movement varied across the sites (Table 1.4). During the year, mean hourly movement was largest during the spring and smallest during the winter. Observed mean hourly movement was larger during the diurnal period than the nocturnal period. Only 3% of nocturnal hourly movements were $\geq$ 100 m, indicating that bobwhite rarely move significant distances during this period. We found that bobwhite had two distinct movement peaks (9:00–10:00 and 17:00–20:00 depending on the season) throughout the diurnal period (Figure 1.5).

We evaluated 14 different models to determine how diel and seasonal rhythms and site differences as well as interactive effects influenced bobwhite hourly movement. The only competitive model included season and the two-way interaction between diel period and site (Table 1.3). According to this model, bobwhite moved more during the diurnal period than the nocturnal period, regardless of site (Figure 1.6). However, within the diurnal period, the model indicated that hourly movement was variable across the sites. In contrast, bobwhite movement during the nocturnal period were similar across sites. Furthermore, the model indicated that hourly movement was shortest during the winter, but similar across the rest of year (Figure 1.6). Based on our daily mean hourly movement data, bobwhite appeared to be more sedentary during the middle of winter, but as the year progressed, daily mean hourly movement increased until plateauing at the beginning of summer before declining and plateauing at a lower level during the fall (Figure 1.7).

DISCUSSION

Our study shows that diel and seasonal rhythms shape the movement ecology of a non-migratory terrestrial species. Because movement influences the spatial and temporal distribution of animals on the landscape connecting various aspects of an animal’s life impacting survival and population connectivity (Zollner and Lima 2005, Nathan et al. 2008, Earl et al. 2016), understanding how animals move is paramount to conservation because of the critical role that movement has on the life of an animal. In particular, the variation in movement pattern in relation to diel and seasonal rhythms can provide broad implications for understanding the resiliency and adaptability of other species to cope with daily and seasonal changes in their environment (Shaw 2020). This variation in bobwhite movement patterns also suggests that their movements are influenced by potentially complex interrelationships of diel and seasonal rhythms and environmental and climatic variables. Future studies should investigate the role specific factors that change with these rhythms such as weather, food availability, predation risk, habitat requirements have on movement (Arndt 2003, Sperry et al. 2008, Ramos Pereira et al. 2010, Lamb et al. 2020). Further, our findings add to a growing body of literature that suggests that diel rhythms influence the movement ecology of many animals similarly, suggesting that some animals can exhibit similar movement patterns despite occurring in different regions of the globe (Bourgoin et al. 2011, Owen-Smith and Goodall 2014, Carroll et al. 2015, Rakowski et al. 2019). As GPS technology increases in accessibility, there is an increased call to better understand the movement ecology of animals to better inform conservation efforts (Allen and Singh 2016). Our findings aid in that call by recognizing the variability of movement patterns in bobwhite and suggesting that a multitude of mechanisms, including diel and seasonal rhythms likely influence the movement of bobwhite and other species.

Daily bimodal movement patterns have been found in birds and mammals (Bourgoin et al. 2011, Owen-Smith and Goodall 2014, Carroll et al. 2015, Rakowski et al. 2019). Similarly, we found a distinct bimodal movement pattern, with peak movements occurring during 9:00–10:00 CDT and another during 17:00–20:00 CDT dependent on season. Given the energetic costs of thermal stress and the risk of predation, it is possible that avoidance of thermal stress and predators could be an explanation for this bimodal pattern. During thermal extremes, some species, including bobwhite, become more sedentary by sheltering in suitable thermal refuge to mitigate thermal stress (Carroll et al. 2015, Rakowski et al. 2019, Alston et al. 2020). Thus, this behavior could explain a reduction in movement during midday. However, individuals were sedentary during midday throughout each season suggesting that thermal stress may not be the only factor driving this pattern. Several studies have shown that prey experience temporal variation in predator risk on a daily and seasonal basis (Metcalfe and Ure 1995, Sperry et al. 2008, Lang et al. 2019). In our study, it is possible that predator (i.e., raptors) activity during midday may have resulted in bobwhites being more sedentary to lower predation risk. Interestingly, Lang et al. (2019) suggested that songbird predators (i.e., *Accipiter* hawks that also prey on bobwhite) match the activity patterns of their prey species, which suggests that linking movement patterns to predator avoidance may be problematic. Another explanation for the bimodal pattern could be that energy and foraging demands resulted in the peak movements occurring during morning and late afternoon. Some avian species during the winter begin to forage before sunrise and increase their foraging rate abruptly before sunset likely as a strategy to reduce starvation risk during the night (Bonter et al. 2013). We hypothesize that bobwhite may be altering their movements throughout the day to build and replenish energy reserves before and after the night, especially during periods when energy demand is high. However, foraging demands may not influence movement across all seasons because the energy demands of bobwhite change in response to seasonal differences in life history requirements and environmental conditions (Guthery 1999). Given the complex nature of these factors and their potential influence on movement, it is difficult to attribute one factor to the bimodal pattern we observed. However, thermal stress, predation risk, and foraging demands all likely alter movement patterns on a daily or seasonal basis depending on environmental conditions, predator activities, and physiological needs. In fact, animals likely make frequent decisions in response to these factors on a daily basis as they move across landscapes and assess risks to their survivability (Hernández and Laundré 2004, Zollner and Lima 2005). The complexity of these relationships is further increased as animals move across different landscapes (e.g., anthropogenic-influenced landscapes vs. natural landscapes) as evident by the fact that we observed different daily movement patterns for bobwhite among our different study sites.

We found that the movement ecology of bobwhite changed across seasonal rhythms. This aligns with previous research that determined that the movement ecology of many animals is influenced by seasonal rhythms (Owen-Smith and Goodall 2014, Lenz et al. 2015, Ellington et al. 2020, McMillan et al. 2021). Furthermore, this pattern was consistent across all sites suggesting a broad-scale response to seasonal rhythms. This is contrary to previous research that found that bison at different sites moved differently during the fall, which McMillan et al. (2021) suggested was caused by topographical differences between these sites. Seasonal rhythms appeared to influence bobwhite net displacement the most during spring. This matches previous studies that determined that bobwhite disperse the farthest during the spring (Fies et al. 2002, Townsend et al. 2003, Carroll et al. 2017). Shifts in resources and life history potentially influence the seasonal movements of some non-migratory avian species (Lenz et al. 2015). Unlike movements during the spring, seasonal differences in cumulative distance and hourly movement showed that bobwhite became most sedentary during the winter. Limited movement may infer that large portions of the landscape were unsuitable to bobwhite during the winter. A previous study determined that mortality in bobwhite was highest during periods of extreme cold when large portions of the landscape became unsuitable (Tanner et al. 2017). For non-migratory species, especially in more northern latitudes, winter could be the most limiting time during their annual cycle since many of these species typically rely on predictable resources within a fixed home range (Maron et al. 2015). Given these challenges during winter for non-migratory species, it is likely that the reduced winter movements that we observed in bobwhite were a function of birds avoiding exposure during cold temperatures by being immobile, but reduced movements could also be related to limited food resources (i.e., seeds) and cover causing individuals to remain in close proximity to these resources. Our findings suggests that seasonal rhythms can influence the movement ecology of a non-migratory bird.

Examining nocturnal movement patterns of animals typically characterized as diurnal can yield interesting results. In our study, we found that despite being considered diurnal, bobwhite do engage in limited nocturnal movements, although these movements tend to be limited with few being ≥100 m. Several factors may play a role in causing movement during the nocturnal period. Many animals including bobwhite are depredated by both diel and nocturnal predators (Marti and Kochert 1995, Brennan et al. 2020), which could cause some individuals to engage in nocturnal movements in response to perceived threats. Further, as bobwhites roost in coveys during the night, disturbances near coveys can result in nocturnal movements (Brennan et al. 2020). Alternatively, it is also possible that nocturnal movements in bobwhite may be related to energetic requirements. Some avian species have been documented to begin foraging before sunrise during the winter to likely meet foraging demands (Bonter et al. 2013). Furthermore, captive bobwhites have been observed foraging at night (Kirkpatrick 1957, Hiller and Guthery 2004); however, this behavior has not been observed in wild bobwhites to our knowledge. Our data indicated that hourly movements were occasionally >100 m early in the morning before sunrise, which may indicate that bobwhite moved to foraging areas during the low light dawn period. This observation potentially has interesting management and research implications. For example, fall covey call counts used to estimate population abundance assume individuals calling before sunrise are sedentary at the roost suggesting that individuals moving before sunrise could potentially inflate or bias abundance estimates (Wellendorf and Palmer 2005). Such findings could translate to other techniques used to determine population abundance estimates for species deemed diurnal if those species engage in nocturnal movements when assumed to be sedentary. Finally, many species require suitable refuge to survive thermal extremes or inclement weather (Janke et al. 2015, Rakowski et al. 2019, Alston et al. 2020). Nocturnal movements may be a response to individuals attempting to locate suitable cover to survive harsh conditions caused by inclement weather and thermal extremes. Lastly, our data determined that cumulative distance during the nighttime was largest during the spring and summer. We suspect that these differences are likely due to seasonal differences in daylight and not truly reflecting seasonal differences in nocturnal movement in bobwhite. However, without additional research examining the role of predation, foraging demands, and weather extremes on the nocturnal movements of primarily diurnal animals, these hypotheses are merely speculative. We encourage future studies to consider investigating nocturnal movement patterns of primarily diurnal animals to better understand the mechanisms that cause these species to move at night.

Diel and seasonal rhythms influence the daily lives of animals (Owen-Smith and Goodall 2014, Ellington et al. 2020). We determined that even a non-migratory, terrestrial bird species with a small home range can have complex movement patterns. Our study aligns with previous research that indicates that some animals including bobwhite exhibit a bimodal movement pattern throughout the day (Bourgoin et al. 2011, Owen-Smith and Goodall 2014, Rakowski et al. 2019). Furthermore, bobwhite are most sedentary during the winter stating the importance of studying movement across all seasons because movement pattern varies with season. This has broad implications for the survival of species and potentially others if individuals are unable to access resources during a specific season. Future research should investigate if the movement of other non-migratory species is most constrained during the winter. Specifically, regarding bobwhite creating areas with suitable woody cover within their winter home range would likely aide in the conservation of winter bobwhite populations because access to woody cover increases the winter survival of bobwhite (Janke et al. 2015). Disentangling how diel and seasonal rhythms influence the movement ecology of organisms advances our understanding of movement pattern, ultimately aiding in our ability to conserve these species and the ecosystems they inhabit. As habitat loss and fragmentation continue to be major threats throughout the world (Coppedge et al. 2001, Radeloff et al. 2005), understanding how animals move is critical to developing management plans that maintain survival and population connectivity and thereby furthering the conservation of the species.

TABLES

Table 1.1: Mean, standard error, and range of net displacement between site, and season obtained from global positioning system telemetry data of northern bobwhite (*Colinus virginianus*) in western Oklahoma, USA, 2019–2020.

Net Displacement (m)			
Site	N	Mean±SE	Range
Beaver River	91	133.9±10.6	2.0–455.8
Cross Timbers	119	122.3±9.7	3.6–646.2
Packsaddle	615	155.5±5.3	1.1–1248.4
Sandy Sanders	23	153.5±28.9	2.5–536.1
Season†			
Winter	146	140.8±8.5	2.9–463.9
Spring	407	163.1±7.0	2.0–1248.4
Summer	222	126.5±6.5	1.8–452.6
Fall	73	148.8±15.9	1.1–825.3

†During 2019 seasons: winter, December 21 – March 19; spring, March 20 – June 20; summer, June 21 – September 22; and fall, September 23 – December 20.

During 2020 seasons: winter, December 21 – March 18; spring, March 19 – June 19; summer, June 20 – September 21; and fall, September 22 – December 20.

Data from 2021 only occurred in winter (January).

Table 1.2: Mean, standard error, and range of cumulative distance between site, and season obtained from global positioning system telemetry data of northern bobwhite (*Colinus virginianus*) in western Oklahoma, USA, 2019–2020.

	Daytime			Nighttime		
Site	N	Mean±SE	Range	N	Mean±SE	Range
Beaver River	27	776.0±115.0	66.3–2519.5	64	211.0±23.5	2.9–1354.1
Cross Timbers	32	458.1±40.7	196.6–1197.4	87	171.0±14.0	24.2–939.4
Packsaddle	271	599.2±20.8	53.3–2202.6	344	216.0±8.7	2.8–1312.4
Sandy Sanders	10	365.0±57.0	35.8–581.0	13	203.9±56.5	11.6–802.2
Season†						
Winter	71	407.3±19.8	122.2–1231.1	75	152.8±11.5	24.6–464.5
Spring	187	653.2±30.8	35.8–2519.5	220	260.4±13.1	3.0–1354.1
Summer	49	545.8±42.8	203.7–2191.1	173	187.4±9.6	2.8–802.2
Fall	33	727.3±42.2	361.8–1497.3	40	103.8±10.9	17.2–284.2

†During 2019 seasons: winter, December 21 – March 19; spring, March 20 – June 20; summer, June 21 – September 22; and fall, September 23 – December 20.

During 2020 seasons: winter, December 21 – March 18; spring, March 19 – June 19; summer, June 20 – September 21; and fall, September 22 – December 20.

Data from 2021 only occurred in winter (January).

Daytime: (7:00–19:00 [CDT]). Nighttime: (19:00–7:00 [CDT]).

Table 1.3: Model comparison table showing models investigated to understand how changes in diel and seasonal rhythms and site influence the hourly movement, net displacement, and cumulative distance of Northern Bobwhite (*Colinus virginianus*) in western Oklahoma, USA, 2019-2020.

Model Variables	Df	dAICc	AICc Weight
Hourly Movement			
Diel Period*Site + Season	13	0.0	1
Diel Period*Site	10	33.6	<0.001
Diel Period*Season + Site	13	52.0	<0.001
Diel Period*Season	10	73.9	<0.001
Season*Site + Diel Period	19	150.2	<0.001
Diel Period + Season + Site	10	184.7	<0.001
Diel Period + Season	7	207.6	<0.001
Diel Period + Site	7	221.5	<0.001
Diel Period	4	247.5	<0.001
Season*Site	18	4608.4	<0.001
Season + Site	9	4739.8	<0.001
Season	6	4670.3	<0.001
Site	6	4690.4	<0.001
Null	3	4721.9	<0.001
Net Displacement			
Diel Period + Season + Site	10	0.0	0.390
Diel Period	4	0.6	0.300
Diel Period + Season	7	1.5	0.180
Diel Period + Site	7	2.1	0.130
Season + Site	9	17.8	<0.001
Season	6	22.0	<0.001
Site	6	22.0	<0.001
Null	3	22.9	<0.001
Cumulative Distance (Daytime[†])			
Season + Site	9	0.0	0.544
Season	6	1.1	0.319
Null	3	3.7	0.086
Site	6	4.7	0.051
Cumulative Distance (Nighttime[‡])			
Season + Site	9	0.0	0.870
Season	6	3.8	0.130
Null	3	32.7	<0.001
Site	6	34.2	<0.001

†Daytime: (7:00–19:00 [CDT]). ‡Nighttime: (19:00–7:00 [CDT]).

Table 1.4: Mean, standard error, and range of hourly movement between site, season and diel period obtained from global positioning system telemetry data of northern bobwhite (*Colinus virginianus*) in western Oklahoma, USA, 2019–2021.

Site	N	Mean±SE (m)	Range (m)
Beaver River	13,286	57.5±0.9	0.1–1882.5
Cross Timbers	7,988	34.4±0.6	0.04–777.5
Packsaddle	20,409	53.8±0.6	0.1–1693.8
Sandy Sanders	3,917	43.3±1.2	0.1–1234.8
Season†			
Winter	3,669	32.6±0.9	0.2–1234.8
Spring	23,810	52.4±0.5	0.04–1882.5
Summer	11,059	55.0±0.8	0.1–1538.5
Fall	7,062	46.6±0.9	0.1–1034.0
Diel period‡			
Diurnal	40,067	55.8±0.4	0.04–1882.5
Nocturnal	5,533	12.4±0.5	0.1–677.4

†During 2019 seasons: winter, December 21 – March 19; spring, March 20 – June 20; summer, June 21 – September 22; and fall, September 23 – December 20.

During 2020 seasons: winter, December 21 – March 18; spring, March 19 – June 19; summer, June 20 – September 21; and fall, September 22 – December 20.

Data from 2021 only occurred in winter (January).

‡Diurnal (sunrise–sunset) and nocturnal (sunset–sunrise).

FIGURES

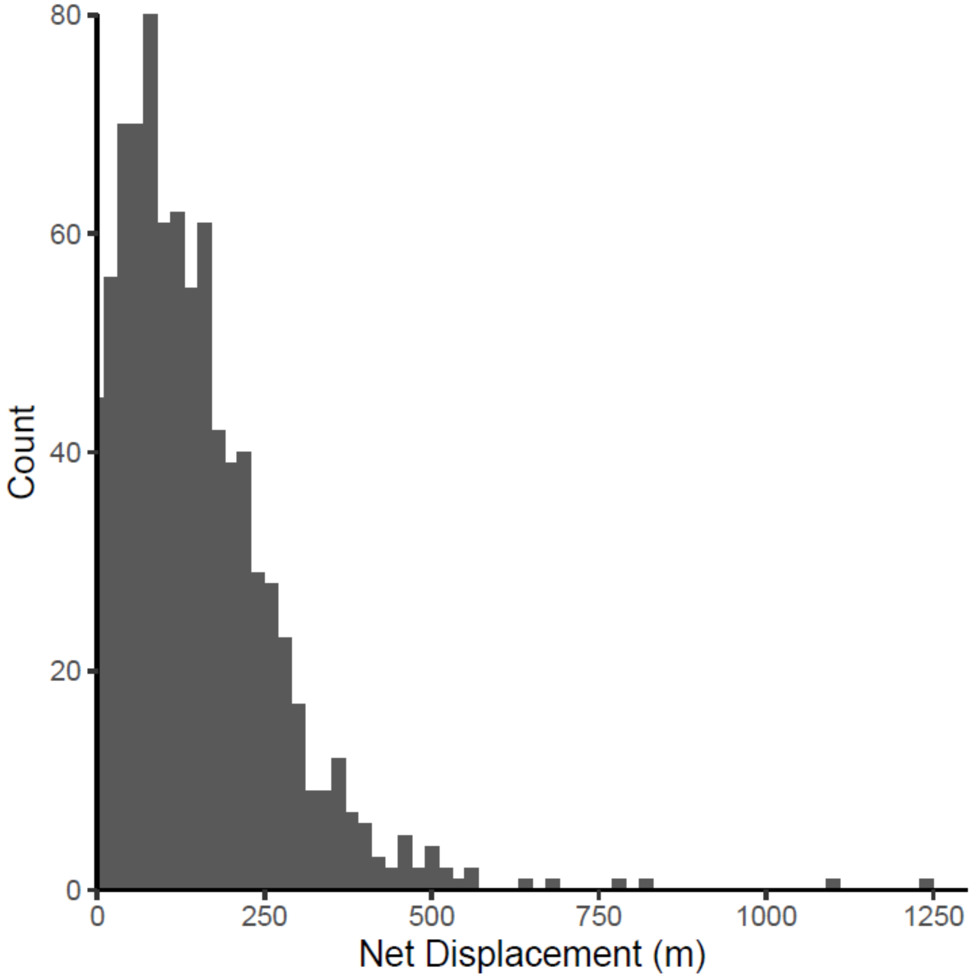


Figure 1.1: A histogram showing the distribution of Northern Bobwhite (*Colinus virginianus*) net displacement across a 12-hour path from individuals tracked in western Oklahoma during 2019–2020.

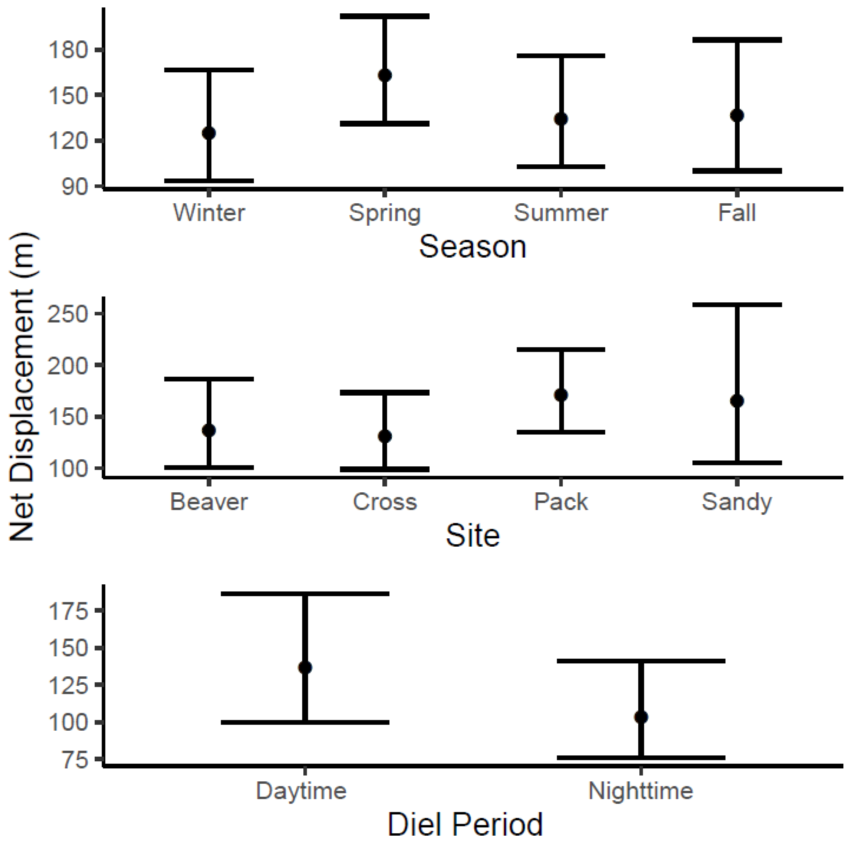


Figure 1.2: Model predictions from the top model that best described the relationship between the net displacement of Northern Bobwhite (*Colinus virginianus*) across a 12-hour period in response to changes in diel period, season and site during 2019–2020 in western Oklahoma. We defined 7:00–19:00 (CDT) as daytime and 19:00–7:00 (CDT) as nighttime. In 2019 the last days of winter, spring, summer, and fall occurred on March 19, June 20, September 22, and December 20, respectively, and in 2020 on March 18, June 19, September 21, and December 20, respectively. Data from 2021 only occurred during winter (January). Beaver, Cross, Pack, and Sandy refer to Beaver River, Cross Timbers, Packsaddle, and Sandy Sanders, respectively. Error bars refer to 95% confidence intervals for each prediction.

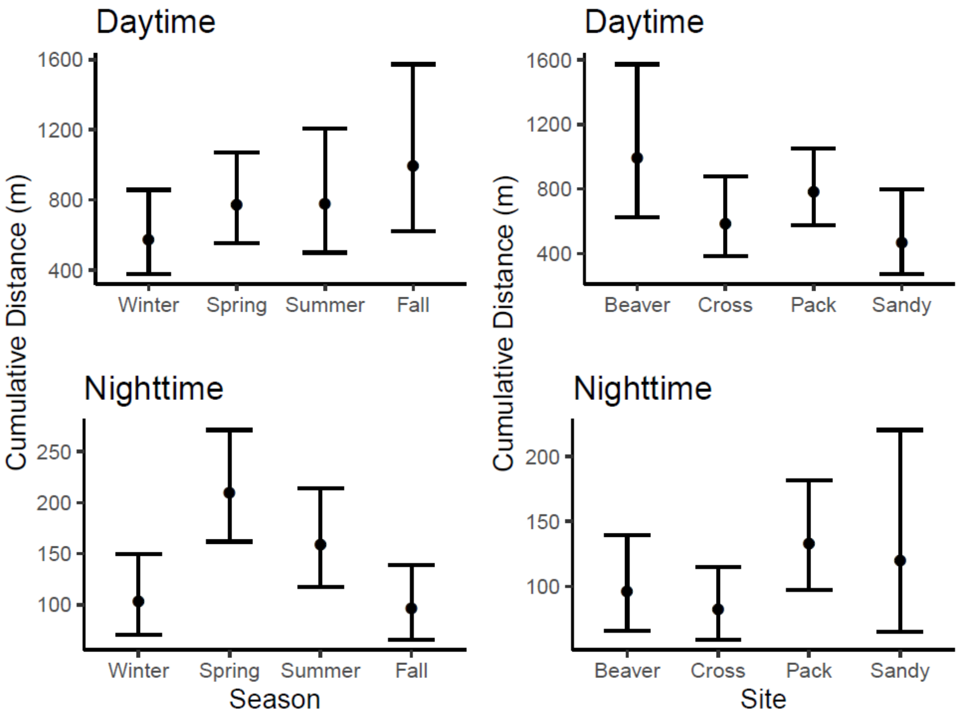


Figure 1.3: Model predictions from the top model that best described the relationship between the cumulative distance of Northern Bobwhite (*Colinus virginianus*) across a 12-hour period in response to changes in season and site during daytime and nighttime during 2019–2020 in western Oklahoma. Because the number of consecutive fixes differed between daytime and nighttime, we could not compare cumulative distance between these periods. We defined 7:00–19:00 (CDT) as daytime and 19:00–7:00 (CDT) as nighttime. In 2019 the last days of winter, spring, summer, and fall occurred on March 19, June 20, September 22, and December 20, respectively, and in 2020 on March 18, June 19, September 21, and December 20, respectively. Data from 2021 only occurred during winter (January). Beaver, Cross, Pack, and Sandy refer to Beaver River, Cross Timbers, Packsaddle, and Sandy Sanders, respectively. Error bars refer to 95% confidence intervals for each prediction.

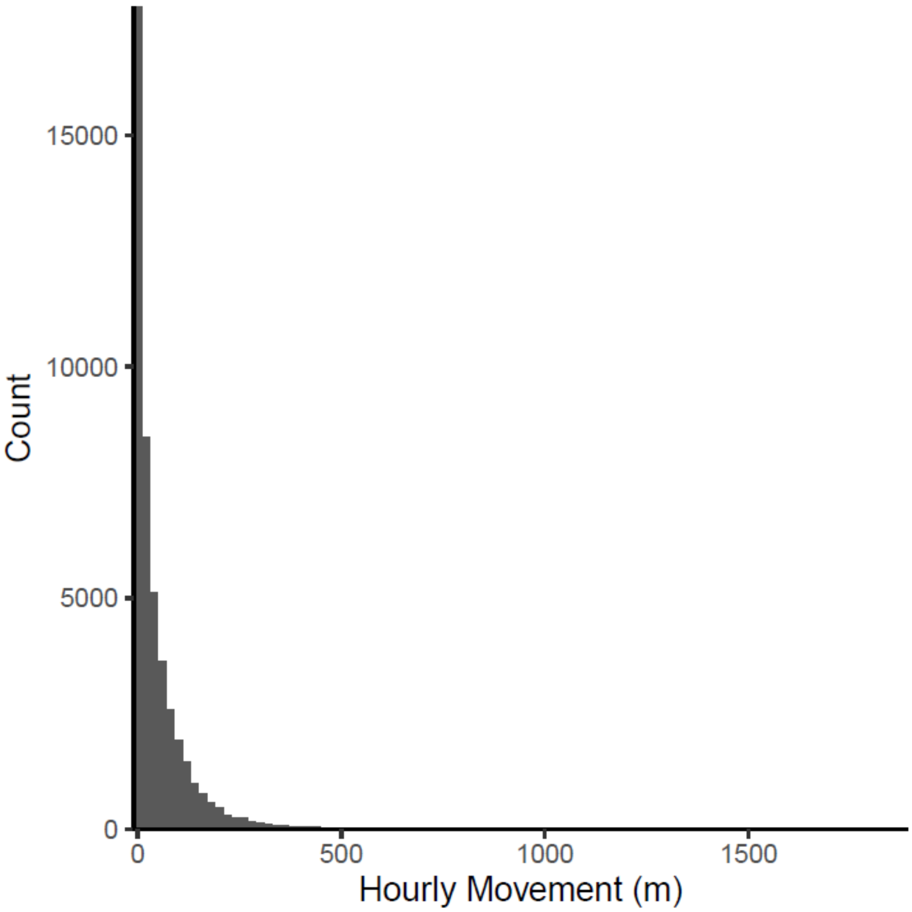


Figure 1.4: A histogram showing the distribution of Northern Bobwhite (*Colinus virginianus*) hourly movement from individuals tracked in western Oklahoma during 2019–2021.

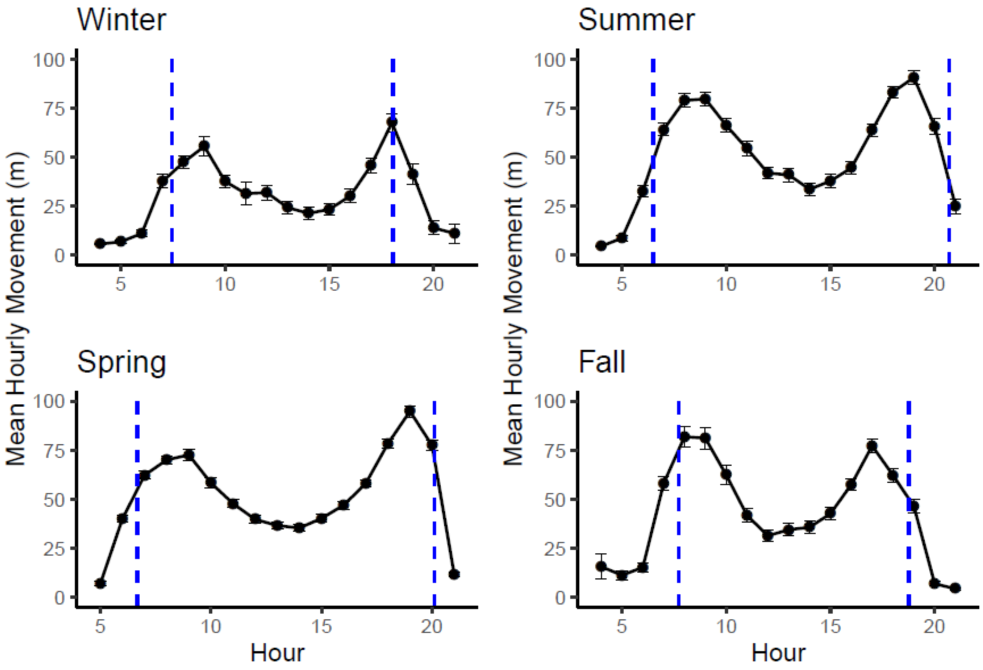


Figure 1.5: Mean hourly movement split by season from global positioning data of Northern Bobwhite (*Colinus virginianus*) in Oklahoma, USA, 2019–2021. Each point represents an hourly interval of movement. The point is the beginning of each interval. The bars on each data point represent standard error for that mean. The dashed blue line indicates mean sunrise and sunset times for each respective season. In 2019 the last days of winter, spring, summer, and fall occurred on March 19, June 20, September 22, and December 20, respectively, and in 2020 on March 18, June 19, September 21, and December 20, respectively. Data from 2021 only occurred during winter (January).

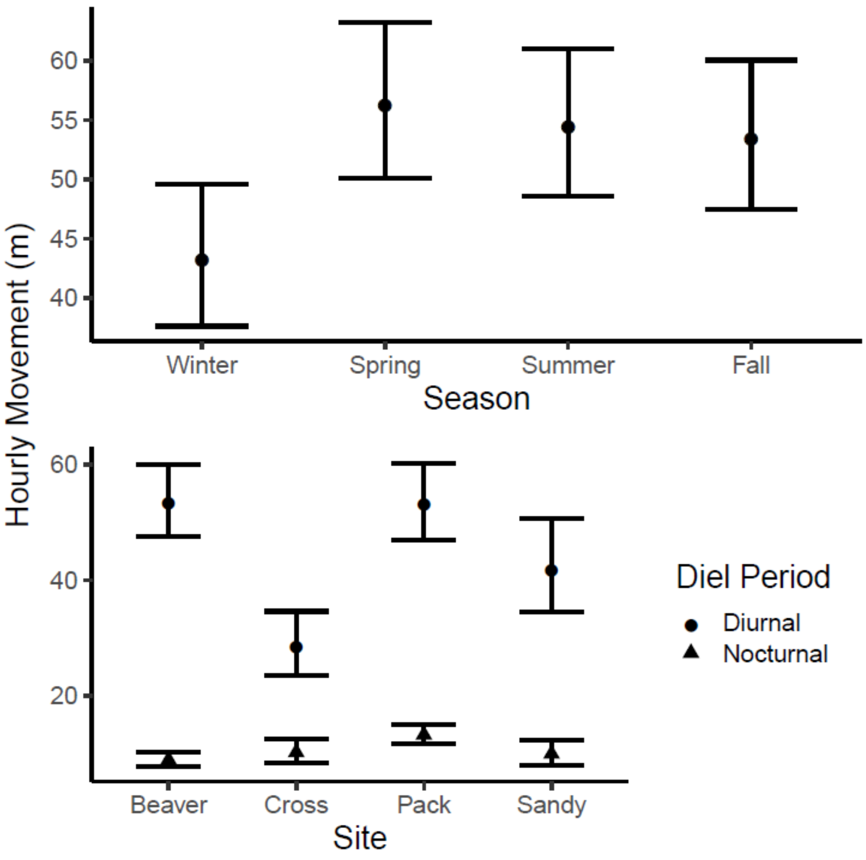


Figure 1.6: Model predictions from the top model that best described the relationship between the hourly movement of Northern Bobwhite (*Colinus virginianus*) in response to changes in diel period, season and site. We defined sunrise–sunset as diurnal and sunset-sunrise as nocturnal. In 2019 the last days of winter, spring, summer, and fall occurred on March 19, June 20, September 22, and December 20, respectively, and in 2020 on March 18, June 19, September 21, and December 20, respectively. Data from 2021 only occurred during winter (January). Beaver, Cross, Pack, and Sandy refer to Beaver River, Cross Timbers, Packsaddle, and Sandy Sanders, respectively. Error bars refer to 95% confidence intervals for each prediction.

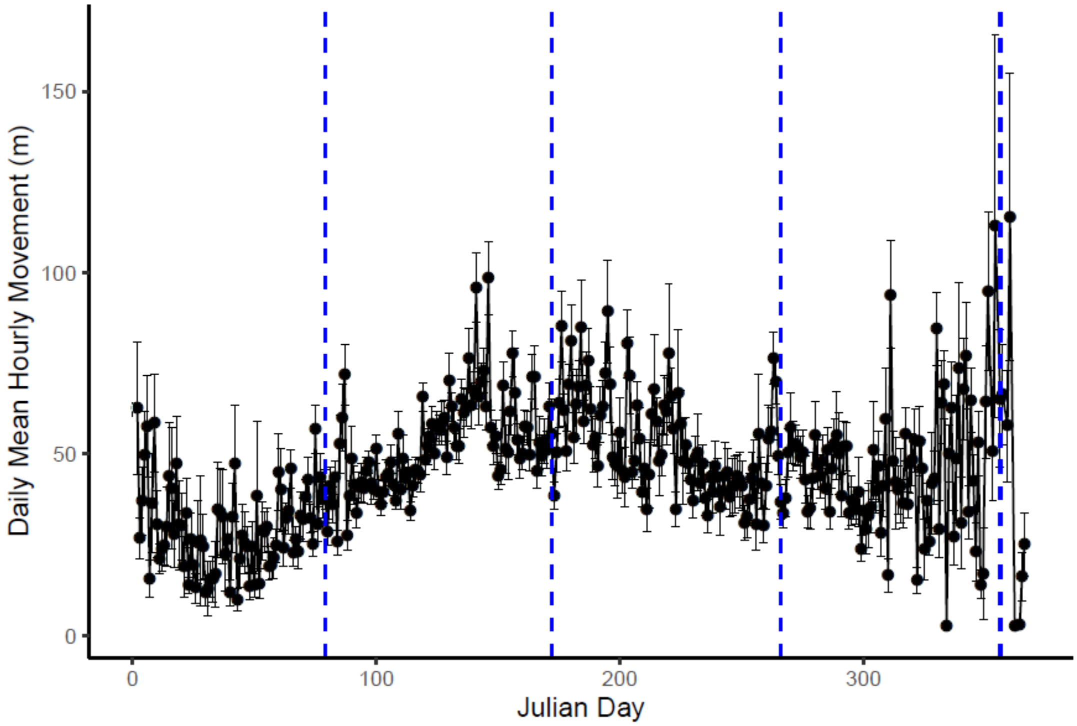


Figure 1.7: Daily mean hourly movement across the year obtained from global positioning telemetry data of Northern Bobwhite (*Colinus virginianus*) in Oklahoma, USA, 2019–2021. The bars on each data point represent standard error for that mean. The dashed blue line indicates the beginning of spring, summer, fall and winter, respectively.

CHAPTER II

THE IMPORTANCE OF UNDERSTANDING THE ROLE OF SPECIFIC CLIMATE VARIABLES ON THE MOVEMENT OF TERRESTRIAL GROUND-DWELLING ANIMALS

ABSTRACT

Climate change is predicted to increase the intensity and frequency of climate extremes that will likely threaten biodiversity and alter ecosystems. Climate is comprised of many different climate variables including air temperature, barometric pressure, solar radiation, wind, relative humidity, and precipitation that interact to make climate. Because movement connects various aspects of an animal's life, understanding how different climate variables influence movement will be critical to the long-term conservation of species. Increased enviromental variability caused by climate change may increasingly threaten non-migratory species because these species typically rely on predictable resources within a fixed home range. We used Northern Bobwhite (*Colinus virginianus*) as a model to understand how different climate variables and their interactions alters the movement ecology of a non-migratory species at a fine temporal scale (hourly timescales). We collected global positioning system data on Northern Bobwhite from across western Oklahoma during 2019–2020 and paired this data with meteorological data from nearby Mesonet stations. For our analysis, we calculated two movement metrics: hourly movement (displacement between two consecutive geographic fixes an hour apart) and sinuosity (a form of tortuosity that determines the amount of curvature of a random search path). We used a generalized linear-mixed modeling approach to analyze our data. Hourly movement decreased as the interactions between solar radiation and air temperature and between solar radiation and average wind speed increased. Variability in hourly movement appeared most limited when air temperature was ≤0 or ≥30 °C regardless of solar radiation intensity. The 3-hour movement paths of bobwhite exhibited a positive relationship in response to the interactions between air temperature and solar radiation and solar radiation and average wind speed. Our study showed that bobwhite became more sedentary during climate extremes. Increased climate extremes will likely force animals to make behavioral adjustments limiting their movement and ability to access resources which could affect survival. This has the potential to impact the long-term survival of populations. Because of these challenges managers and scientists will need to rethink how to manage non-migratory species in the future.

INTRODUCTION

As climate change continues to affect biodiversity and alter ecosystems understanding the importance of different climate variables on animal behavior is critical to the conservation and management of wildlife (McCarty 2001, King 2005). Climate is comprised of many different climate variables including air temperature, barometric pressure, solar radiation, wind, relative humidity, and precipitation that interact to make climate (Ahrens and Henson 2016). As climate change continues, climate extremes (e.g., extreme heat or cold, drought, floods) are projected to increase in frequency and intensity (IPCC 2013, Cohen et al. 2018). Many animals have specific behavioral strategies to cope with climate extremes (Melin et al. 2014, Pattinson and Smit 2017, Cunningham et al. 2021). For example, some species adjust their immediate position on the landscape to seek cooler temperatures to mitigate extreme heat (Melin et al. 2014, Mason et al. 2017, Tanner et al. 2017, Pattinson and Smit 2017). However, these strategies can have major consequences on the survival and population dynamics of species by reducing foraging efficiency, reproduction success and an animal's ability to access resources (Pattinson and Smith 2017, van de Ven et al. 2020, Tanner et al. 2017). Furthermore, increased climate extremes is expected to cause catastrophic population declines by increasing resource bottlenecks (Maron et al. 2015) and or fragment and isolate the geographic distributions of some species by altering plant communities (Murray et al. 2017). Until recently, constraints in technology have prevented researchers from determining how changes in different climate variables alters animal behavior at fine temporal scales (e.g., hourly timescales; Cagnacci et al. 2010). As climate change continues, understanding how different climate variables alter animal movement is critical to promote the long term persistence of species affected by climate change.

Movement connects various aspecects of an animal's life shaping the life of an animal (Nathan et al. 2008). Changes in an animal's environment (Etzenhouser et al. 1998, Alston et al. 2020) and life history (Fies et al. 2002, Lenz et al. 2015) directly influence the movement ecology of animals. These changes alter the spatial and temporal arrangement of individuals across landscapes impacting the survival of individuals (Zollner and Lima 2005, Somveille et al. 2015), nutrient and energy flow within and across ecosystems (Earl and Zollner 2014), gene flow (Clobert et al. 2001), and structural and distributional shifts in populations (Nathan et al. 2008, Knowlton and Graham 2010, Earl et al. 2016). Movement can be split into two distinct behaviors: long-distance dispersal and local movement (Earl et al. 2016, Rakowski et al. 2019). Changes in climate alter movement differently depending on the type of movement. For example, some species engage in long-distance dispersal (i.e., seasonal migration) in response to seasonal changes in climate (Somveille et al. 2015, Nicholson et al. 2016). In other species, extreme temperatures can cause animals to become more sedentary by constraining them to areas with suitable thermal refuge (Carroll et al. 2015, Rakowski et al. 2019, Alston et al. 2020). Because local movement directly influences animals by allowing them to accomplish daily activities (e.g., foraging, predator avoidance, and reproductive duties) important to maintaining their own and species long-term survival on the landscape (Hernández and Laundré 2005, Geary et al. 2020, Precioso et al. 2020), it is important we understand how the local movement of animals is impacted by different climate variables. Climate change may disrupt these activities by causing animals to devote more time to behavioral thermogulation potentially influencing their survival and long-term persistence of their species on the landscape (Cunningham et al. 2021). Therefore, understanding how animals alter their local movements in response to specific climate variables at a fine temporal scale better informs how climate change may effect the daily lives of animals. As climate change continues to threaten ecosystems and biodiversity (McCarty 2001), such knowledge is important to maintain species resiliency on a changing landscape.

As climate change continues, non-migratory species may be at a higher risk for extinction because they rarely disperse long distances (Townsend et al. 2003, Earl et al. 2016). Because climate change is predicted to fragment and isolate the populations of some species (Murray et al. 2017), populations that become disjunt maybe more genetically isolated and experience reduced fitness in the future (Luquet et al. 2011, van de Kerk et al. 2019). The sedentary nature of non-migratory species increases their risk for this. Furthermore, adaptations and strategies used by many species to combat climate extremes may become ineffective or negatively impact the fitness of an animal (Carroll et al. 2016, Cunningham et al. 2021). In the future, climate change may intensify the thermal conditions of some landscapes leaving some animals without the ability to locate suitable thermal refuge to survive extreme thermal conditions (Carroll et al. 2016). Non-migratory species would be adversely impacted by these threats, especially if populations become isolated by climate change. Finally, because non-migratory species typically depend on predictable resources within their home range, increased resource bottlenecks caused by climate change may negatively impact the long-term survival of many non-migratory species (Maron et al. 2015). Given the increased likelihood of increased climate extremes in the future (IPCC 2013), it is necessary we understand how different climate variables influence the movement of non-migratory species at a fine temporal scale (e.g, hourly timescales). Historically, many studies have only investigated how a specific climate variable (i.e., temperature) influences movement (Mason et al. 2017, Rakowski et al. 2019, Alston et al. 2020) or analyzed responses to movement at a broad temporal scale (i.e., daily movement; Garstang et al. 2014, Gong et al. 2019). Thus, because of climate change there is an increased need to understand how different climate variables alter movement at finer temporal scales. Having this knowledge could better equip us to manage landscapes that buffer animals from climate extremes (Elmore et al. 2017).

The Northern Bobwhite (*Colinus virginianus*; hereafter, bobwhite) is a non-migratory species that rarely engages in long-distance movements and typically remain within a few kilometers of their natal area during their lifetime (Townsend et al. 2003, Brennan et al. 2020). Because of their wide distribution across North America, bobwhite frequently experience climate extrmes in the western edge of their distribution, where periodic drought and extreme heat are common, making them an ideal species to study how different climate variables influence movement (Arndt 2003, Carroll et al. 2017, Brennan et al. 2020). Recent advancements in global positioning technology (GPS) now allow bobwhite to be fitted with this technology (Cagnacci et al. 2010) allowing us to study their movement at fine temporal scales (e.g., hourly timescales). Previous research has found that bobwhite respond to changes in their thermal environment by using taller woody cover during hotter periods and that individuals begin to show signs of thermal stress around 30 ^{o}C (Guthery et al. 2005, Carroll et al. 2017). However, studies have not explored how bobwhite change their movement in response to specific climate variables across hourly timescales. Therefore, we used bobwhite as a model to understand how a non-migratory species alters its movements in response to this. Our objective was to understand how different climate variables affect the movement ecology of a non-migratory species at a fine temporal scale (e.g, hourly timescales). Specifically, we investigated how air temperature, barometric pressure, solar radiation, relative humidity, average wind speed, average vector wind direction, fractional water index and their interactions alter the movement characteristics (i.e., hourly movement and sinuosity of a 3-hour path) of a non-migratory species throughout the day.

METHODS

Study Areas

We collected GPS data at the following wildlife management areas across western Oklahoma, USA: Cross Timbers (33.964043, -97.366169), Packsaddle (35.895249, -99.717387), Sandy Sanders (35.071182, -99.837630), and Beaver River (36.832998, -100.608260; Figure 2.1). These sites represent the wide range in climate that exists throughout western Oklahoma. During 2019-2020, air temperature ranged between -18.0–44.1 °C across our sites with mean (± SE) air temperature being 15.3 °C ±0.4 (Brock et al. 1995, McPherson et 2007). Mean (± SE) annual rainfall across these sites during 2019–2020 was 812.8 mm ±120.6, while ranging between 431.8–1,168.4 mm (Oklahoma Climatology Survey 2021). Common tree species at these sites included eastern cottonwood (*Populus deltoides*) and post oak (*Quercus stellate*). Across these sites common shrub species included shinnery oak (*Quercus havardii*), sand sagebrush (*Artemisia filifolia*), and Chickasaw plum (*Prunus angustifolia*).

Data Collection

During the study, we captured male and female bobwhite year-around using Stoddard walk-in funnel traps (Stoddard 1931, Smith et al. 1981) baited with a mixture of cracked corn (*Zea mays*) and milo (*Sorghum bicolor*) at all four wildlife management areas. Individual birds were aged, sexed, and weighed and then fitted with a 7.2 g, solar-powered GPS transmitter (Lotek, Wareham, United Kingdom; average location accuracy <15 m) that was attached by a backpack-style harness made from 4.76-mm tubular Teflon® ribbon. If we trapped a covey, we only fitted a maximum of four individuals from that covey with transmitters. This was done to maintain an adequate number individuals within a covey while maximizing the number of coveys with marked individuals as much as possible. Transmitters were only attached to bobwhite weighing ≥150 g to ensure that the transmitter weights did not exceed 5% of the bird's body weight (Bridge et al. 2011). GPS transmitters were programmed to collect 18 hourly fixes per day between 0500–2200 central daylight savings time (CDT), but fewer hourly fixes occasionally occurred due to poor satellite transmission or a low battery voltage. We did not sample between the hours of 2200–500 to conserve battery life. All trapping and handling protocols were approved by Oklahoma State University Animal Care and Use Committee (ACUP AG-18-7).

Because climate consists of many different climate variables (e.g, air temperature, solar radiation, relative humidity; Ahrens and Henson 2016) we utilized the Oklahoma Mesonet, an extensive environmental monitoring network that collects meteorological data at fine temporal across each county in Oklahoma to obtain meteorological data (Brock et al. 1995, McPherson et al. 2007). From January 2019 to December 2020 (bobwhite monitoring period), we acquired hourly weather data (air temperature, average wind speed, average vector wind direction, relative humidity, solar radiation, barometric pressure, and calibrated delta-T; Table 2.1) from the following Mesonet stations: Beaver (Beaver WMA), Arnett (Packsaddle WMA), Erick and Elk City (Sandy Sanders WMA), and Burneyville (Cross Timbers WMA). We could not record instantaneous precipitation events because Mesonet was unable to collect such data; however, collecting barometric pressure and calibrated delta-T can provide an index for rainfall events (Illston et al. 2008, Ahrens and Henson 2016). We standardized barometric pressure across all four sites by using the following equation to reduce barometric pressure to sea level (Keisan 2018):

PRES (Reduced to Sea Level) =

$p*(1-(0.0065*h)/(T\ ^{\circ}\mathrm{C}+273.15+0.0065*h))^\wedge-5.257$,

where p is barometric pressure, h is altitude, and T is air temperature.

We grouped average vector wind direction into the four cardinal directions based on their corresponding degrees. We used calibrated delta-T to calculate fractional water index (FWI) a drought index using the following equation (Illston et al. 2008):

FWI = (3.96 $^{\circ}$C – Reference Temperature Difference)/(3.96 $^{\circ}$C – 1.38 $^{\circ}$C).

Data Analysis

We excluded the first day of data collection for each bird to allow it to acclimate to the GPS transmitter. To account for GPS error, we removed all GPS fixes that were based on <4 acquired satellites or had an indicated dilution of precision >3.9. Following these corrections to the GPS fixes, average GPS error was confirmed to be <15 m (K. Andersson, Oklahoma State University, unpublished data). We also removed any duplicate fixes with the same timestamp. Because different movement metrics have been developed to describe different structural aspects of a movement path (consecutive relocations in a time series of geographic fixes), we analyzed two different movement metrics: hourly movement (displacement between two consecutive geographic fixes an hour apart) and sinuosity (form of tortuosity that determines the amount of curvature of a random search path; Bovet and Benhamou 1988, Benhamou 2004, Almeida et al. 2010, Seidel et al. 2018).

Hourly Movement: To understand how specific climate variables alter the hourly movement of bobwhite, we used the R package "amt" to calculate hourly movement (Signer et al. 2019, R Core Team 2021). We used the functions *track_resample*, *filter_min_n_burst*, and *steps_by_burst* to resample our entire dataset into a continuous series of 1-hour movements across each individual and to calculate hourly movement (Signer et al. 2019, R Core Team 2021). Using hourly movement allowed us to understand how changes in specific weather variables influence the movement of a small, non-migratory animal at a fine temporal scale. At the beginning timestamp for each hourly movement, we paired each hourly movement with the appropriate meteorological data that aligned with the correct site and timestamp.

To analyze our data, we used linear mixed-models with a log-transformed response variable using the R package "lme4" (Bates et al. 2015, R Core Team 2021) to develop models that investigate how different climate variables, and their interactions alter the hourly movement of bobwhite. We chose a linear mixed-modeling approach over a generalized mixed modeling approach with a log-link function because it better fit the distribution and model assumptions of our data. Within each model we included id nested in site as a random intercept to account for individual heterogeneity, potential pseudo-replication, uneven sampling among individuals and environmental differences between sites potentially influencing bobwhite behavior (Gillies et al. 2006, Cady et al. 2021). We removed any individuals that had less than 10 hourly movements because of data constraints when fitting a random effect structure within our models. In addition, we removed all 0 m movements were removed from the analysis because of challenges with model convergence. We scaled each continuous independent variable using the scale function because of differences in scale across the continuous independent variables (R Core Team 2021). When modeling the data, we did not include the following combinations together in models after performing a Pearson’s correlation test and graphing our data determined these combinations were moderately correlated with one another barometric pressure: air temperature (r = -0.60) and solar radiation: relative humidity (r = -0.57). Because air temperature and barometric pressure had a quadratic relationship, both variables were fit with a quadratic polynomial term when present in a model (Ostertagová 2012).

For development and testing of our models, we used an *a priori* approach to determine the most appropriate models given our data (Burnham et al. 2011). We quantified which model best supported the data by using Akaike Information Criterion using the R package “bbmle” (Bolker and R Core Team 2021). We considered models competitive if a modal had a Δ AICc <2.0 (Burnham and Anderson 2002). We graphed the raw data according to the top model by parsing solar radiation into three categories (low, medium, and high); which represented the lower 25th, 25th – 75th, and upper 75th percentiles of the data.

Sinuosity: To understand how bobwhite change their sinuosity in response to different climate variables, we used the R package “amt” to calculate sinuosity (Signer et al. 2019, R Core Team 2021). As a path becomes more tortuous, sinuosity increases in value; however, as a path become straighter the value becomes closer to 0 (Duffy et al. 2011). We used the functions *track_resample* and *filter_min_n_burst* to resample our entire dataset into a continuous series of 1-hour movements across each individual (Signer et al. 2019, R Core Team 2021). At the top of each hour, we paired each GPS location to the appropriate meteorological data that aligned with the correct site and timestamp. Because calculating sinuosity requires paths with multiple fixes, we were unable to analyze sinuosity at a one-hour scale (Duffy et al. 2011). Therefore, we split each individual bird's data into continuous 3-hour paths. We calculated sinuosity for each 3-hour path using the function *sinuosity* (Signer et al. 2019, R Core Team 2021). We also averaged each climate variable across each 3-hour path.

To analyze the data, we used gamma distributed generalized linear mixed models with log link functions using the R package "lme4" (Bates et al. 2015, R Core Team 2021) to develop models that investigate how different climate variables, and their interactions shape the sinuosity of bobwhite movements. Within each model, we included id nested in site as a random intercept. We removed paths where movement did not occur because they resulted in extreme sinuosity values, creating challenges modeling the data to a specific statistical distribution. Because barometric pressure had a quadratic relationship, we fit it with a quadratic polynomial term when included in a model (Ostertagová 2012). Our approach to model development, testing and graphing sinuosity was similar to our approach to model development and testing for hourly movement.

RESULTS

Hourly movement

During our study, we analyzed 44,026 hourly movements from 281 bobwhite, with 45% of the movements from Packsaddle (*n* = 19,814), 28% from Beaver River (*n* =

12,309), 18% from Cross Timbers (*n* = 8,010), and 9% from Sandy Sanders (*n* = 3,893). In our dataset, mean (± SE) hourly movement was 50.5 m ± 0.40 with a range from 0.04–1,882.5 m. While 99.5% (*n* = 43, 825) of hourly movements were $\leq$500 m.

We investigated 30 models to understand how different climate variables and their interactions influence the hourly movement of bobwhite. The best fit model was the interaction between air temperature and solar radiation and the interaction between solar radiation and average wind speed (Table 2.2). As the interaction between air temperature and solar radiation increased hourly movement decreased suggesting that bobwhite became more sedentary (Table 2.3). Bobwhite hourly movement exhibited a similar relationship to the interaction between solar radiation and average wind speed (Table 2.3). Across all solar radiation groups, variability in hourly movement increased as air temperature increased until 25–30 ^{o}C when hourly movement variability began to decrease (Figure 2.2). This pattern was largest during medium (38.83–666.59 Wm^{-2}) and high solar radiation (666.60–1203.12 Wm^{-2}; Figure 2.2). Variability in hourly movement was also constrained when air temperatures $\leq$0 ^{o}C occurred regardless of solar radiation intensity (Figure 2.2). During each solar radiation category, hourly movement variability was highest during periods of low average wind speed (0–5 m/s; Figure 2.3). Bobwhite became more sedentary as average wind speed increased regardless of solar radiation (Figure 2.3).

Sinuosity

We analyzed 10,008 3-hour paths from 207 bobwhite. Forty-five percent of the movements occurred at Packsaddle (*n* = 4,545), 28% at Beaver River (*n* = 2,796), 18% at

Cross Timbers (*n* = 1,836), and 8% at Sandy Sanders (*n* = 831). Mean (± SE) sinuosity for 3-hour paths across our study was 0.5 ± 0.01 with a range of 0.0003–41.4.

Similar to hourly movement, we evaluated 30 models to understand how the sinuosity of bobwhite relative to a 3-hour path is influenced by different climate variables and their interactions. The model that best described the data was the interaction between air temperature and solar radiation and the interaction between solar radiation and average wind speed (Table 2.2). Sinuosity experienced a positive relationship in response to both interactions meaning that the 3-hour path of bobwhite became more tortuous as these interactions increased (Table 2.3). However, graphing the data showed only a minimal relationship between sinuosity and these interactions (Figures 2.4–2.5).

DISCUSSION

Our study aligns with a growing body of research that indicates that specific climate variables alter animal movement (Bourgoin et al. 2011, Rakowski et al. 2019, Alston et al. 2020, Gong et al. 2020). Our findings determined that the movement of bobwhite is influenced by the interaction between climate variables. Specifically, we found that the interaction between solar radiation and air temperature and the interaction between solar radiation and average wind speed best described hourly movement. Because climate is comprised of multiple climate variables influencing each other (Ahrens and Henson 2016), it should not be surprising that some animals alter their movement in response to interactions between different climate variables. In addition, our results suggest that movement was most constrained during climate extremes. For example, variability in hourly movement was most limited when air temperatures ≤ 0 or

≥30 °C occurred throughout all solar radiation categories. Previous studies show that temperature extremes can alter an animal's position on the landscape, which can lead to constraints in useable space increasing mortality in some animals (Aublet et al. 2009, Melin et al. 2013, Carroll et al. 2015, Tanner et al. 2017). Because non-migratory species typically rely on predictable resources within a fixed home range (Maron et al. 2015), our findings suggest that increased climate extremes associated with climate change could impact the survival of many non-migratory species if animals become more sedentary and unable to access available resources (IPCC 2013).

Changes in hourly movement in response to the interaction between air temperature and solar radiation may reflect behavioral tradeoffs associated with increased hyperthermia risk caused by extreme heat (≥30 °C) and solar radiation (Boyles et al. 2011, Norris and Kunz 2012, Cunningham et al. 2021). Some animals adjust their behavior to lower hyperthermia risk by reducing their movement (Rakowski et al. 2019), locating thermal refuge to limit thermal stress (Carroll et al. 2015, Alston et al. 2020), adjusting foraging behavior (Pattinson and Smit 2017) and changing their posture (Maloney et al. 2005, Norris and Kunz 2012). However, these behavioral adjustments can be costly (Cunningham et al. 2021), as increased behavioral thermoregulation caused by increased air temperature can reduce the reproduction and foraging success (Cunningham et al. 2013, Pattinson and Smit 2017, van de Ven et al. 2020). Such implications could have lasting effects on the ability for populations to persist (Pattinson and Smit 2017, van de Ven et al. 2020). Our findings suggest that non-migratory species like bobwhite may experience increased challenges surviving climate extremes and maintain population connectivity in the future. These challenges have the potential to increase the risk of disjunct populations by disrupting gene flow and the ability to recruit individuals from nearby populations, ultimately leading to the decline of populations (Opdam 1991, Luquet et al 2011, Earl et al. 2016). However, predator avoidance could also cause shifts in movement. Because animals often use the same cover to reduce thermal and predation risks (Hiller and Guthery 2005, Milling et al. 2017), disentangling which influences movement more is challenging. Despite this, that bobwhite were more sedentary during periods of extreme hot air temperature across all solar radiation categories suggests that hyperthermia risk, not predation risk, was the primary driver of bobwhite movement during these periods. However, during thermally stressful times, predators could seek thermal refuge potentially increasing the predation risk of bobwhite in these areas.

Many studies have focused on understanding how extreme heat influences animal behavior (Carroll et al. 2017, van de Ven et al. 2020, Cunningham et al. 2021). This is warranted given that extreme heat is predicted to increase with climate change (IPCC 2013). However, climate change can cause extreme winter weather suggesting that other conditions beyond extreme heat could negatively impact animals too (Cohen et al. 2018). Some animals reduce their activity during extreme cold temperatures, likely to conserve energy (Cotton and Parker 2000). A previous study determined that mortality in bobwhite is highest when extreme cold occurs, likely a response from limited space use associated with these extremes (Tanner et al. 2017). Furthermore, increased wind speed increases the metabolic rates of some birds by heightening physiologically demands during periods with colder temperatures (Wolf and Walsberg 1996, Burger et al. 2017). During our study, air temperatures ≤0 °C occurred across 257 days suggesting that animals like bobwhite frequently experience air temperatures below freezing. Our findings show that variability in hourly movement was limited when bobwhite experienced air temperatures ≤ 0 °C in conjunction with solar radiation suggesting that these conditions can limit animal movements.

Even though we determined that the interaction of specific climate variables best described sinuosity, we found little indication that different climate variables dramatically influenced the sinuosity of this species relative to a 3-hour path. Given that our study sites represent quality habitat for this species, bobwhite may have moved directly to areas with thermal refuge during periods of thermal stress thus maintaining a straighter path. In addition, changing the temporal scale of an animal’s movement path can yield different results (Kay et al 2017). It is possible that the sinuosity of bobwhite is influenced more strongly by different climate variables at broader scales. Therefore, investigating sinuosity at a different temporal scale could have determined a stronger relationship between the sinuosity of bobwhite and specific climate variables.

As climate change continues, increasing the intensity and frequency of extreme heat and precipitation (IPCC 2013), understanding how animals respond to different climate variables is paramount to their conservation. We added to the growing body of literatures that attempts to understand how the movements of animals are influenced by climate (Aublet et al. 2009, Bourgoin et al. 2011, Alston et al. 2020, Gong et al. 2020). Our findings show that increased climate extremes could constrain the movements of bobwhite and potentially other non-migratory species. However, changes in behavior caused by these extremes could negatively impact the fitness of an individual and population dynamics of a species (Mason et al. 2017, van de Ven et al. 2020, Cunningham et al. 2021). Increased heat or cold may render large portions of the landscape unsuitable for species that require adequate thermal refuge (Carroll et al. 2016, Tanner et al. 2017). Because changes in movement patterns influence the connectivity of individuals and populations, increased climate extremes may impact the long-term survival of populations (Nathan et al. 2008, Knowlton and Graham 2010, Luquet et al. 2011, Murray et al. 2017). Therefore, managing landscapes that promote survival and population connectivity will be critical in the future. Investigating the role that the interaction of landscape and different climate variables have on animal movement is an important next step to understand how animals respond to environmental change. Such knowledge and management will be critical to the conservation of species like the bobwhite in the face of climate change.

TABLES

Table 2.1: Description of climate variables including those collected from Beaver, Arnett, Erick, Burneyville, and Elk City mesonet stations located across western Oklahoma and those calculated from mesonet data during 2019–2020. Calibrated Delta-T was used to calucate fractional water index (Illston et al. 2008).

Climate Variable	Abbrv	Units	Collection Specifics	Observed Range 2019-2020
Air Temperature	TAIR	^{o}C	1.5 m above ground	-18.0–44.1
Average Wind Speed	WS2M	ms^{-1}	2 m above ground, 5-minute average	0–17.9
Average Wind Direction	WDIR	Degrees	10 m above ground, 5-minute average	0–360
Relative Humidity	RELH	%	1.5 m above ground	5.5–100.0
Solar Radiation	SRAD	Wm^{-2}	-	0–1203.1
Barometric Pressure	PRES	Mb	-	892.7–1013.4
Fractional Water Index	FWI	-	5 cm below ground	-0.03–1.04

Table 2.2: Model comparison table showing the top 10 best fit models of the 30 models that we tested that investigated how different climate variables and their interactions alter the hourly movement and sinuosity (3-hour path) of Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019–2020.

Model Variables	df	dAICc	AICc Weight
Hourly movement			
TAIR*SRAD + TAIR^2*SRAD + WS2M*SRAD	10	0.0	1
TAIR*SRAD + TAIR^2*SRAD	8	637.6	<0.001
TAIR + TAIR^2 +WS2M*SRAD	8	654.9	<0.001
PRES*SRAD + PRES^2*SRAD + WS2M*SRAD	10	910.3	<0.001
WS2M*SRAD	6	975.4	<0.001
TAIR*WS2M + TAIR^2*WS2M + SRAD	9	1275.8	<0.001
TAIR + TAIR^2 + SRAD + FWI + WS2M + WDIRF	11	1373.6	<0.001
TAIR + TAIR^2 + FWI*SRAD	8	1383.1	<0.001
TAIR + TAIR^2 + WS2M*WDIRF + SRAD	13	1406.6	<0.001
TAIR*FWI + TAIR^2*FWI + SRAD	9	1418.8	<0.001
Sinuosity			
TAIR*SRAD + WS2M*SRAD	8	0.0	1
TAIR*SRAD	6	31.9	<0.001
PRES*SRAD + PRES^2*SRAD + WS2M*SRAD	10	35.9	<0.001
PRES*SRAD + PRES^2*SRAD	8	54.2	<0.001
TAIR + WS2M*SRAD	7	70.9	<0.001
WS2M*SRAD	6	76.6	<0.001
TAIR*FWI + SRAD	7	96.8	<0.001
TAIR + FWI*SRAD	7	97.8	<0.001
TAIR*WS2M + SRAD	7	98.5	<0.001
PRES+ PRES^2 + FWI*SRAD	8	99.0	<0.001

TAIR: air temperature; SRAD: solar radiation; WS2M: average wind speed;
WDIR: average wind vector direction; PRES: barometric pressure;
FWI: fractional water index

Table 2.3: Model output from each top model predicting hourly movement, and sinuosity (3-hour path) of Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019–2020.

Fixed Effects	Estimate	Std.Error	t-value	p-value	Random Effect (SD)
Hourly movement					
Intercept	2.946834	0.039206	75.163	<0.001	0.6180
TAIR	0.185582	0.011745	15.801	<0.001	
TAIR^2	0.035814	0.007702	4.650	<0.001	
SRAD	-0.101749	0.009887	-10.291	<0.001	
WS2M	0.052109	0.007753	6.721	<0.001	
TAIR:SRAD	-0.237976	0.009632	-24.707	<0.001	
TAIR^2:SRAD	-0.057339	0.006737	-8.511	<0.001	
SRAD:WS2M	-0.176990	0.007044	-25.128	<0.001	
Sinuosity					
Intercept	-0.89260	0.03916	-22.791	<0.001	0.7661
TAIR	-0.01920	0.01678	-1.144	0.253	
SRAD	0.08727	0.01367	6.383	<0.001	
WS2M	-0.01471	0.01222	-1.204	0.229	
TAIR:SRAD	0.10057	0.01180	8.521	<0.001	
SRAD:WS2M	0.06428	0.01093	5.882	<0.001	

TAIR: air temperature; SRAD: solar radiation; WS2M: average wind speed

FIGURES

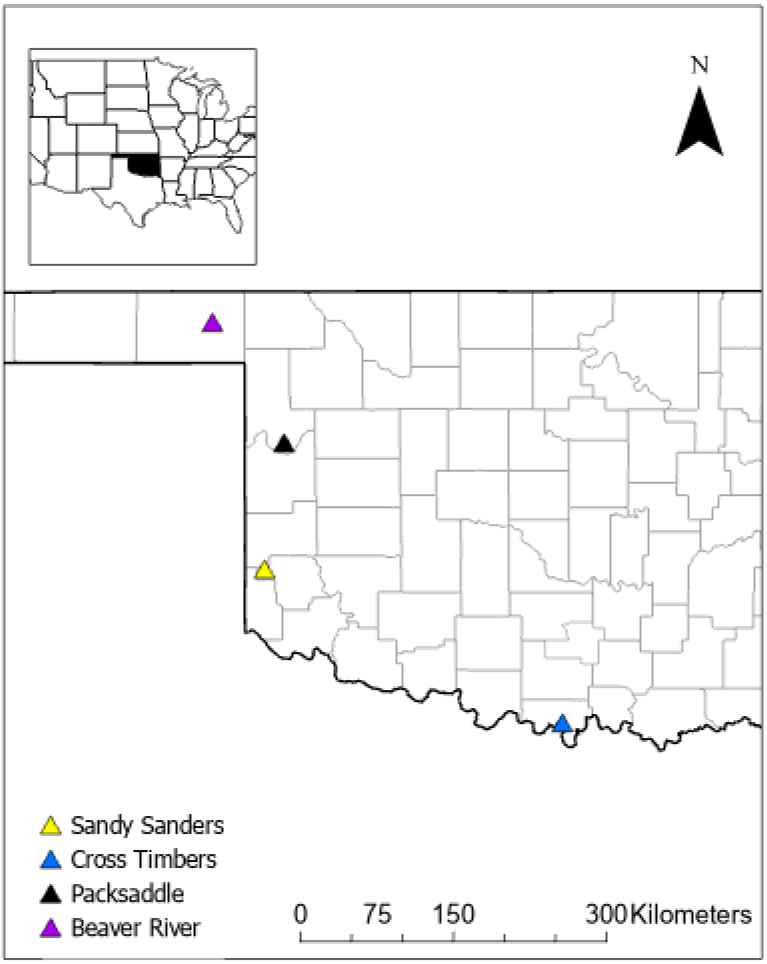


Figure 2.1: Location of the four study sites in Oklahoma where Northern Bobwhite (*Colinus virginianus*) were fitted with GPS technology and tracked during 2019–2020.

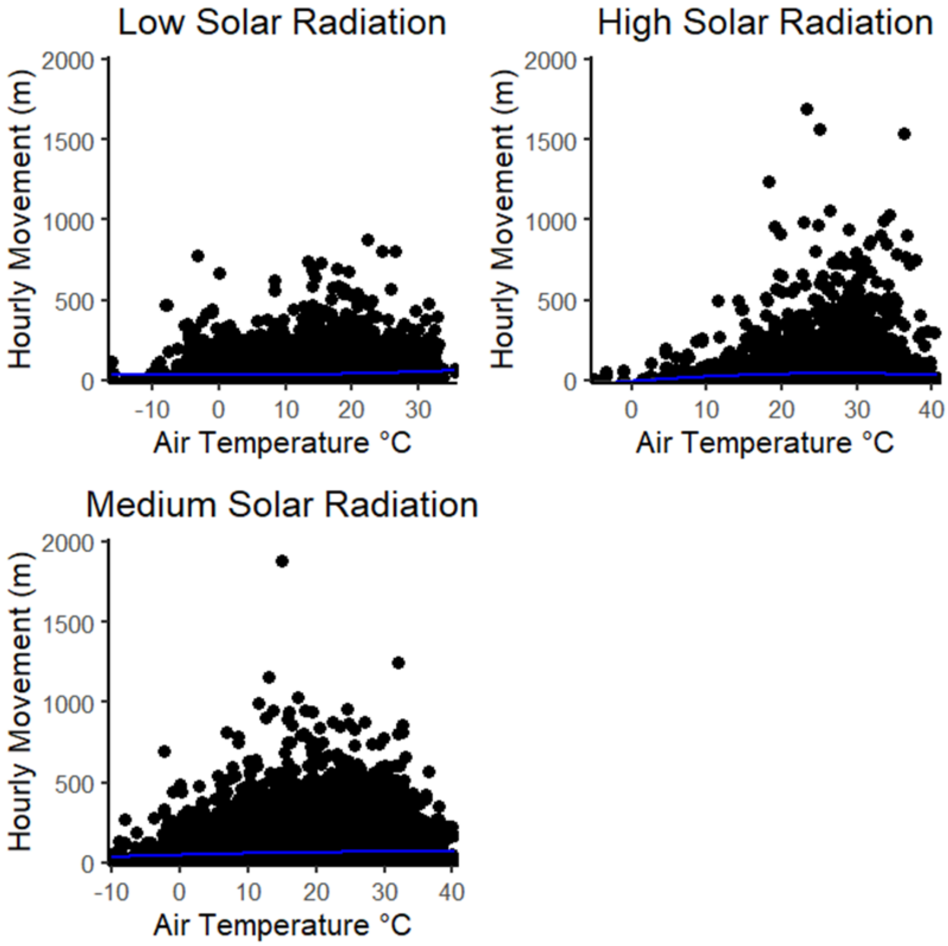


Figure 2.2: The interactive effect of air temperature and solar radiation on hourly movement from Northern Bobwhite (*Colinus virginianus*) GPS data collected from across western Oklahoma during 2019-2020. Solar radiation is displayed categorically as low (0–38.82 Wm^{-2}), medium (38.83–666.59 Wm^{-2}), and high (666.60–1203.12 Wm^{-2}); which represents the lower 25th, 25th – 75th, and upper 75th percentiles of the data. The blue line represents a regression line fitted to each solar radiation group. Because air temperature exhibited a non-linear relationship, we fit the regression line with a polynomial.

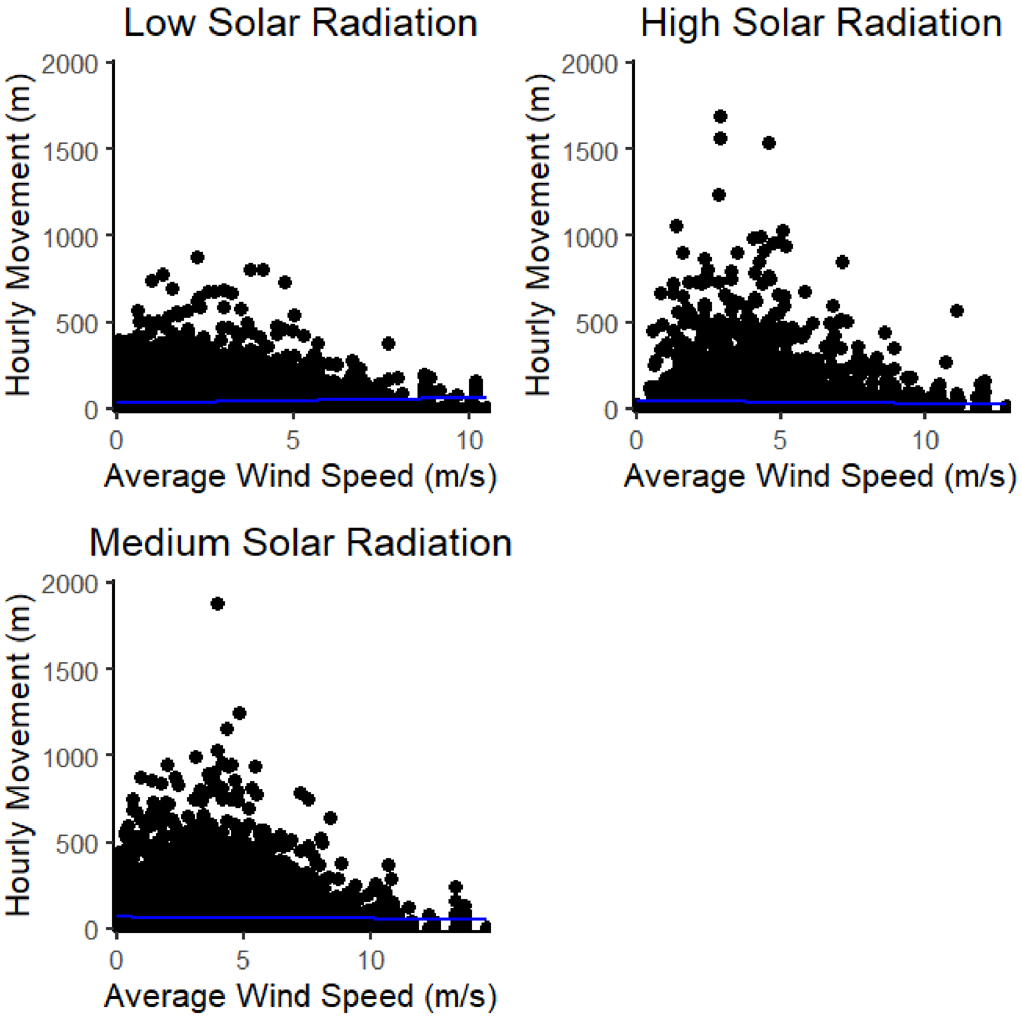


Figure 2.3: The interactive effect of average wind speed and solar radiation on hourly movement from Northern Bobwhite (*Colinus virginianus*) GPS data collected from across western Oklahoma during 2019-2020. Solar radiation is displayed categorically as low (0–38.82 Wm^{-2}), medium (38.83–666.59 Wm^{-2}), and high (666.60–1203.12 Wm^{-2}); which represents the lower 25th, 25th – 75th, and upper 75th percentiles of the data. The blue line represents a regression line fitted to each solar radiation group.

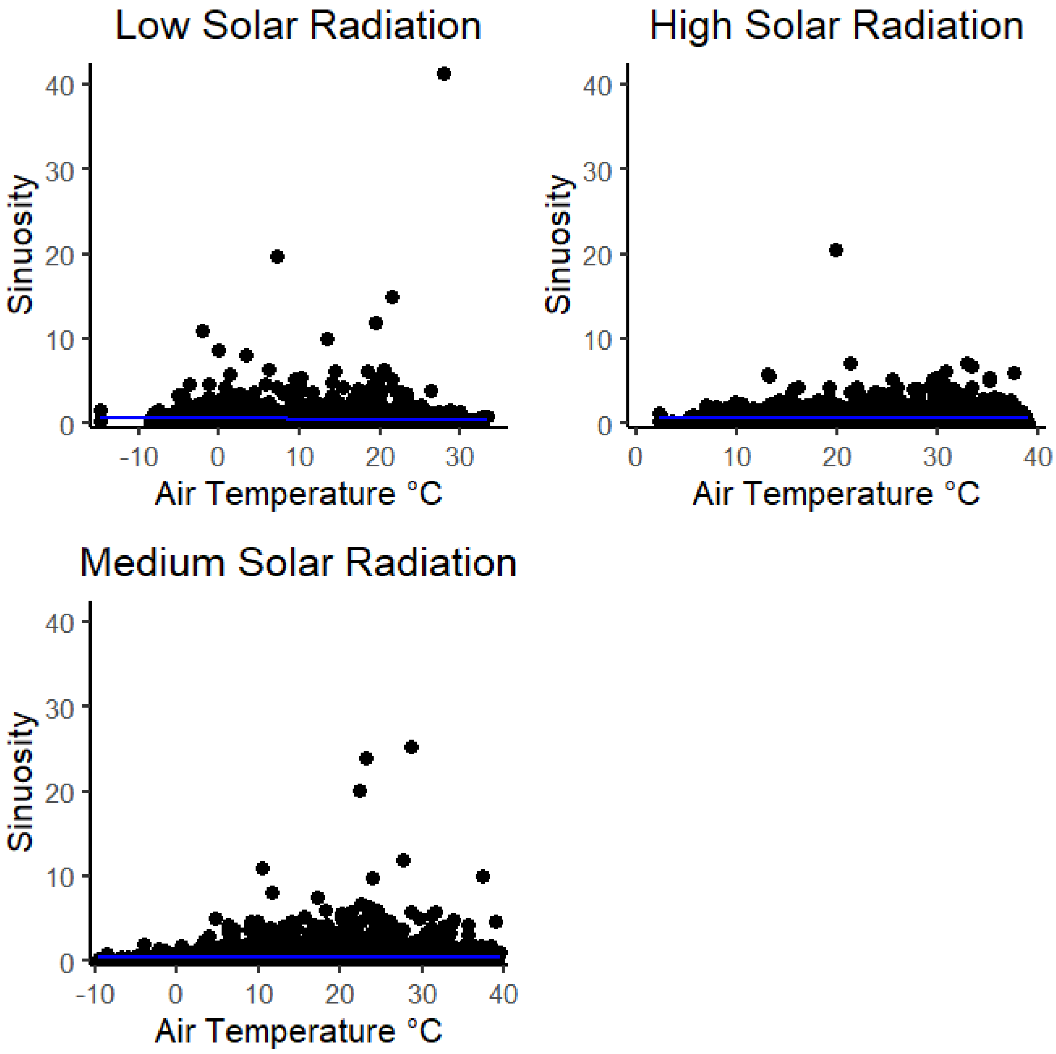


Figure 2.4: The interactive effect of air temperature and solar radiation on sinuosity calculated from 3-hour movement paths from Northern Bobwhite (*Colinus virginianus*) GPS data collected from across western Oklahoma during 2019-2020. Solar radiation is displayed categorically as low (0–90.696 Wm^{-2}), medium (90.97–659.79 Wm^{-2}), and high (659.791–1009.065 Wm^{-2}); which represents the lower 25th, 25th – 75th, and upper 75th percentiles of the data. As a path becomes more tortuous sinuosity increases in value (Duffy et al. 2011). The blue line represents a regression line fitted to each solar radiation group.

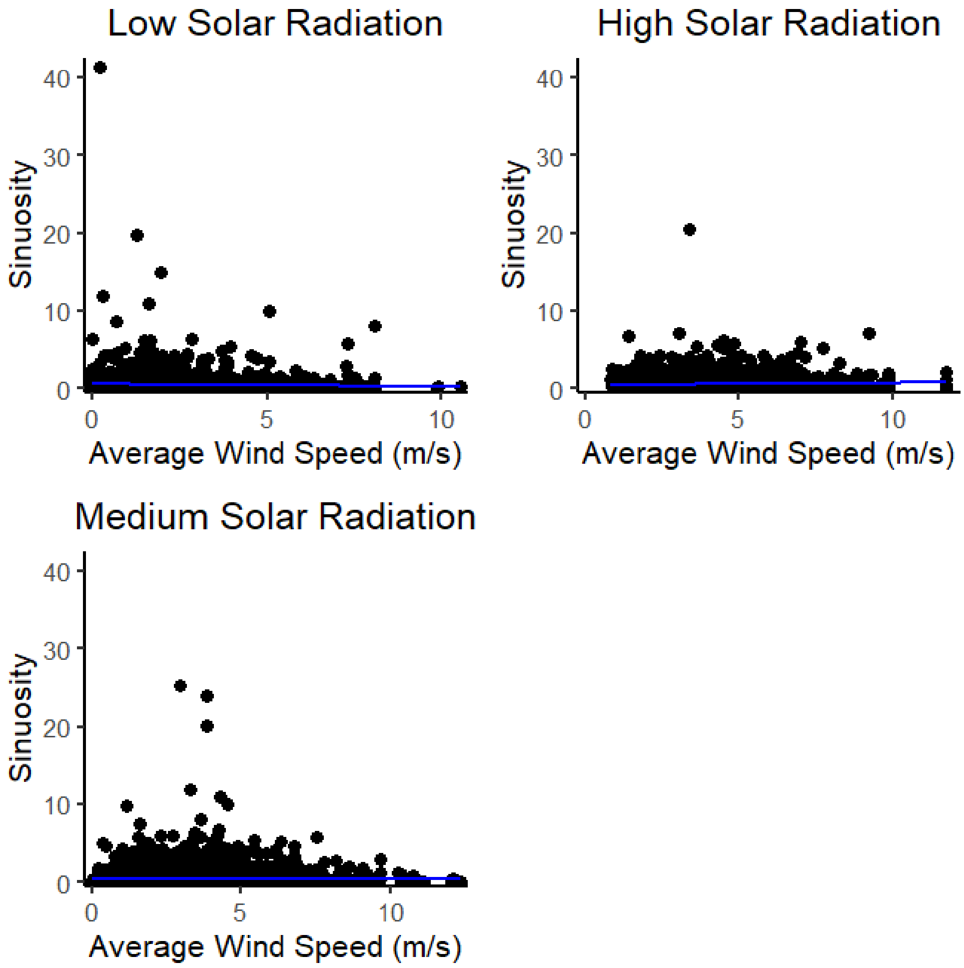


Figure 2.5: The interactive effect of average wind speed and solar radiation on sinuosity calculated from 3-hour movement paths from Northern Bobwhite (*Colinus virginianus*) GPS data collected across western Oklahoma during 2019-2020. Solar radiation is displayed categorically as low (0–90.696 Wm^{-2}), medium (90.97–659.79 Wm^{-2}), and high (659.791–1009.065 Wm^{-2}); which represents the lower 25^{th}, 25th – 75^{th}, and upper 75^{th} percentiles of the data. As a path becomes more tortuous sinuosity increases in value (Duffy et al. 2011). The blue line represents a regression line fitted to each solar radiation group.

CHAPTER III

CLIMATE EXTREMES ALTER HABITAT USE AND MOVEMENT OF A NON-MIGRATORY BIRD

ABSTRACT

Climate change is predicted to increase the intensity and frequency of climate extremes (e.g., extreme heat and drought) threatening species. Maintaining landscape heterogeneity has been argued as a potential conservation strategy to buffer animals from climate extremes. Because movement shapes survival and population connectivity, understanding how animals use habitat and move across the landscape during climate extremes will be critical for the conservation of animals effected by climate change. Non-migratory species are predicted to be more negatively impacted by climate extremes because they require predictable resources. We used the Northern Bobwhite (*Colinus virginianus*) as a model to study how climate extremes influence when a non-migratory animal uses a specific habitat and moves through the landscape. We collected global positioning system data on Northern Bobwhite across western Oklahoma during 2019–2020 and paired this data with meteorological and vegetation data. We analyzed our data differently using hourly points and 12-hour paths. Regarding our 12-hour paths analysis, we calculated three different movement metrics: cumulative distance, net displacement, sinuosity. We used a generalized linear-mixed modeling approach to analyze our data. We found that bobwhite used denser tree cover and higher normalized difference vegetation index values when hotter air temperatures and more intense solar radiation occured. Bobwhite used denser shrub cover as air temperature and average wind speed increased; however, during periods with low average wind speed bobwhite used denser shrub cover when air temperature was at or below freezing. Regarding movement, during hotter air temperatures bobwhite moved further as NDVI variance increased. However, when air temperatures at or below freezing occurred increased NDVI variance had little effect on the movement of this species. Our findings suggest that bobwhite use habitat differently during different climate extremes reinforcing the need to manage habitat that allows animals to tolerate a wide range of climate extremes. Furthermore, different climate extremes alter how animals move in respond to changes on the landscape differently. Thus, managing for landscape heterogeneity is critical to allow animals to tolerate increased climate extremes by increasing their realized thermal niche on the landscape.

INTRODUCTION

As climate change increases the intensity and frequency of climate extremes (Schär et al. 2004, IPCC 2013, Cohen et al. 2018), undersanding how animals use and move through the landscape has important implications for the long-term persistence of species impacted by climate change. Already, climate change is increasing the risk of extinction and altering the geographic distribution of some species by negatively impacting their reproduction or causing the northward expansion of species (McCarty 2001). However, the long-term impacts of climate change are likely to affect animals differently than discrete extreme climate events (McCarty 2001, Maron et al. 2015). Despite being relatively rare, climate extremes, such as extreme heat or cold, drought, can have a pronounced impact on animals (Smith et al. 2011, Maron et al. 2015, Tanner et al. 2017). For instance, climate extremes can reduce the foraging success (Pattinson and Smith 2017, van de Ven et al. 2019), body performance (Boyles et al. 2011), and movement of some animals (Carroll et al. 2015, Alston et al. 2020). Furthermore, some animals experience constraints in useable space or alter their position on the landscape in response to climate extremes (Broders et al. 2012, Tanner et al. 2017, Rakowski et al. 2019). These constraints can cause resource bottlenecks in food, water and suitable habitat leading to high mortality events potentially causing rapid declines in population size and directly altering the population dynamics of a species (Maron et al. 2015, Tanner et al. 2017). However, despite this knowledge, few studies have explicitly investigated the role that climate extremes have on the movement of animals across landscapes. Therefore, because climate extremes are projected to increase in intensity and frequency (IPCC 2013), there is a growing need to understand whether climate extremes how alter animals move across the landscape and when they use specific habitat during these extremes.

Landscape heterogeneity has been found to be important at moderating impacts of climate change by providing thermal refuge and moderating temperature on the landscape (Hovick et al. 2014, Carroll et al. 2016, Carroll et al. 2017, Londe et al 2020). Because of this, maintaining landscape heterogeneity has been argued as a potential conservation strategy to allow animals to tolerate thermal extremes (Elmore et al. 2017). We define landscape heterogeneity as the variability in vegetation structure, composition, density and biomass across a landscape that is driven by climate, disturbance events, and topographic factors (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004, Reed et al.

2009, Godfree et al. 2011). Many species regularly seek out thermal refuge during periods of extreme heat to moderate thermal conditions (Hovick et al. 2014, Melin et al. 2014, Carroll et al. 2017, Rakowski et al. 2019). Furthermore, increased landscape heterogeneity has the potential to increase the ability for animals to locate thermal refuge (Elmore et al. 2017, Londe et al. 2020). However, despite knowledge gained from previous studies (Hovick et al. 2014, Carroll et al. 2016, Carroll et al. 2017, Londe et al 2020), we know little how animals move across landscapes in the face of climate extremes and how landscape heterogeneity and connectivity of habitat influence their response to these extremes. Therefore, understanding the role of landscape heterogeneity on animal movement and habitat use during climate extremes is important for the conservation of species effected by climate change.

Non-migratory species have the potential to be negatively impacted by climate change because their limited ability to disperse long distances (Townsend et al. 2003, Maron et al. 2015, Earl et al. 2016). Climate change is predicted to alter plant communities, influencing the geographic distribution of species and increasing the potential of isolating populations (Murray et al. 2017). Because of their life history, populations of non-migratory species suffer the risk of becoming increasingly isolated, which could impact population connectivity and cause some populations to experience genetic loss reducing fitness decreasing survival (Luquet et al. 2011, van de Kerk et al. 2019). Furthermore, extreme heat restricts the ability of some animals to access more productive foraging areas on the landscape by forcing them into areas with more suitable thermal conditions (Cunningham et al. 2017, Mason et al. 2017, Pattinson and Smit 2017). This has the potential to negatively impact population dynamics by limiting access to food. Because non-migratory species typically require predictable resources, they are expected to be more severely impacted by resource constraints than other species (Maron et al. 2015). Thus, understanding how non-migratory animals move across landscapes in response to climate extremes is critical to the long-term persistence of these species, potentially threatened by increased climate extremes. Until recently, understanding movement at a fine temporal and spatial scale was limited because of technological constraints (Cagnacci et al. 2010). However, advancements in global positioning system (GPS) technology now allow a broad suite of species to be fitted with this technology creating an opportunity to understand how animals move through the landscape during climate extremes (Cagnacci et al. 2010).

The Northern Bobwhite (*Colinus virginianus*; hereafter; bobwhite) is an excellent model to investigate how climate extremes alter how an animal moves through landscape and when it uses specific habitat. Recent technological advancements now allow this species to be fitted with GPS technology. Bobwhite are a non-migratory species that frequently experience climate extremes in the western edge of their distribution, where periodic drought and heat waves are common (Arndt 2003, Carroll et al. 2017). Because bobwhite have been extensively studied (Hernández and Guthery 2012), much is known on the habitat needs and physiological limitations of this species (Guthery et al. 2005, Carroll et al. 2015, Janke et al. 2015). For instance, bobwhite readily use woody cover as thermal refuge during extreme heat (Carroll et al 2015a). In addition, bobwhite experience increased physiological demands during periods of extreme cold or heat as well as increased wind speed (Guthery et al. 2005, Burger et al. 2017). This knowledge allows us to use bobwhite as a model species to understand how climate extremes influence the movement of a non-migratory species across landscapes and when they use specific habitat.

The objective of our study was to explore how climate extremes alter when a non-migratory animal uses a specific habitat and how they move through the landscape by using movement data collected from bobwhite marked with GPS transmitters in western Oklahoma during 2019-2020. Recent advancements in GPS technology, allow us to study this at fine temporal scale and spatial scales. Because of this, we examined if a non-migratory species responds to climate extremes differently across two unique temporal scales (hourly points, and 12-hour paths; consecutive relocations in a time series of geographic fixes; Seidel et al. 2018). Previous research determined that changes in temporal scale can lead to different conclusions (Kay et al. 2017). Our study had two main objectives. First, investigate if climate extremes alter when bobwhite use specific habitat on the landscape. More specifically, we investigated whether changes in specific climate variables (i.e., air temperature, average wind speed, and solar radiation) influence when bobwhite use different types of woody cover (i.e. tree and shrub cover). Second, we determined if the daily movement of bobwhite across western Oklahoma relative to a 12-hour path changes how a non-migratory animal moves across the landscape in response to climate extremes. More specifically, we analyzed cumulative distance, net displacement, and sinuosity to understand whether bobwhite alter their daily movements in response to specific types of woody cover (i.e., tree and shrub cover) and climate variables (i.e., mean air temperature, mean solar radiation, and mean average wind speed).

METHODS

Study Area

Data were collected at the following wildlife management areas across western Oklahoma, USA: Cross Timbers (33.964043, -97.366169), Packsaddle (35.895249, -99.717387), Sandy Sanders (35.071182, -99.837630), and Beaver River (36.832998, -100.608260). Common tree species at these sites included eastern cottonwood (*Populus deltoides*) and post oak (*Quercus stellate*). Percent tree cover ranged between 0–100 (Allred et al. 2021). Across these sites common shrub species included shinnery oak (*Quercus havardii*), sand sagebrush (*Artemisia filifolia*), and Chickasaw plum (*Prunus angustifolia*). Percent shrub cover spanned between 0–100 (Allred et al. 2021). NDVI ranged between -0.65–1.0. During 2019-2020, air temperature across these sites ranged between -18.0–44.1^{o}C with mean air temperature being 15.3 ^{o}C ± 0.4 (Brock et al. 1995, McPherson et 2007). Mean annual rainfall across these sites during 2019–2020 was 812.8 mm, but ranged between 508–1155.7 mm (Oklahoma Climatology Survey 2021).

Data Collection

During 2019-2020, we captured male and female bobwhite year-around using Stoddard walk-in funnel traps (Stoddard 1931, Smith et al. 1981) baited with a mixture of cracked corn (Zea mays) and milo (Sorghum bicolor) at all four wildlife management areas. Individual birds were aged, sexed, and weighed and then fitted with a 7.2 g, solar-powered GPS transmitter (Lotek, Wareham, United Kingdom; average location accuracy <15 m) that was attached by a backpack-style harness made from 4.76-mm tubular Teflon® ribbon. When we trapped a covey, only a maximum of four individuals from that covey were fitted with transmitters, allowing us to maintain an adequate number individuals within a covey while maximizing the number of coveys with marked individuals. The high mortality rate in bobwhite (Brennan et al. 2020) and variable battery life among GPS transmitters resulted in little overlap in quail location data among individuals from the same covey, reducing pseudo-replication concerns of placing transmitters on individuals from the same covey. To ensure that the weight of the transmitter did not exceed 5% of the bird's body weight, transmitters were only attached to bobwhite weighing >150 g (Bridge et al. 2011). We programmed GPS transmitters to collect 18 hourly fixes per day between 0500–2200 central daylight savings time (CDT), however, fewer hourly fixes occasionally occurred due to poor satellite transmission or a low voltage battery. GPS data was not collected between the hours of 2200–500 to conserve battery life. All trapping and handling protocols were approved by Oklahoma State University Animal Care and Use Committee (ACUP AG-18-7).

To understand when bobwhite use specific habitat and how they move through the landscape in response to climate extremes, we used three different vegetation variables in our analyses: tree and shrub cover, and NDVI. Bobwhite readily use woody cover to survive climate extremes (Carroll et al. 2015, Janke et al. 2015). We obtained tree and shrub cover data by utilizing the rangeland analysis platform, which is a raster dataset that contains annual continuous percent land cover data for a wide variety of plant functional groups at approximately 30 m spatial resolution (Jones et al. 2018; Allred et al. 2021). These land cover data were developed from approximately 60,000 field plots in conjunction with over 200 layers of grided surface data using a random forest model to predict functional cover types across western United States (Jones et al. 2018). We obtained such data for 2018, 2019 and 2020 for each site. Mean absolute error for tree and shrub cover was 2.8 % and 5.8 %, respectively (Cover version 2.0; Allred et al. 2021). Because we were interested in understanding when bobwhite use specific habitat and move across the landscapes in response to climate extremes, utilizing tree and shrub cover from the rangeland analysis platform was appropriate for our objectives. In addition, we obtained 2018, 2019, 2020 Pléiades imagery taken during the summer (approximately 2 m spatial resolution) to calculate NDVI for each site each year when applicable. NDVI is a metric used to measure greenness and vegetation biomass on the landscape, which can be used to infer woody cover, species richness, and to measure landscape heterogeneity broadly across the landscape (Pettorelli et al. 2005, Pettorelli 2013). A previous study studying bobwhite showed that NDVI can be used to determine specific vegetation types on the landscape, including trees and shrubs (Guthery et al. 2005). Because of this, we utilized NDVI as another method to infer woody cover (i.e., trees and shrubs) broadly to understand when bobwhite use specific habitat and how landscape heterogeneity influences movement in response to climate extremes. We calculated NDVI for each year across each site using the NDVI tool in ArcPro (Esri, Redlands, CA). Because cloud cover blocked portions of imagery from Beaver River during 2019, we used the Clip Raster tool in ArcPro to remove portions of the image with clouds to avoid error when calculating NDVI.

We obtained climate data from the Oklahoma Mesonet, which is one of the most extensive environmental monitoring networks in the world that collects meteorological data at fine temporal scales across each county in Oklahoma (Brock et al. 1995, McPherson et al. 2007). We utilized this data to obtain climate data at an hourly temporal scale that fit our GPS data. We acquired hourly meteorological data (air temperature, average wind speed, solar radiation) from January 2019 to December 2020 from the following Mesonet stations: (Beaver [Beaver WMA], Arnett [Packsaddle WMA], Erick and Elk City [Sandy Sanders WMA], and Burneyville [Cross Timbers WMA]).

Data Analysis

We excluded the first day of data collection for each bird to allow it to acclimate to the GPS transmitter. To account for GPS error, we removed all GPS fixes that were marked as “fail” or “corrected” during data retrieval via satellite. This was based on <4 acquired satellites, and or with an indicated dilution of precision > 3.9. Average GPS error was confirmed to be <15 m after these corrections (K. Andersson, Oklahoma State University, unpublished data). We removed any duplicate fixes with the same timestamp.

Points Analysis: To understand if climate extremes alter when bobwhite use specific habitat, we used Program R to pair each point to the appropriate climate data that aligned with the correct site and timestamp using the function merge (R Core Team 2021). We fit each point with the correct vegetation raster data from the correct site by using the extract values to points tool in ArcPro. Because the growing season approximately starts in western Oklahoma in April (Oklahoma Climatological Survey 2021), points before April 1st were matched with the previous year’s vegetation data to better reflect the correct biomass on the ground before the growing season began. Because of this, we fit points within the following time periods with the following vegetation data: January 2019–31 March 2019:2018 data, 1 April 2019–31 March 2020:2019 data, and 1 April 2020–31

December 2020:2020 data. Points that did not have vegetation and or climate data were removed from the analysis.

We analyzed tree, shrub cover and NDVI separately. We used gamma distributed generalized linear-mixed models with log link functions using R package “lme4” (Bates et al. 2015, R Core Team 2021) to develop models that analyze whether changes in specific climate variables (i.e., air temperature, solar radiation, average wind speed), and their interactions influence when bobwhite use specific amounts of tree and shrub cover. To fit tree and shrub cover to a gamma distribution, we added 0.000001 to each value to remove any 0 values. Furthermore, we used a linear-mixed modeling approach to develop models that analyze whether certain climate variables, and their interactions alter when bobwhite use specific NDVI values using R package “lme4” (Bates et al. 2015, R Core Team 2021). For all analyses, we fit each model with a random intercept of site to account for differences in tree, shrub cover and NDVI among sites. A recent study found that bobwhite select habitat differently across different sites, thus accounting for differences across sites is important when studying bobwhite (Cady et al. 2021). We scaled each continuous independent variable using the scale function because of differences in scale across the continuous independent variables (R Core Team 2021). For development and testing of our models for each analysis, we used an a priori approach to determine the most appropriate models to test given our data (Burnham et al. 2011). A Pearson correlation test found no significant correlation ($r < -0.70$ or >0.70; Nettleton 2014) among independent variables (all $r < 0.47$). We quantified which model best supported the data by using Akaike Information Criterion using the R package “bbmle” (Bolker and R Core Team 2021). We considered models competitive if a model had a Δ AICc <2.0 (Burnham and Anderson 2002). For each analysis, we graphed the top model using bar graphs. Because each top model consisted of an interaction, we parsed solar radiation or average wind speed (depending on the top model) into three categories (low, medium, and high); which represented the lower 25th, 25th –75th, and upper 75th percentiles of the data. We also parsed air temperature into three categories (cold, medium, and hot) based on when bobwhite begin to exhibit signs of thermal stress (Guthery et al. 2005). We determined differences between air temperature for each solar radiation or average wind speed group by using a Welch's one-way ANOVA test to account for unequal variance among groups. If significant differences were detected ($p < 0.05$) we used a Games Howell test to determine which pairs between groups were significantly different.

Movement Analysis: We analyzed movement to understand how climate extremes alter how a non-migratory animal moves across the landscape relative to a 12-hour path. Because different movement metrics have been developed to describe different structural aspects of a movement path, we analyzed three different movement metrics: cumulative distance (sum of all Euclidean distances between each consecutive fix along the path), net displacement (the Euclidean distance that a bird moved from the starting fix to the ending fix of its path) and sinuosity (form of tortuosity that determines the amount of curvature of a random search path; Benhamou 2004, Almeida et al. 2010, Chiaverano et al. 2014, Seidel et al. 2018). We separated the data into a continuous series of 1-hour movements for each individual using Program R (R Core Team 2021). To convert to a 12-hour path, we parsed the data into continuous 12-hour paths (13 points) that spanned from 700 to 1900 (CDT) for each individual. One-hour movements not within the 12-hour path framework were not used for this analysis. We chose a 12-hour path because we wanted to understand how the daily movements of a bobwhite respond to specific forms of landscape hand climate extremes. Data constraints prevented us from extending the temporal scale of the path. Along each path we calculated cumulative distance, net squared displacement, and sinuosity using the following functions make_track, cum_dist, nsd, and sinuosity from the R package “amt” (Signer et al. 2019, R Core Team 2021). To convert net squared displacement to net displacement, we calculated the square root of net squared displacement to allow for simpler interpretation of the data. Along each 12-hour path, we fitted each point with the appropriate climate data that aligned with the correct timestamp and site. We averaged the data from each climate variable along each 12-hour path. Regarding vegetation data, we converted each line to a spatial line class using the function points_to_line (https://rpubs.com/walkerke/points_to_line, R Core Team 2021). Using the function extract using the R package “raster”, we extracted vegetation data along each 12-hour path. Similar to the points analysis, we fitted each line with the appropriate vegetation data that aligned with the correct growing season and site. We calculated mean and variance for each vegetation variable along each 12-hour path. Twelve-hour paths that did not contain climate and or vegetation data were removed from the analysis.

We analyzed cumulative distance, net displacement, and sinuosity separately using gamma distributed generalized linear-mixed models with log link functions using the R package “lme4” (Bates et al. 2015, R Core Team 2021) to develop models that investigated whether bobwhite alter their daily movements relative to a 12-hour path in response to woody cover and climate variables and their interactions. To fit net displacement to a gamma distribution, we added 0.000001 to every value to remove any 0 values. For each analysis, we fitted each model with a random intercept of site to account for variance among sites. Data constraints prevented us from including id within the random effect structure to account for individual heterogeneity in movement; however, this did not impact our study because we were primarily interested in understanding how bobwhite across western Oklahoma broadly move across the landscape in response to climate extremes. We scaled each continuous independent variable using the scale function because of differences in scale across the continuous independent variables (R Core Team 2021). Our approach to model development, testing, graphing and detecting differences among groups for each movement analysis was similar to our approach used for the points analysis. A Pearson correlation test found no significant correlation ($r < -0.70$ or >0.70; Nettleton 2014) among independent variables included together in the same model ($r > -0.07, < 0.24$). When graphing, we separated NDVI variance into three categories (low, medium, and high); which represented the lower 25th, 25th–75th, and upper 75th percentiles of the data.

To better understand how bobwhite moved across the landscape in response to what was available to them, we created a random path for each real path in our movement analysis. We used the move to tool within the modify tool in ArcPro to move each real path and create a random path. We used a random number generator to generate a cardinal direction and distance between 50-200 m to move the line. This prevented random lines from overlapping with real paths. Because there were no points associated with each random line, we used the generate points along line tool in ArcPro to generate points 1.9 m from each other to extract NDVI and approximately 27 m from each other to extract woody cover along each random path. Differences in distance between points were a result of differences in spatial resolution between NDVI and woody cover raster data. We used the extract values to points tool in ArcPro to extract vegetation data for each random path. Similar to our movement analysis using real paths, we fit each line with the appropriate vegetation data that aligned with the correct growing season and site. We calculated summary statistics for real and random paths to understand better how bobwhite moved in response to what was available to them on the landscape. To test if there were differences between specific vegetation variables between actual and random paths, we utilized a Welch's t-test to account for unequal variances among groups.

RESULTS

Points Analysis

During the study, we analyzed 61,451 points from 315 bobwhite. Across the sites, 43% of movements were at Packsaddle (n = 26,570), 30% at Beaver River (n = 18,183), 18% at Cross Timbers (n = 11,082), and 9% at Sandy Sanders (n = 5,616). Overall mean ± SE percent tree cover and shrub cover used by bobwhite was 11.8 % ± 0.06 and 15.3 % ± 0.06 even though bobwhite used a wide range of tree and shrub cover (0–100%, 0–97%, respectively). During our study, bobwhite used a mean ± SE NDVI value of 0.54 ± 0.001, while using a wide range of NDVI values from -0.04–0.87.

Tree Cover – We evaluated 7 models to understand whether specific climate variables and their interactions alter when bobwhite use specific amounts of tree cover. The best-fit model was the interaction between air temperature*solar radiation (Table 3.1). We found no evidence for similar competing models (Table 3.1). Overall, the interaction of different climate variables altered when bobwhite used specific amounts of tree cover. Bobwhite used denser tree cover during medium (0.01–29.99 ^{o}C) and hot (30.0–40.62 ^{o}C) air temperature than during cold air temperature (-16.08–0.0 ^{o}C) regardless of solar radiation (Figure 3.1). A Welch's one-way ANOVA showed that during low (0.0–4.979 Wm^{-2}) and medium (4.98–618.60 Wm^{-2}) solar radiation, bobwhite used significantly different amounts of tree cover across air temperature groups (Low: $F_{2, 329.0} = 121.9$, Medium: $F_{2, 2253.1} = 125.3$, all p <0.001). Investigating further, a Games Howell test found that during these solar radiation groups, bobwhite used significantly thicker tree cover during medium and hot air temperature than during cold air temperature (all p <0.001; Figure 3.1). Interestingly, during medium solar radiation, bobwhite used significantly denser tree cover when medium air temperature occurred than during hot air temperature (p <0.001; Figure 3.1). However, mean (± SE) tree cover used by these animals during medium and hot air temperature was similar (12.1 % ± 0.1 and 10.9 % ± 0.2, respectfully) suggesting that this statistical difference may not be biologically significant. During high solar radiation (618.601–1203.12 Wm^{-2}), we found that there were no significant differences in mean tree cover used by bobwhite among air temperature groups ($F_{2, 81.0} = 2.5$, $p = 0.09$). Limited cold air temperature data during high solar radiation likely attributed to this. Despite this, during high solar radiation, bobwhite still used denser tree cover during medium and hot air temperature than cold air temperature.

Shrub Cover – We investigated 7 models to determine whether changes in specific climate variables and their interactions influence when bobwhite use specific amounts of shrub cover. The only competitive model was the interaction between air temperature and average wind speed (Table 3.1). Bobwhite used specific amounts of shrub cover as the interaction between average wind speed and solar radiation increased. Our analysis showed that mean shrub cover used by bobwhite was significantly different among the air temperature groups during low average wind speed (Low: $F_{2,\ 1300.0} = 12.9$, $p < 0.001$). Within this group, we determined that bobwhite used significantly denser shrub cover during cold and medium air temperature than during hot air temperature (all $p < 0.001$; Figure 3.2). In addition, a Welch's one-way ANOVA found that bobwhite used significantly different amounts of shrub cover among air temperature groups when medium and high average wind speed occurred (Medium: $F_{2,\ 2406.9} = 59.5$, High: $F_{2,\ 643.3} = 53.0$, all $p < 0.001$). A Games Howell test showed that when medium or high solar radiation occurred bobwhite used significantly thicker shrub cover between each air temperature group as air temperature intensity increased (all $p < 0.001$; Figure 3.2).

NDVI – Similar to tree and shrub cover, we evaluated 7 models. The best-fit model was the interaction between air temperature and solar radiation (Table 3.1). We found no evidence that other models should be considered (Table 3.1). We determined that bobwhite used significantly different NDVI values among air temperature categories across each solar radiation group (Low: $F_{2,\ 322.5} = 225.2$, Medium: $F_{2,\ 1988.5} = 199.7$, High: $F_{2,\ 80.1} = 29.2$ all $p < 0.001$). Across all solar radiation intensities, a Games Howell test found that bobwhite used significantly higher NDVI values during medium and hot air temperature than when cold air temperature occurred (all $p < 0.001$; Figure 3.3). During medium and high solar radiation, we determined that mean NDVI used by bobwhite was significantly different between medium and hot air temperature, despite being nearly identical, suggesting that these differences may not be biologically significant (all $p < 0.05$; Figure 3.3).

Movement Analysis

We analyzed 812, 12-hour paths (10,556 points) from 195 bobwhite during the study. Across the sites, 55% of movements were at Packsaddle (n = 446), 26% at Beaver River (n = 212), 14% at Cross Timbers (n = 111), and 5% at Sandy Sanders (n = 43). Mean ± SE cumulative distance was 615.9 m ± 14.8 with cumulative distance ranging between 8.5–2,997.1 m. Fifty-two percent (n = 422) of 12-hour paths had a cumulative distance of >500 m. Mean ± SE net displacement was 172.6 m ± 5.5 with net displacement ranging from 0.0–1,583.6 m. Only 3% (n = 22) of 12-hour paths had a net displacement >500 m. Across our dataset, mean ± SE sinuosity was 0.09 ± 0.004 with sinuosity ranging between 0.003–1.15. Two percent (n = 14) of 12-hour paths had a sinuosity value >0.5. We observed that all vegetation variables, except NDVI mean, were similar between actual and random paths suggesting that other factors such as climate extremes drive when bobwhite use specific habitat and move across the landscape (all $p > 0.05$; Table 3.2). A Welch's t-test determined that there were differences between actual and random paths between NDVI mean ($p = 0.04$); however, both paths exhibited similar values suggesting that this difference was not biologically significant (Table 3.2).

Cumulative Distance – We evaluated 28 models to investigate how woody cover and climate variables and their interactions alter the cumulative distance of bobwhite relative to 12-hour path. The top model that best explained our data was the interaction between NDVI variance*mean air temperature (Table 3.3). We found no evidence for similar competing models (Table 3.3). Overall, the interaction between variance on the landscape and changes in temperature altered how bobwhite moved across the landscape. During cold air temperature (-9.61–0.0 ^{o}C) changes on the landscape had little effect on bobwhite cumulative distance. For example, mean cumulative distance was <500 m during cold air temperature regardless of NDVI variance (Figure 3.4). However, during medium (0.01–29.99 ^{o}C) and hot (30.0–34.88 ^{o}C) air temperature variance in the landscape exhibited a pronounced effect on cumulative distance of bobwhite. When these air temperatures occurred, bobwhite exhibited longer cumulative distance as NDVI variance increased (Figure 3.4). A Welch's one-way ANOVA determined cumulative distance moved by bobwhite was only significantly different among NDVI variance categories during medium and hot air temperature (Medium: $F_{2,\ 402.4} = 35.3$, Hot: $F_{2,\ 21.3} = 4.8$, all $p < 0.05$; Figure 3.4). Further, investigation using a Games Howell test showed that within medium air temperature the cumulative distance of bobwhite became significantly larger as NDVI variance increased between groups (all $p < 0.01$; Figure 3.4). Despite noting similar trends during hot air temperature, the mean cumulative distance was only significantly greater between low (0.000048–0.00329) and medium (0.0033–0.010) NDVI variance ($p < 0.05$; Figure 3.4).

Net Displacement – Similar to cumulative distance, we investigated 28 models. The best-fit model was the interaction between NDVI variance and mean air temperature (Table 3.3). Our analysis determined that 1 model (NDVI variance) was competitive to the top model suggesting that mean air temperature may not be an important predictor of net displacement in bobwhite (Δ AICc = 1.1; Table 3.3). The interaction between the landscape and air temperature shaped the net displacement of bobwhite differently. For instance, we found that during cold air temperature bobwhite mean net displacement was similar regardless of NDVI variance (medium: x̄ = 168.1±38.2, low: x̄ = 116.0±29.4, high: x̄ = 99.4±36.0). However, changes in landscape heterogeneity in conjunction with warmer air temperatures influenced bobwhite net displacement. As NDVI variance increased, mean net displacement of bobwhite increased when medium (low: x̄ = 125.6±9.4, medium: x̄ = 185.7±8.4, high: x̄ = 201.8±12.4) and hot air temperature (low: x̄ = 107.5±19.8, medium: x̄ = 139.4±23.1, high: x̄ = 241.2±67.8) occurred. Despite these trends, a Welch's one-way ANOVA test determined that bobwhite net displacement was only significantly different among NDVI variance groups during medium air temperature ($F_{2, 415.9} = 16.1$, $p < 0.001$). Within medium air temperature, a Games Howell test found that during medium and high (0.010001–0.039) NDVI variance bobwhite exhibited longer mean net displacement than during low NDVI variance (all $p < 0.001$).

Sinuosity – Between the 28 models that we tested the top model was the interaction between NDVI variance and mean solar radiation (Table 3.3). We found that 1 model (NDVI variance*mean average wind speed) was competitive against the top model suggesting that other climate variables when interacting with NDVI variance may influence sinuosity (Δ AICc = 1.1; Table 3.3). We determined that the movement paths of bobwhite were most tortuous when they were in areas with low NDVI variance regardless of mean solar radiation group (Figure 3.5). However, a Welch's one-way ANOVA only showed that mean sinuosity of bobwhite was only significantly different among NDVI groups during medium (329.29–546.81 Wm^{-2}) and high (546.811–669.83 Wm^{-2}) solar radiation (Medium: $F_{2, 213.9} = 7.0$, High: $F_{2, 85.3} = 5.5$, all $p < 0.01$; Figure 3.5). Within groups, a Games Howell test determined that during these solar radiation categories, bobwhite movement paths were significantly less tortuous during medium and high NDVI variance than during low NDVI variance (all *p* <0.01; Figure 3.5).

DISCUSSION

Our study determined that habitat use and animal movement is linked together by the interaction between changes on the landscape and climate extremes. We analyzed our GPS data using a unique approach by analyzing both hourly points and 12-hour paths. Both analyses found that simply analyzing how an animal uses habitat and moves across the landscape without accounting for climate extremes would likely lead to erroneous results. Previous studies show that some species alter their position on the landscape in response to climate extremes (Aublet et al. 2009, Carroll et al. 2015, Rakowski et al. 2019, Alston et al. 2020). However, we went further by quantifying how an animal uses a particular habitat type during specific climate extremes. For example, bobwhite used denser tree cover as it got hotter regardless of solar radiation. Our findings show that non-migratory species such as bobwhite likely will increasingly require woody cover to survive hotter climate extremes in the future, potentially creating a conservation paradox given the ongoing concerns regarding the impacts of increased woody encroachment on the conservation of North American grasslands (Ratajczak et al. 2012, Archer et al. 2017). Furthermore, we noted that bobwhite moved differently in response to the interaction between changes on the landscape and climate extremes. For example, during cold air temperature increased variance on the landscape had little effect on bobwhite movement; however, during hotter air temperatures bobwhite moved further as they experienced increased variance on the landscape. Previous studies show that animal movement is altered by climate extremes (George et al. 2015, Pattinson and Smith 2017, Alston et al. 2020). However, our findings suggest that to fully understand animal movement we must include landscape and climate related factors when studying movement. Finally, both analyses determined that a non-migratory animal uses specific habitat and move through the landscape differently in response to different climate extremes. Thus, managing for landscape heterogeneity to provide animals with an increased realized thermal niche will be essential to conserve species effected by climate change in the future (Elmore et al. 2017).

We determined that climate extremes change when a non-migratory bird uses a specific habitat. For instance, bobwhite used denser woody cover as the interaction between air temperature and solar radiation increased. This aligns with previous studies that show that some animals use habitat differently based on changes in air temperature (Carroll et al. 2017, Alston et al. 2020). Therefore, analyzing habitat use without accounting for climate extremes could hinder our ability to understand how animals use habitat by oversimplifying our understanding of the drivers behind habitat selection. Furthermore, we argue that analyzing habitat from a use versus available perspective is irrelevant to animals whose survival may hinge on locating a specific habitat type during a particular climate extreme. Previous research show that climate extremes can cause constraints in useable space and increase mortality (Tanner et al. 2017). In addition, climate change is expected to exacerbate resource bottlenecks including both food and cover increasing mortality (Maron et al. 2015). Therefore, an animal’s survival may depend on it locating a particular set of habitat requirements during certain climate extremes. Our study determined that bobwhite use habitat differently during different climate extremes. Because of this analyzing habitat selection broadly from a use vs available perspective is not practical in a future with increase climate extremes. This is likely to be further exacerbated in the future when finding suitable thermal refuge is likely to become even more critical and difficult because of climate change (Carroll et al. 2016). For sedentary species like bobwhite, these concerns are amplified because of their inability to move long distances (Brennan et al. 2020, Marson et al. 2015). Thus, accounting for climate extremes when modeling habitat use is critical if we want to understand how to conserve species effected by climate change. Our study suggests that some animals require a broad range habitat requirement to survive a multitude of climate extremes. Thus, managing for landscape heterogeneity to increase the ability for species to tolerate climate extremes is increasingly important for the long-term survival of species like bobwhite in a changing world.

Landscape heterogeneity may influence the role that climate extremes have on animal movement. For example, our findings determined that bobwhite moved further during extreme heat as NDVI variance increased. This is contrary to previous studies that suggest that some animals reduce their movement during hotter air temperatures (Carroll et al. 2015, Alston et al. 2020, Gong et al. 2020). We hypothesize that bobwhite present in highly heterogenous landscapes moved to areas with thermal refuge when extreme heat occurred, increasing their movement. However, individuals present in rather homogeneous environments were likely in a resource scarce environment with nowhere to go when extreme heat occurred. We noted additional support for this hypothesis given that paths became straighter as NDVI variance increased, in conjunction with solar radiation, suggesting that individuals in landscapes with increased variance were moving directly to a resource. Our findings clearly show that changes on the landscape and climate extremes together influence animal movement. However, differences in movement pattern related to this interaction may have their own costs. For example, changes in behavior caused by extreme heat can limit an animal's ability to forage efficiently and care for young, possibly negatively impacting survival and population dynamics of a species (van de Ven et al. 2019, van de Ven et al. 2020, Cunningham et al. 2021). In addition, because extreme heat increases resting metabolic rate in animals (Whitfield et al. 2015, Cunningham et al. 2021), animals may be forced to forage during these extremes increasing their exposure to predation. These findings further stress the point that managing for landscape heterogeneity is crucial for animal's ability to tolerate thermal stress by increasing its realized thermal niche on the landscape (Elmore et al. 2017).

During cold air temperature, increased variance on the landscape had little effect on the movement of bobwhite. For example, when cold air temperature occurred mean cumulative distance was <500 m regardless of NDVI variance. Unlike our previous findings showing that bobwhite moved further as NDVI variance increased during medium and hot air temperature, our findings suggest that cold air temperatures alone may influence movement more strongly than the interaction between cold air temperature and changes on the landscape. This further indicates that different climate extremes alter how some animals move in response to changes on the landscape differently Our study is not the first to indicate that some animals reduce their movement during colder air temperatures (Cotton and Parker 2000, George et al. 2015). However, other animals increase their movement during colder air temperatures (Alston et al. 2021). Physiological and behavioral differences associated with temperature could cause animals to move differently during colder air temperatures (Terrien et al. 2011, Buckley et al. 2012). Our study suggests that colder climate extremes alone shape movement differently than other climate extremes. Despite this, mean cold air temperature and mean low solar radiation rarely occurred during a 12-hour path during our study thus limiting our data on this topic. Future studies should investigate this relationship in colder or wetter climates where these extremes occur more frequently.

As climate continues to threaten ecosystems and biodiversity across the globe (McCarty 2001), managing landscapes that buffer animals from climate extremes will be vital to the long-term persistence of animals impacted by climate change. Our findings stress the importance of managing landscapes in a heterogeneous way that provide species with habitat across a broad range of climate extremes. Managing for landscape heterogeneity can increase and stabilize species diversity and ecosystem functions (Isbell et al. 2011, Hovick et al 2015, Fuhlendorf et al. 2017). Because climate extremes can constrain space use and increase mortality (Maron et al. 2015, Tanner et al. 2017), managers need to manage for the extremes compared to the average to promote the survival and connectivity of populations on the landscape. As climate extremes increase in intensity and frequency (IPCC 2013), climate change will exacerbate the need to manage this way. Our data shows that traditional methods analyzing habitat as use vs available may not be useful in a changing world. Lastly, we determined that climate influences how some animals use habitat and move through a landscape. Future studies should consider both landscape and climate when attempting to understand animal habitat use and movement. This knowledge betters equips scientists and managers with the ability to conserve species effected by climate change promoting the long-term persistence of populations in a changing world.

TABLES

Table 3.1: Model comparison table investigating the influence of air temperature, average wind speed, and solar radiation on tree and shrub cover and NDVI used by Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019-2020.

Model Variables	df	Δ AICc	AICc Weight
Tree Cover			
Air Temperature*Solar Radiation	6	0.0	1
Solar Radiation	4	18.1	<0.001
Solar Radiation*Average Wind Speed	6	18.2	<0.001
Air Temperature*Average Wind Speed	6	51.0	<0.001
Air Temperature	4	84.9	<0.001
Average Wind Speed	4	105.6	<0.001
Null	3	135.8	<0.001
Shrub Cover			
Air Temperature*Average Wind Speed	6	0.0	0.9938
Air Temperature*Solar Radiation	6	10.2	0.0062
Air Temperature	4	31.2	<0.001
Solar Radiation*Average Wind Speed	6	82.7	<0.001
Solar Radiation	4	93.9	<0.001
Null	3	96.4	<0.001
Average Wind Speed	4	96.9	<0.001
NDVI			
Air Temperature*Solar Radiation	6	0.0	1
Air Temperature*Average Wind Speed	6	78.4	<0.001
Air Temperature	4	96.0	<0.001
Solar Radiation*Average Wind Speed	6	262.7	<0.001
Solar Radiation	4	296.0	<0.001
Average Wind Speed	4	704.4	<0.001
Null	3	707.4	<0.001

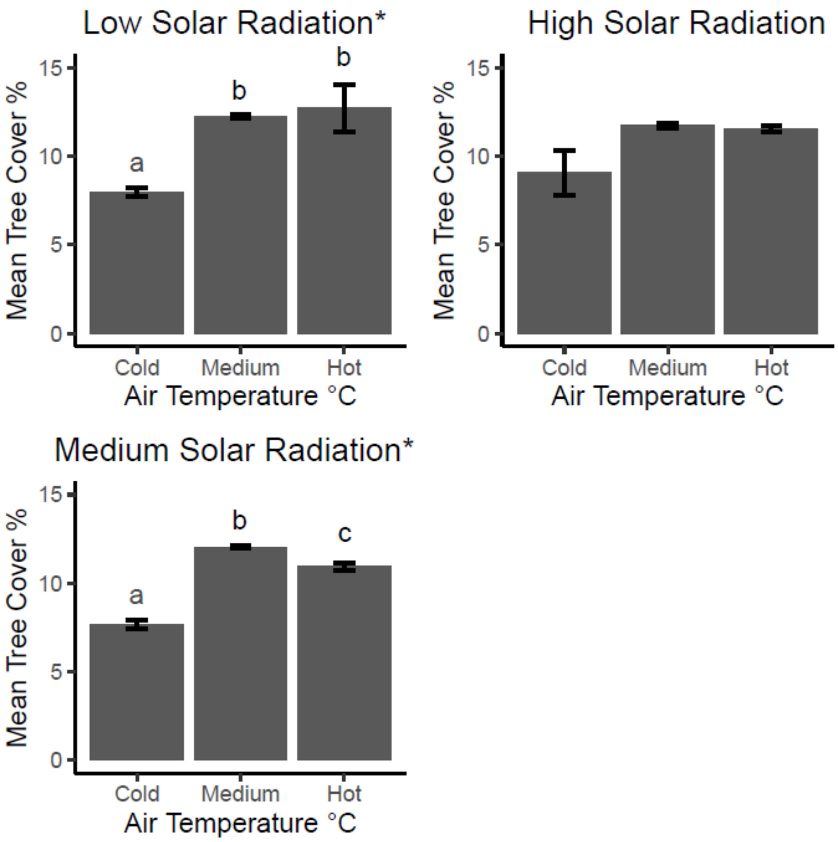
Table 3.2: Summary statistics calculated for each vegetation variable from actual and random paths generated from 812 12-hour Northern Bobwhite (*Colinus virginianus*) paths during 2019-2020.

Actual Paths			
Landscape Variable	Mean±SE	SD	Range
Trees Mean (%)	10.0±0.4	11.1	0.2–67.4
Trees Variance	26.4±1.8	51.5	0.0–447.4
Shrubs Mean (%)	16.0±0.4	12.6	0.0–67.9
Shrubs Variance	61.8±3.4	95.9	0.0–1086.2
NDVI Mean	0.50±0.01	0.14	0.17–0.83
NDVI Variance	0.01±0.0002	0.01	0.00005–0.04
Mean Air Temperature ^{o}C	18.9±0.3	8.7	-9.6–34.9
Mean Solar Radiation (Wm^{-2})	428.2±5.1	144.6	47.8–669.8
Mean Average Wind Speed (m/s)	3.5±0.1	1.5	0.7–12.3
Random Paths			
Landscape Variable	Mean±SE	SD	Range
Trees Mean (%)	9.8±0.4	11.5	0.0–100.0
Trees Variance	30.4±2.3	66.9	0.0–575.8
Shrubs Mean (%)	15.9±0.5	12.9	0.0–66.8
Shrubs Variance	67.0±4.1	118.0	0.0–1338.5
NDVI Mean	0.48±0.01	0.14	0.15–0.85
NDVI Variance	0.01±0.0002	0.01	0.00002–0.05

Table 3.3: Model comparison table showing the top 5 best fit models that investigated the influence of woody cover and different climate variables on cumulative distance, net displacement, and sinuosity relative to a 12-hour path from Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019-2020.

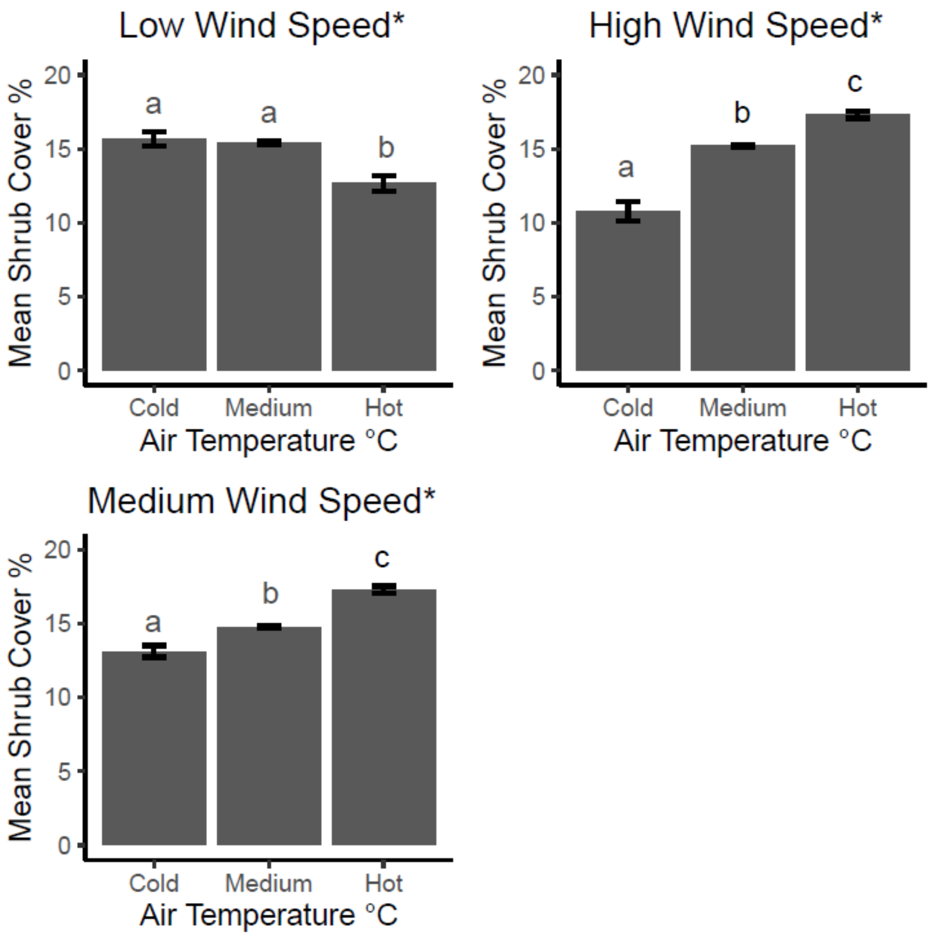
Model Variables	Df	Δ AICc	AICc Weight
Cumulative Distance			
NDVI Variance*Mean Air Temperature	6	0.0	0.9946
NDVI Variance*Mean Solar Radiation	6	11.5	0.0031
NDVI Variance	4	13.4	0.0012
Tree Variance*Mean Air Temperature	6	14.9	<0.0010
NDVI Variance*Mean Average Wind Speed	6	15.0	<0.0010
Net Displacement			
NDVI Variance*Mean Air Temperature	6	0.0	0.4037
NDVI Variance	4	1.1	0.2356
NDVI Variance*Mean Solar Radiation	6	2.2	0.1353
Tree Variance*Mean Air Temperature	6	3.9	0.0562
Tree Mean*Mean Air Temperature	6	4.2	0.0492
Sinuosity			
NDVI Variance*Mean Solar Radiation	6	0.0	0.5890
NDVI Variance*Mean Average Wind Speed	6	1.1	0.3470
NDVI Variance	4	5.5	0.0390
NDVI Variance*Mean Air Temperature	6	6.3	0.0250
Shrub Variance*Mean Average Wind Speed	6	26.4	<0.0010

FIGURES



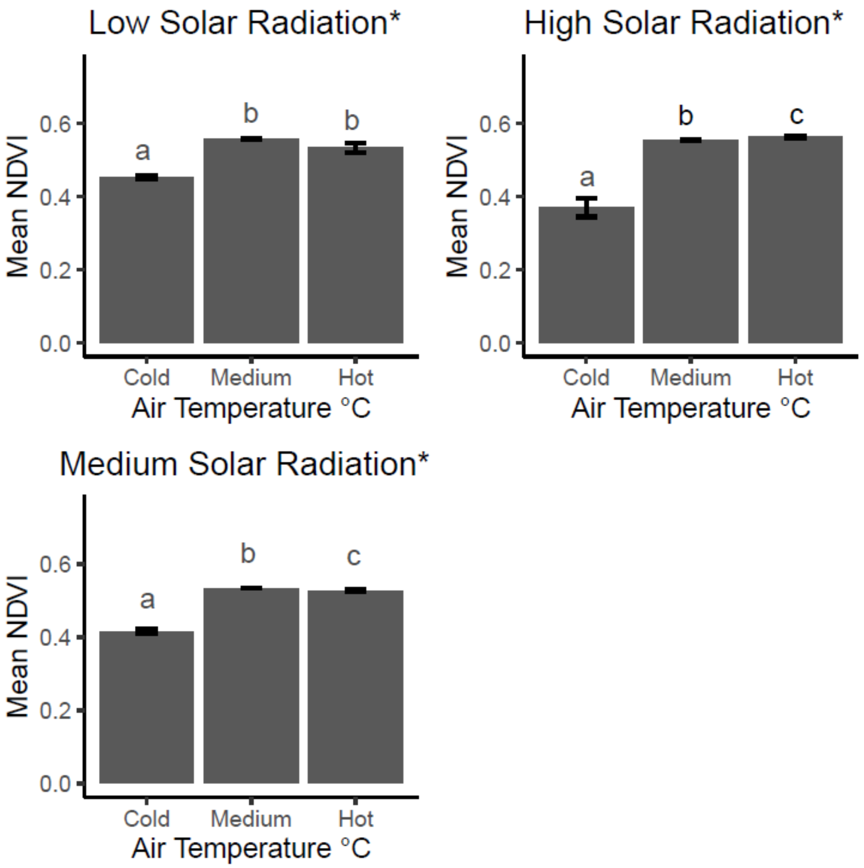
* Welch’s ANOVA *p* <0.001

Figure 3.1: Mean tree cover used by Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019-2020 in response to the interaction of solar radiation and air temperature. Solar radiation was grouped categorically as low (0–4.979 Wm^{-2}), medium (4.98–618.60 Wm^{-2}), and high (618.601–1203.12 Wm^{-2}); which represents the lower 25th, 25th – 75th and upper 75th percentiles of the data. Air temperature was grouped categorically as cold (-16.08–0.0 ^{o}C), medium (0.01–29.99 ^{o}C), and hot (30.0–40.62 ^{o}C) based on freezing and when bobwhite show signs of thermal stress (Guthery et al. 2005). Standard error bars shown to show the spread of the mean. Means with different letters are significantly different (Games Howell test, $p \leq 0.001$).



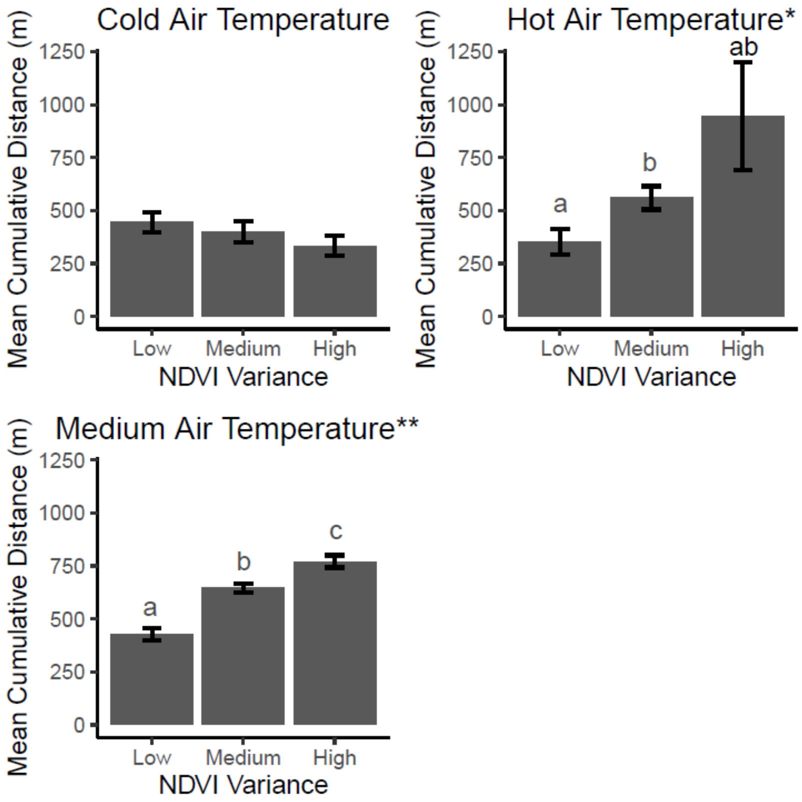
* Welch's ANOVA p <0.001

Figure 3.2: Mean shrub cover used by Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019-2020 in response to the interaction of average wind speed and air temperature. Average wind speed is grouped categorically as low (0–1.679 m/s), medium (1.680–4.38 m/s), and high (4.381–16.69 m/s); which represents the lower 25th, 25th – 75th and upper 75th percentiles of the data. Air temperature was grouped categorically as cold (-16.08–0.0 ^{o}C), medium (0.01–29.99 ^{o}C), and hot (30.0–40.62 ^{o}C) based on freezing and when bobwhite show signs of thermal stress (Guthery et al. 2005). Standard error bars shown to show the spread of the mean. Means with different letters are significantly different (Games Howell test, p <0.001).



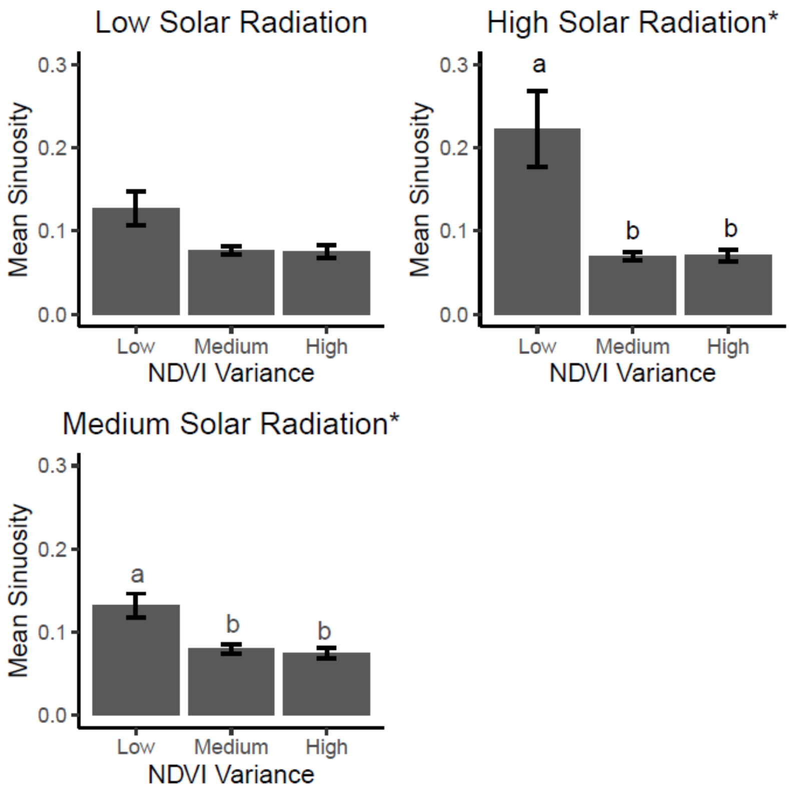
* Welch's ANOVA *p* <0.001

Figure 3.3: Mean NDVI used by Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019-2020 in response to the interaction of solar radiation and air temperature. Solar radiation was grouped categorically as low (0–4.979 Wm^{-2}), medium (4.98–618.60 Wm^{-2}), and high (618.601–1203.12 Wm^{-2}); which represents the lower 25th, 25th – 75th and upper 75th percentiles of the data. Air temperature is grouped categorically as cold (-16.08–0.0 ^{o}C), medium (0.01–29.99 ^{o}C), and hot (30.0–40.62 ^{o}C) based on freezing and when bobwhite show signs of thermal stress (Guthery et al. 2005). Standard error bars shown to show the spread of the mean. Means with different letters are significantly different (Games Howell test, *p* <0.05).



* Welch’s ANOVA p <0.05
** Welch’s ANOVA p <0.001

Figure 3.4: Mean cumulative distance from 812 12-hour movement paths from Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019-2020 in response to the interaction between NDVI variance and mean air temperature. NDVI variance was grouped categorically as low (0.000048–0.00329), medium (0.0033–0.010), and high (0.010001–0.039); which represents the lower 25th, 25th – 75th, and upper 75th percentiles of the data. Mean air temperature was grouped categorically as cold (-9.61–0.0 °C), medium (0.01–29.99 °C), and hot (30.0–34.88 °C) based on freezing and when bobwhite show signs of thermal stress (Guthery et al. 2005). Standard error bars shown to show the spread of the mean. Means with different letters are significantly different (Games Howell test, p <0.05).



* Welch's ANOVA p <0.01

Figure 3.5: Mean sinuosity from 812 12-hour movement paths from Northern Bobwhite (*Colinus virginianus*) in western Oklahoma during 2019-2020 in response to the interaction between NDVI variance and mean air temperature. NDVI variance was grouped categorically as low (0.000048–0.00329), medium (0.0033–0.010), and high (0.010001–0.039). Mean solar radiation was grouped categorically as low (47.84–329.289 Wm^{-2}), medium (329.29–546.81 Wm^{-2}), and high (546.811–669.83 Wm^{-2}). Both groups represent the lower 25th, 25th – 75th, and upper 75th percentiles of the data. Standard error bars shown to show the spread of the mean. Means with different letters are significantly different (Games Howell test, *p* <0.01).

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VITA

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