Extreme climatic events constrain space use and survival of a ground-nesting bird

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Abstract

Two fundamental issues in ecology are understanding what influences the distribution and abundance of organisms through space and time. While it is well established that broad-scale patterns of abiotic and biotic conditions affect organisms' distributions and population fluctuations, discrete events may be important drivers of space use, survival, and persistence. These discrete extreme climatic events can constrain populations and space use at fine scales beyond that which is typically measured in ecological studies. Recently, a growing body of literature has identified thermal stress as a potential mechanism in determining space use and survival. We sought to determine how ambient temperature at fine temporal scales affected survival and space use for a ground-nesting quail species (*Colinus virginianus*; northern bobwhite). We modeled space use across an ambient temperature gradient (ranging from −20 to 38 °C) through a MAXENT algorithm. We also used Andersen–Gill proportional hazard models to assess the influence of ambient temperature-related variables on survival through time. Estimated available useable space ranged from 18.6% to 57.1% of the landscape depending on ambient temperature. The lowest and highest ambient temperature categories (<−15 °C and >35 °C, respectively) were associated with the least amount of estimated useable space (18.6% and 24.6%, respectively). Range overlap analysis indicated dissimilarity in areas where *Colinus virginianus* were restricted during times of thermal extremes (range overlap = 0.38). This suggests that habitat under a given condition is not necessarily a habitat under alternative conditions. Further, we found survival was most influenced by weekly minimum ambient temperatures. Our results demonstrate that ecological constraints can occur along a thermal gradient and that understanding the effects of these discrete events and how they change over time may be more important to conservation of organisms than are average and broad-scale conditions as typically measured in ecological studies.

Introduction

Two fundamental issues in ecology are understanding what influences the distribution and abundance of organisms (Krebs, 1988). Resource bottlenecks have been suggested as potential limiting periods in which resources for an organism are restricted, which can influence the size and distribution of populations (Maron *et al.*, 2015). These periods of resource bottlenecks have been linked to extreme climatic events (ECEs) and stochastic perturbations that populations are exposed to (Parmesan *et al.*, 2000; Maron *et al.*, 2015). However, how researchers define spatial and temporal scales is important and can influence our understanding of how extreme events can directly affect organisms (Mooij *et al.*, 2002). At fine temporal and spatial scales, resource use is highly dynamic and

can vary based on the availability of other necessary resources (Mooij *et al.*, 2002; Beerens *et al.*, 2015), environmental conditions (Mooij *et al.*, 2002; Hovick *et al.*, 2014; Carroll *et al.*, 2015a), or with biotic interactions (Ryder & Sillet, 2016). These patterns may exist at smaller scales of resolution than typically studied (Dunbar *et al.*, 2009; Maron *et al.*, 2015), and as a result, extreme events may facilitate changes in space use and/or survival at both fine temporal (Carroll *et al.*, 2015a) and spatial (Hovick *et al.*, 2014) scales. Understanding how extreme events can lead to constraints in space use and/or survival (i.e., an ecological constraint) across scales is a high priority in the context of climate change.

It is important to explicitly define what constitutes an ECE within the context of specific research objectives to facilitate comparisons across studies (Smith, 2011; Bailey & van de Pol, 2016). Here, we combine both climatological and biological definitions of ECEs, in which ECEs are events where the conditions occurring are

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rare relative to the distribution of those conditions (i.e., occurring <5% of the time; Smith, 2011). Furthermore, these events must also result in an extreme negative biological response for an organism (i.e., constraining a response parameter to the lower tail of the parameter's distribution; Bailey & van de Pol, 2016). However, this pattern can exist at smaller temporal scales (i.e., weather) when environmental conditions fluctuate to extreme values within daily and weekly time periods (Brown & Brown, 1998). These fine-scale ECEs can constrain the ecological or selective space available to an organism which may have survival implications (Fig. 1).

Constraints in space use and/or survival can occur across multiple temporal and spatial scales, and the implications are dependent on the phenotypic variation among species or individuals (Bestion et al., 2015), as well as landscape heterogeneity that might provide buffering or refugia for organisms to escape these extreme periods (Hovick et al., 2014; Carroll et al., 2015a,b). Thus, the direct effects of these events are
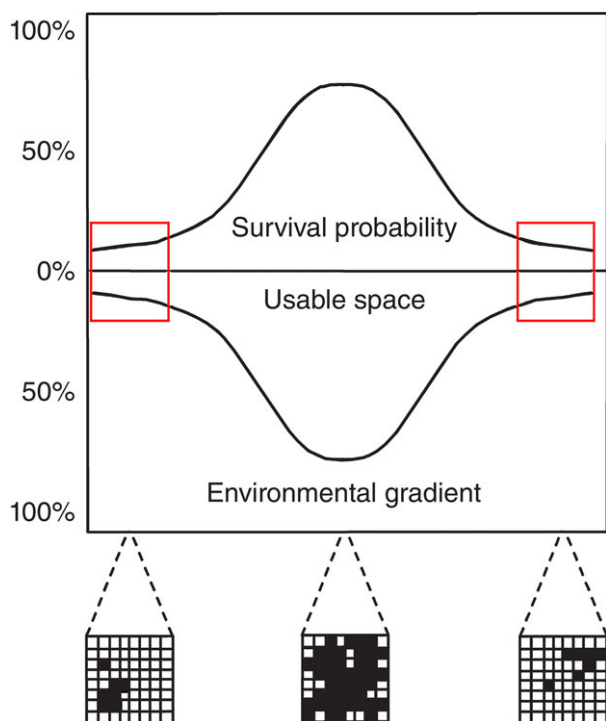

Fig. 1 A theoretical model illustrating potential extreme climatic events and a subsequent negative biological response (outlined by red boxes) resulting in ecological constraints, which may occur at both ends of an environmental gradient. Insets illustrate how usable space might vary along the environmental gradient assuming that the organism is directly constrained by the environmental gradient. Individual species responses could be highly variable along various gradients.

organism-specific. It is important to not only understand when ECEs ecologically constrain organisms, but to estimate how the frequency and magnitude of these events may be altered in future due to the trajectory of global change as this has population and species persistence implications.

There are multiple climatic variables that could constrain organisms during extreme events, but temperature is an obviously relevant variable given the rapid changes in temperatures occurring across the globe (Parmesan et al., 2000). Specifically, temperature may constrain the amount of space usable by organisms (Carroll et al., 2015a) and decrease vital rates (McKechnie & Wolf, 2010; Sanz-Aguilar et al., 2012), thus potentially increasing the effects of extreme events related to thermal conditions. It has been suggested that heterogeneity in plant community structure can play a role in the stabilization of faunal populations through increased opportunities in establishing climatic niches (Parmesan et al., 1999; Hampe & Petit, 2005; Hovick et al., 2015). However, despite thermal tolerances being a long understood ecological driver of species distributions (Begon et al., 2006), it was only recently that studies began to scale down to assess how organisms respond to fine-scale patterns of thermal heterogeneity that are driven by landscape structure and heterogeneity (Hovick et al., 2014; Melin et al., 2014; Carroll et al., 2015a; Marchand et al., 2015). Furthermore, previous literature has often focused on annual means in relation to thermal constraints on organisms, and few studies have examined fine-scale spatiotemporal variability in thermal conditions to estimate ecological constraints related to these conditions (Dunbar et al., 2009).

Structural patterns in a landscape can drive ecological processes (Turner, 1989), and moderation of thermal conditions is an important aspect of landscape patterns that may be critical in maintaining flora and fauna in the face of climate change (Hovick et al., 2014; Carroll et al., 2015a; Marchand et al., 2015). Considering the predicted increases in annual global temperatures by climate models (IPCC, 2014), species that are unable to adapt or that exhibit strong niche conservatism face threats of declines or possible extinction (Parmesan, 2006; Wiens et al., 2012). Predictive climatic models indicate that the frequency and intensity of extreme events will increase (Easterling et al., 2000; Schär et al., 2004; Cook et al., 2015), and ecological models predict that these changes will likely limit demographic rates (Frederiksen et al., 2008; McKechnie & Wolf, 2010; Selwood et al., 2015) and restrict or cause shifts in species distributions (Lawler et al., 2009; Thomas, 2010). If habitat selection can influence survival of individuals (Block & Brennan, 1993), extreme thermal conditions could

lead to unique patterns in habitat selection that may have direct (e.g., mortality from exposure) or indirect (e.g., limitations in resource availability) survival implications (Mysterud & Østbye, 1999). This would result in an organism's available space being pinched if only small amounts of the landscape provided adequate refuge from stressful abiotic conditions.

It is likely that ecological constraints caused by ECEs have played an important role in shaping distributions and community structure through evolutionary pressure (Skelly & Freidenburg, 2010; Maron *et al.*, 2015). However, future conditions projected from climate models will likely alter the frequency and severity of extreme events. Coupled with changes in resources facilitated by human-induced rapid environmental change (HIREC; Sih *et al.*, 2011), the potential ecological consequences of extreme events will likely be exacerbated for many organisms exhibiting niche conservatism. Changes in the occurrence of extreme events will not only influence the way organisms may or may not adapt to novel conditions, but will also have implications on how researchers study these organisms. Methods of population monitoring and analysis that are focused on long-term averages in conditions or resources could discount the importance of discrete extreme events at fine scales, in which vital rates (Welbergen *et al.*, 2008) and space use (Angilletta *et al.*, 2009; Carroll *et al.*, 2015a) are unique relative to average conditions. Therefore, understanding at what scale these events occur and how they influence individuals and/ or species will have important implications for conservation efforts within the context of global change.

To better understand how space use and survival are constrained during periods of extreme thermal conditions, we studied *Colinus virginianus* (northern bobwhite) on the western periphery of their distribution. *Colinus virginianus* is a ground-nesting, shrub-obligate Galliform that has generally experienced distribution-wide declines (Sauer *et al.*, 2014) due to habitat loss and fragmentation (Hernández *et al.*, 2013). However, along the western periphery of their distribution, local abundance is highly variable and driven by stochasticity in weather patterns (Lusk *et al.*, 2001, 2002; Guthery *et al.*, 2002; Perez *et al.*, 2002). As ground-nesting avifauna tend to be more susceptible to extreme thermal conditions (Albright *et al.*, 2010), we sought to determine whether available space can become restricted and whether survival decreases during periods of thermal extremes across full annual cycles. We used occurrence locations and survival data obtained through radiotelemetry efforts between 2012 and 2015 and modeled predicted space use and adult survival across a thermal gradient through an ecological niche modeling algorithm and a time-varying proportional hazard

model, respectively. Specifically, our objectives were to: (i) determine whether space use was constrained during periods of thermal extremes (i.e., periods in which habitat availability was much less during extreme thermal conditions), (ii) determine whether areas used during temperature extremes were different from areas used under dominant moderate conditions, (iii) use climate change projections to understand the implications of thermal extremes on future potential space use for *Colinus virginianus*, and (iv) determine how periods of extreme thermal conditions (ECEs) constrain survival of *Colinus virginianus*. Through these objectives, we demonstrate that fine-scale changes in thermal conditions can lead to ECEs which cause ecological constraints, thus negatively impacting space use and survival.

Materials and methods

To determine how periods of extreme thermal conditions ecologically constrained *Colinus virginianus*, we analyzed radiotelemetry data, which were collected from April 2012 to March 2015. We assigned ambient temperatures to telemetry locations based on local weather station data. We then estimated usable space across the annual thermal gradient through a maximum entropy algorithm using occurrence data and vegetation information on our study site. Finally, we estimated *Colinus virginianus* survival at a weekly temporal scale based on weekly values of weather data associated with ambient temperatures. We collated both of these analyses to identify periods of extreme thermal conditions throughout the full annual cycle that would elucidate an extreme biological response in *Colinus virginianus*.

Study area

We conducted our research on the Beaver River Wildlife Management Area (WMA), located in Beaver County, Oklahoma (lat 36°50′21.62″N, long 100°42′15.93″W), which consists of approximately 11 315 ha managed by the Oklahoma Department of Wildlife Conservation (ODWC). A majority of the WMA consists of upland rangelands and the floodplain of the Beaver River (Tanner *et al.*, 2015). Much of the upland areas are dominated by Tivoli fine sand soils, while the floodplain is dominated by Lesho silty clay loam.

At no time was the WMA out of meteorological drought conditions during our study, as determined through data from a partnership between The National Drought Mitigation Center (Lincoln, Nebraska, USA), the US Department of Agriculture, and the National Oceanic and Atmospheric Administration. Furthermore, the WMA was classified under D2 (severe drought) conditions 23.8% of the period, D3 (extreme drought) conditions 48.7% of the period, and D4 (exceptional drought) conditions 27.5% of the period based on weekly drought data provided by The National Drought Mitigation Center, Lincoln, Nebraska, USA. Conditions during our study were drier than the long-term average (1895–2014) in

2012 and 2014 (Table S1). Furthermore, average summer (May–July) temperatures generally exceeded the long-term average in 2013 and 2014, while average winter (December–February) temperatures were greater than the long-term average in all years of our study (Table S1). Ambient temperature averages were calculated by averaging all five-minute interval observations during the day at the closest Mesonet station. Climate data were obtained from the Beaver Mesonet station (Brock *et al.*, 1995; McPherson *et al.*, 2007).

Space use analysis

Occurrence data. To determine whether usable space became constrained, we used *Colinus virginianus* locations (known presence points) obtained from radiotelemetry to estimate space use across different ambient temperature categories. Individuals were located 5–7 times per week via radiotelemetry. Telemetry methods followed protocol described by Tanner *et al.* (2015) and all trapping and handling methods complied with the Oklahoma State University's Institutional Animal Care and Use Committee (Permit No. AG-11-22). Radiotelemetry locations ranged from 0600 to 2032 in time of day. Average telemetry error during the course of our study was estimated as 8.97 m [95% confidence interval (CI) = 6.48 to 11.46; Tanner *et al.*, 2016]. Bird locations were split into categories representing varying ranges of ambient temperatures. Ambient temperature (°C) values were obtained from the nearest Mesonet weather station (~2 km from nearest WMA boundary; Brock *et al.*, 1995; McPherson *et al.*, 2007) and were recorded every five minutes. All bird locations were matched with weather data corresponding to the nearest minute. Ambient temperature categories were arbitrarily split by every 5 °C. This resulted in a range of ambient temperatures from −20 to >35 °C (Table S2), with actual values ranging from −20 to 38.3 °C. Identical occurrence locations (i.e., same coordinates for individuals occurring in a covey) were removed from our dataset. We also eliminated any locations that occurred outside of the extent of vegetation data included in our analysis (discussed below).

Vegetation data. Variables used to estimate *Colinus virginianus* space use were related to the configuration and structure of vegetation on our study site. We chose to use vegetation (and associated landscape metrics described below) to model *Colinus virginianus* space use in relation to ambient temperature as this species is known to behaviorally modify their selection of vegetation during periods of thermal stress (Carroll *et al.*, 2015a; Janke *et al.*, 2015). An Iso Cluster Unsupervised classification method from 2-m-resolution satellite imagery was used to delineate vegetation. This method is an unsupervised classification approach that incorporates the Iso Cluster algorithm (to determine the natural grouping of pixels) and maximum likelihood to create a classified raster based on satellite imagery. The primary cover types on our study site are mixed shrub [consisting of sand plum (*Prunus angustifolia*), fragrant sumac (*Rhus aromatic*)], sand sagebrush (*Artemisia filifolia*), mixed grass [little bluestem (*Schizachyrium scopariu*), switchgrass (*Panicum virgatum*), bromes (*Bromus* spp.)], short-

grass/yucca (*Yucca glauca*), sparse vegetation/exposed soil, bare ground, and salt cedar (*Tamarix spp.*).

We used FRAGSTATS 4.2.1.603 (McGarigal *et al.*, 2012) to incorporate class and landscape metrics based on our vegetation classification into our assessment of *Colinus virginianus* space use. We used previous research to help eliminate redundancy and narrow our selection of variables included in our analysis (Ritters *et al.*, 1995; Fuhlendorf *et al.*, 2002). Furthermore, because we scaled up our vegetation map from 2 to 30 m in our analysis, we also limited Fragstats variable selection to those variables least affected by changes in spatial resolution as indicated by results from Lustig *et al.* (2015). A list of variables initially included in our analysis is provided in Table S3. To scale from the 2 m to the 30 m grain sizes, we used the Block Statistics and Resample tools with a majority rule in ARCGIS 10.2 (ESRI, 2011). The 30-m-resolution layers were used as the base layers for all subsequent Fragstats analysis. We reclassified all 'no data' cells for Fragstats layers within the extent of our study area to 0 before incorporating them into our modeling procedures (Foley *et al.*, 2008).

Maximum entropy modeling. A maximum entropy algorithm, MAXENT version 3.3.3 (Phillips & Dudik, 2008) with default options, was used to model *Colinus virginianus* space use in relation to our vegetation variables and ambient temperature categories. Although this algorithm has been traditionally used for species distribution modeling at large geographic scales (Elith *et al.*, 2011), MAXENT can be used to estimate space use or habitat selection at smaller extents using presence-only data (Baasch *et al.*, 2010). Presence information used in our modeling approach was separated into the 5 °C categories (12 total categories), resulting in 12 separate MAXENT models with idiosyncratic vegetation variables used for each model run. Our highest and lowest ambient temperature categories were represented with the least amount of observations (Table S2). However, these sample sizes are within the range of necessary observations needed to provide meaningful MAXENT models (Hernandez *et al.*, 2006; Wisz *et al.*, 2008).

We eliminated highly correlated variables ($r \geq 0.70$; Dormann *et al.*, 2013) and variables that had ≤5% contribution to accuracy gain (Sahlean *et al.*, 2014) of preliminary models that we ran for each weather category to further increase the robustness of our space use models. After examining the results of correlation analysis and removing poorly performing variables, we retained 21 of the original 39 variables (Table S4).

To test the validity of our models, we used a bootstrap method with 100 replicates (Araújo *et al.*, 2014), in which 25% of our data were held out for testing through random selection and 75% of our data were used for training our models (Bahn & McGill, 2012; Sahlean *et al.*, 2014; Sohl, 2014). We used 10 percentile training presence as the threshold method to convert continuous occurrence probability estimates into binary, presence–absence maps (Sahlean *et al.*, 2014), which we used as our measure of usable space available to *Colinus virginianus*. To evaluate our model results, we assessed the average area under the curve (AUC) of the receiver operating characteristic

(ROC) and the average omission error, which was calculated using test occurrence data and the binary occurrence maps.

To verify that the predicted trend in space use relative to ambient temperature categories was not an artifact of sample size discrepancies (Table S2), we used ENMTOOLS v1.4.4 (Warren *et al.*, 2010) to compare values of predicted usable space across 100 replicates of MAXENT models for ambient temperature categories with the lowest sample size (−20 to−15 °C) and the highest sample size (15–20 °C). The same unique combination of vegetation variables used for our initial analysis was also retained for this exercise. For each replication in the 15–20 °C ambient temperature category, we randomly retained a sample of occurrences equal to the number of occurrence points used in the −20 to −15 °C ambient temperature category analysis ($n = 39$). We then created a histogram comparing the variability between estimates of usable space across all replications. Furthermore, as we arbitrarily chose 5 °C ambient temperature categories, we also verified that the predicted trend in space use relative to ambient temperature categories existed by collapsing ambient temperature categories at every 10 °C. Vegetation variables used in this analysis were determined using identical methods described previously in this section, and all MAXENT settings were identical to previous analyses.

Colinus virginianus habitat selection can vary seasonally (Lohr *et al.*, 2011; Brooke *et al.*, 2015), although previous research has suggested that seasonal variation in habitat use by *Colinus virginianus* on our study site is lacking (Tanner *et al.*, 2015). However, to verify this result, we collated occurrence locations into breeding (1 April–30 September) and nonbreeding (1 October–31 March) seasons (Tanner *et al.*, 2015). We then estimated usable space for these seasonal models using identical methods described previously in this section. We used the range overlap metric in ENMTOOLS v1.4.4 (Warren *et al.*, 2010) to compare the amount of overlap in areas predicted suitable across seasons. The values of this metric range from 0 (no overlap) to 1 (complete overlap). As overlap in seasonal models was high (0.87), we discounted any seasonal influences related to our usable space results.

Post hoc analysis. We compared similarities of empirical space use across ambient temperature categories using ENMTOOLS v1.4.4 (Warren *et al.*, 2010) with the range overlap metric. We compared overlap between four categories: the two thermal extreme categories (>35 °C; −20 to −15 °C), the category predicting the highest amount of space use (15–20 °C), and the category containing the freezing point of water (0–5 °C). We included the category containing the freezing point of water as *Colinus virginianus* have been shown to behaviorally respond to freezing weather events to increase fitness levels by adaptively selecting woody cover, which resulted in increased adult survival during these events (Janke *et al.*, 2015). All pairwise comparisons of range overlap estimates across ambient temperature categories are presented in the supplementary material (Table S5).

Finally, we incorporated future climate change projections to evaluate the difference in the percentage of time occurring within each ambient temperature category during the course of our study (current) vs. 2050 and 2080. We selected five random general circulation models (GCMs) and high, medium, and low emission scenarios (A2, A1B, and B1 scenarios, respectively) using data provided by Climate Wizard (Girvetz *et al.*, 2009; www.climatewizard.org). The five random GCMs included ncar_pcm1.1, csiro_mk3_0.1, ukmo_hadcm3.1, gfd1_cm21.1, and giss_model_e_r.1 and were based on the IPCC Fourth Assessment (IPCC, 2007). Future climate projections were based on downscaling methods as described by Maurer *et al.* (2007) and were used to compare projected changes in ambient temperatures to future decades (2040–2069 and 2070–2099) with baseline climate data (1951–2006). Models were obtained for each month to capture variability in GCMs across months.

Survival analysis

To determine whether *Colinus virginianus* survival became constrained, we used the Andersen–Gill model and estimated hazard rates in relation to weather variables (Andersen & Gill, 1982) using the survival package in Program R (ver. 3.1.1, R Foundation for Statistical Computing, Vienna, Austria). We analyzed *Colinus virginianus* survival in relation to age and weekly variation in weather variables related to ambient temperature. These consisted of average, minimum, maximum, and variance of ambient temperatures within a week, and the average, minimum, and maximum wind chill values estimated within a week.

All variables met the linearity assumption based on plots of Martingale-based residuals (Therneau *et al.*, 1990; Fox, 2002). However, the proportional hazard assumption was not met for the average weekly ambient temperature, weekly maximum ambient temperature, and variance in weekly ambient temperature variables. To address this issue, we created an interaction term for these variables to have them vary over time (Fox, 2002). After incorporating these interactions, all global tests of nonzero slopes for the Schoenfeld residuals were nonsignificant for each model (maximum $\chi^2 = 4.79$, $P = 0.78$), indicating the proportional hazard assumption was met.

We used Akaike's information criterion adjusted for small sample sizes (AIC$_c$) to rank models relating covariates to hazard rates for *Colinus virginianus*. We considered models with a ΔAIC$_c$ <2 plausible models and determined the most parsimonious model based on model weights (w_i) and ΔAIC$_c$ values (Burnham & Anderson, 2002). Because we used a ΔAIC$_c$ <2 threshold for determining plausible models and because we met the $n/K > 40$ assumption, we used 85% CI to assess variable significance and relationships to competing models (Arnold, 2010). We also estimated a concordance index using the package 'PEC' in Program R to estimate a measure of discrimination for our hazard models (Harrell *et al.*, 1982). This index ranges from 0 to 1 and estimates the relative frequency in which paired individuals are correctly classified based on the model evaluated (i.e., a higher risk is assigned to the individual that survives less time). We built models that we found biologically meaningful or models that specifically addressed our research questions. These models included variables used to assess extreme heat

(average and maximum weekly ambient temperatures Guthery, 2000; Lusk *et al.*, 2001), extreme cold (average and minimum weekly ambient temperatures; average, minimum, and maximum weekly windchill; Janke *et al.*, 2015), and a global model. We also created a model (age) to test whether or not *Colinus virginianus* were more susceptible to weekly variation in weather based on being juveniles or adults. To illustrate trends in adult hazard rates related to the most significant parameter, we used the SMOOTHHR package in Program R (Meira-Machado *et al.*, 2013). As this package requires a reference point to be specified, we used a biologically relevant reference point (Cadarso-Suárez *et al.*, 2010) based on the variable being plotted.

Results

Space use

Using locations from 895 individual birds, we found that usable space significantly decreased during periods of extreme heat (>35 °C) and cold events (<−15 °C) when compared to intermediate ambient temperatures (Fig. 2). The least amount of usable space available as predicted through MAXENT (18.6%) was during the coldest ambient temperature category. The maximum amount of usable space was estimated within the 15–20 °C ambient temperature category, with a total of 57.1% of the landscape predicted as usable (Fig. 2). This same trend existed when ambient temperature categories were collapsed into 10 °C ambient temperature categories (Fig. S1). Although the two extreme ambient temperature categories were associated with the highest AUC values, these two categories also had the highest test omission values. Overall, all AUC values indicated useful model predictions across ambient temperature categories (test AUC range: 0.73–0.84; Swets, 1988), while test omission values also indicated good performance for most models (test omission range: 0.11–0.19). Only the −20 to −15 °C and >35 °C ambient temperature categories had test omission >0.20 (0.25 and 0.29, respectively), suggesting higher uncertainty for these two models.

There was little support for any effect of seasonality on our space use analysis, in which the overlap analysis suggested that nonbreeding and breeding season ranges overlapped by 0.87. Furthermore, we were able to verify that differential space use across ambient temperature categories was related to ambient temperature and not occurrence sample size. When adjusted for sample size, the range in predicted usable space for *Colinus virginianus* in the ambient temperature category with the largest sample size (15–20 °C) never overlapped with the range in predicted usable space for the ambient temperature category with the smallest sample size (<−15 °C; Fig. S2).
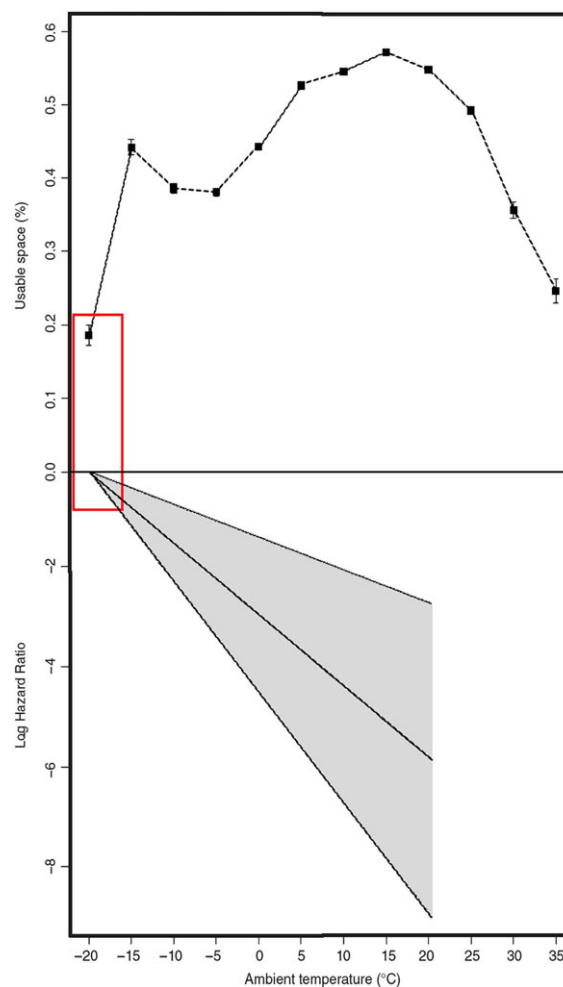

Fig. 2 Evidence of multiple ecological constraints during an extreme climatic event [ambient temperatures <−15 °C (outlined by red box)] as indicated by the percent usable space (± 1 standard error) for *Colinus virginianus* across an ambient temperature gradient (°C) as determined through MAXENT and estimated log hazard ratios[1] based on the top Andersen–Gill proportional hazard model[2,3]. Data were collected during 2012–2015 at Beaver River WMA, Beaver County, OK, USA. Vegetation data were analyzed at 30 m resolution. [1]Hazard ratios with larger negative values indicate a lower risk of experiencing mortality during the study. [2]The −20 °C ambient temperature category was used as the biologically relevant reference point as this value had the highest hazard ratio based on our top model. [3]The hazard ratio curve is based on the minimum weekly ambient temperature variable, which had the highest predicted hazard ratio of all variable analyzed. Values >20 °C are not plotted because they did not exist during our study.

A spatially explicit illustration of space use trends indicates dissimilarities in usable space during the extreme ambient temperature events (blue, red, and green areas in Fig. 3) when compared to overall estimated usable space across all ambient temperature categories (gray in Fig. 3). These variations in estimated
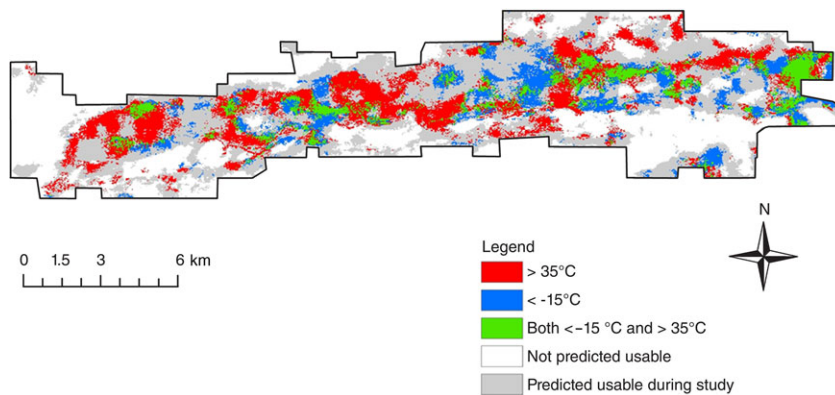
Fig. 3 Disparity in usable space for *Colinus virginianus* across high (>35 °C, shown in red), low (<−15 °C, shown in blue), and both high and low (>35 °C and <−15 °C, shown in green) ambient temperature categories when compared to areas predicted usable (shown in gray) at any ambient temperature category. Observations were collected from 2012 to 2015 at Beaver River WMA, Beaver County, OK, USA. Data were analyzed using 30-m-resolution vegetation data using a MAXENT algorithm.

usable space suggest that during extreme and discrete events, areas that are considered usable during average conditions may no longer be usable. Range overlap values (Table 1) between our hottest and coldest ambient temperature categories indicate that the overlap of space usable to *Colinus virginianus* during these ambient temperatures events is not highly comparable (0.38 estimated overlap; Fig. 3). However, the highest ambient temperature category (>35 °C) and the lowest ambient temperature category (<−15 °C) both overlapped considerably with an intermediate ambient temperature category (0–5 °C) and the ambient temperature category with the highest predicted space use (15–20 °C; 0.76–0.89).

Projections in temporally explicit thermal conditions (the percent of time per month) occurring within each ambient temperature category show a distinct shift to

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

Ambient temperature category (°C)	>35	15 to 20	0 to 5	−20 to −15
>35	1.00	0.88	0.76	0.38
15 to 20	0.88	1.00	0.88	0.87
0 to 5	0.76	0.88	1.00	0.89
−20 to −15	0.38	0.87	0.89	1.00

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

hotter ambient temperature categories (Fig. 4a–f) based on future climate model predictions. However, an increase in the percent of time occurring within the hottest ambient temperature category (>35 °C) is most evident beginning in May and continuing through October. Moreover, the magnitude of this increase is much greater during July–August (Fig. 4d), in which ambient temperatures that are >10 °C higher than the hottest ambient temperatures during May–June (Fig. 4c) are expected to occur. The future predicted percent of time occurring during the coldest ambient temperature category (<−15 °C) does not reflect any major increases when compared to the hottest ambient temperature category. These data represent predictions from five random GCMs within the 2080 A2 (high emissions) scenario for simplicity. Data indicating potential changes across the remaining five scenarios (2050 A2, A1B, B1; 2080 A1B and B1) are presented in the supplementary material (Figs S1–S5).

Survival

The most influential variable on survival of the 895 individuals was weekly minimum ambient temperature [hazard ratio (HR) = 0.87, 85% CI = 0.82 to 0.92, $P < 0.001$], suggesting that *Colinus virginianus* survival was constrained during periods of extreme cold ambient temperatures. The top model for survival was the global model (Table 2), which carried the majority of the weight in our modeling framework (0.94). Other significant variables in this model included the variance in the weekly ambient temperatures (HR = 0.97, 85% CI = 0.96–0.98, $P < 0.001$), weekly average windchill (HR = 1.10, 85% CI = 1.04–1.16, $P = 0.01$), and weekly minimum windchill (HR = 0.94, 85% CI = 0.91–0.98,
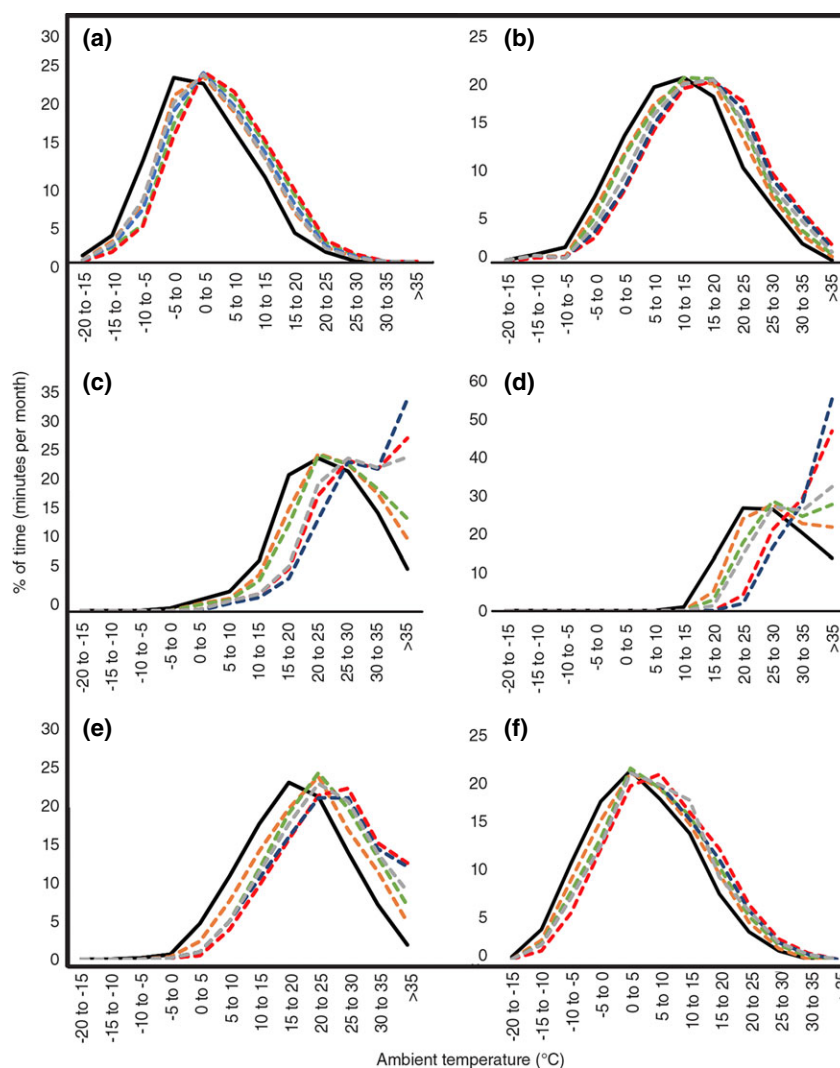
Fig. 4 Percent time (min month^{-1}) occurring within ambient temperature categories (°C) during 2012–2015 (black line) compared to future climate conditions at Beaver River WMA, Beaver County, OK, USA. Ambient temperatures were recorded every five minutes at a local weather station. Climate projections[1] are based on five general circulation models[2] under a high emission scenario (A2) and projected to the year 2080. Data are presented for: January–February (a), March–April (b), May–June (c), July–August (d), September–October (e), and November–December (f). [1]Climate data obtained on June 20, 2016, from www.climatewizard.org. [2]General circulation models are represented as: ncar_pcm1.1 (orange dashed line), csiro_mk3_0.1 (green dashed line), ukmo_hadcm3.1 (red dashed line), gfd1_cm21.1 (blue dashed line), and giss_model_e_r.1 (gray dashed line). All models are from the IPCC Fourth Assessment (IPCC, 2007).

$P = 0.04$). The hazard ratio for weekly minimum ambient temperature indicated that relative to every unit increase in the minimum ambient temperature during the week, individuals were 13% less likely to experience mortality. For instance, individuals exposed to ambient temperatures of −20 °C were 13% more likely to experience mortality than if the same individuals were exposed to −19 °C. This trend indicated that individuals were exposed to the highest hazard rates when ambient temperatures were <−15 °C (Fig. 2; range of minimum ambient temperatures: −20 to 20.6 °C).

Similarly, relative to every unit increase in variance of weekly ambient temperatures, individuals were 3% less likely to experience mortality, and were also 6% less likely to experience mortality relative to every unit increase in weekly minimum windchill values. Conversely, individuals were 10% more likely to experience mortality relative to every unit increase in weekly average windchill values. The global model was the most parsimonious, with the second best competing model (weekly maximum ambient temperature + weekly minimum ambient temperature) having a Δ7.99.

Table 2 Model selection of Andersen–Gill hazard models for *Colinus virginianus* survival from 1 April 1, 2012, to March 31, 2015, at Beaver River WMA, Beaver County, Oklahoma, USA

Model*	$K^\dagger$	AIC_c	ΔAIC_c	AIC_c weight	Cumulative weight	Model likelihood	Concordance index‡
Global	9	2994.00	0.00	0.94	0.94	−1488.99	0.57
tmax + tmin	3	3001.99	7.99	0.02	0.96	−1498.99	0.52
tmax × tmin	4	3002.40	8.41	0.01	0.97	−1498.20	0.53
tmin	2	3002.86	8.86	0.01	0.98	−1500.43	0.43
tavg	3	3003.96	9.97	0.01	0.99	−1499.98	0.53
tmax × time	3	3004.31	10.31	0.01	0.99	−1500.16	0.43
tmin + wchillmin	3	3004.51	10.51	0.00	1.00	−1500.25	0.43
Age	2	3008.80	14.80	0.00	1.00	−1503.40	0.51
wchillmin	2	3009.24	15.24	0.00	1.00	−1503.62	0.42
Null	1	3009.83	15.83	0.00	1.00	−1504.91	–
tvariance × time	3	3010.20	16.20	0.00	1.00	−1503.10	0.44
wchillavg	2	3011.10	17.10	0.00	1.00	−1504.55	0.36
wchillmax	2	3011.28	17.28	0.00	1.00	−1504.64	0.45

*Variables in models are as followed: tmin, tmax, tavg, and tvariance are the minimum, maximum, average, and variance of weekly ambient temperatures; wchillmin, wchillmax, and wchillavg are the minimum, maximum, and average windchill values; age is either juvenile or adult. The global model includes additive effects of all variables included in our analysis.
†Number of parameters in model.
‡The concordance index is a measure of discrimination for survival models. It is an estimate of the relative frequency that paired individuals correctly receive a higher predicted risk when surviving a shorter period during the study and ranges from 0 to 1, with one being the greatest value.

Discussion

We found that space use of *Colinus virginianus* on the landscape was constrained during discrete and extreme temperature events when compared to more moderate thermal conditions. Specifically, space use was most limited during extreme periods of cold. Further, we found that these discrete cold temperature events negatively influenced survival, and compounding effects of limited space use coupled with decreased survival lead to ecological constraints during these periods. Similar to cold periods, we found constrained space use during hot periods although survival was not affected in our data. Despite the lack of survival effects from heat events in our data, the implications of space loss related to extreme heat events may become more important than space loss related to cold events, at least within the southern Great Plains, based on future climate projections (Carroll *et al.*, 2016). Furthermore, range overlap analysis suggests that there was a dissimilarity between space use during periods of extreme heat vs. extreme cold. This suggests heterogeneity of vegetation composition, and structure may alleviate stress from environmental conditions by creating heterogeneous thermal conditions that allow for individuals to behaviorally moderate the conditions they experience and seek refugia (Hovick *et al.*, 2014; Carroll *et al.*,

2015a). The implications of these findings are that analysis of space use or habitat selection averaged across years or seasons will not appropriately identify the most critical habitat elements required for population persistence through variable environmental conditions. This has been demonstrated in limited instances with both endotherms (Carroll *et al.*, 2015a) and ectotherms (Angilletta *et al.*, 2009) in which individuals selected for areas that were representative of ~7% of the landscape or <1% of their home ranges during discrete life-history stages, respectively. In both cases, these selected areas had unique thermal conditions relative to the surrounding landscape. Failure to account for the impacts of discrete and fine-scale ECEs can limit our ability to identify factors affecting populations.

Progress in research continues to illustrate the importance of landscape patterns on habitat selection in response to changes in the thermal environment (Sears *et al.*, 2011; Hovick *et al.*, 2014; Melin *et al.*, 2014; Carroll *et al.*, 2015a). Heterogeneity of vegetation, topography, and/or geology can alter the thermal environment and create microclimates (Chen *et al.*, 1999; Begon *et al.*, 2006; Sears *et al.*, 2011) that allow individuals to thermoregulate (Kearney *et al.*, 2009; Sears *et al.*, 2011; Briscoe *et al.*, 2014). The distribution of thermal refugia available to organisms during times of thermal stress influences their activity patterns (Grubb, 1978) and

ability to behaviorally thermoregulate (Huey & Slatkin, 1976; Sears *et al.*, 2011). This suggests that available habitat is variable depending on weather conditions and that future climate shifts will potentially create novel conditions for these organisms.

Our data suggest that, based on observed *Colinus virginianus* space use, the distribution of thermal refuge areas may be more limiting during extreme ambient temperature events, as usable space was predicted to significantly decrease during times of extreme heat and cold (Fig. 3; Table 1). This concept has been suggested as a key question for future ECE research (Bailey & van de Pol, 2016), and our results show empirical evidence that the selective landscape can change and be reduced (maximum reduction of the selective landscape: ~67%; Fig. 2) during extreme thermal conditions. Ground-nesting avifauna have been shown to be more susceptible to stress compared to other avifauna during periods of extreme heat (Albright *et al.*, 2010), and are known to behaviorally moderate thermal conditions that they experience during different life-history stages (Hovick *et al.*, 2014; Carroll *et al.*, 2015a,b) by exhibiting unique patterns of space use (Forrester *et al.*, 1998; Guthery *et al.*, 2005; Martin *et al.*, 2015). This behavior has also been shown to occur when decoupled from the potential influence of predation risk (Hiller & Guthery, 2005). Furthermore, avifauna may have behavioral or physiological traits that help with thermoregulation and fitness during periods of extreme cold (Swanson, 2010; Carr & Lima, 2014), which could result in variable space use during these temperature events as a result of species' specific traits (Lima, 1990; Carrascal *et al.*, 2001). For example, *Colinus virginianus* have been shown to select woody cover during snow events to increase survival (Janke *et al.*, 2015). Thus, the process of fine-scale selection of microclimates to improve individual fitness during ECEs must be considered beyond the scope of predator avoidance. Under moderate ambient temperatures that fall within an organism's thermal tolerance, we would expect space use decisions to be made primarily based on other factors such as food availability and predator avoidance. But when an organism experiences extreme environmental conditions, food and predation risk may become secondary considerations toward survival. This places obvious selection pressure on populations and species.

Beyond variability in space use, our data suggest that demographic (i.e., vital rates) variability can be influenced by small-scale changes in environmental conditions. We found a nearly twofold increase in *Colinus virginianus* hazard ratios within a 10 °C increase in weekly minimum ambient temperatures during our study (Fig. 2). Although severe winters have been attributed to decreased demographic rates in avifauna (Moynahan *et al.*, 2006; Sanz-Aguilar *et al.*, 2012), we show that ecological constraints can occur due to even discrete weather events and can limit the space use or vital rates of organisms. Our results also indicated that increased variability in weekly ambient temperatures decreased the chance of mortality for *Colinus virginianus*. Although this may be counterintuitive, this relationship could be related to shifts in weekly ambient temperatures away from critical thermal levels. For example, when considering thermal performance curves (Huey, 1982), low variability in weekly ambient temperatures could be detrimental to survival if ambient temperatures stabilize near the critical thermal maximum or minimum level for a species. This positive response with increased variability in weekly temperatures could have important implications for *Colinus virginianus* adapting to future climate conditions as temperature variability is predicted to increase, which in turn will increase the probability of extreme high temperature events throughout midlatitudinal regions globally (Meehl *et al.*, 2000; Meehl & Tebaldi, 2004; Boer, 2009).

Evidence of extreme environmental perturbations has long been understood as an influential force on the demographic rates of organisms (Finlayson, 1932; Welbergen *et al.*, 2008), yet recent discussions have illustrated that this knowledge is often limited to dramatic discrete (i.e., cyclones, extreme winters) or long-term (i.e., drought) events (Maron *et al.*, 2015). We suggest that demographic rates can be constrained at finer temporal scales during extreme conditions, such as the fluctuation in ambient temperatures to the upper and lower tails of the annual distribution. Such changes in ambient temperatures at daily or weekly intervals can lead to a negative biological response (Fig. 1), even though the temperatures are within the normal distribution of climatic variability (Smith, 2011). These ecological constraints related to temporally explicit weather events will become increasingly important for the conservation of organisms as variability and occurrence of extreme events in future decades are predicted to increase (Meehl *et al.*, 2000; Meehl & Tebaldi, 2004). However, depending on the resolution of monitoring and analysis of survival data, discrete events might not be identified which could lead to erroneous conclusions on the importance of various habitat components in mitigating such events.

Although extreme cold ambient temperatures were more important to survival during the course of our study, these results should not preclude an understanding in the importance of extreme heat when it comes to the impacts of ECEs. For example, both Hovick *et al.* (2014) and Carroll *et al.* (2015a,b) illustrate how extreme

heat can influence space use of ground-nesting avifauna during the breeding season. These extreme heat events will likely become more important to survival of nonbreeding individuals within the context of future climate change (McKechnie & Wolf, 2010). Our study site is predicted to have a four times greater frequency in periods with ambient temperatures >35 °C based on our results from the GCM with the greatest predicted increase in ambient temperatures (Fig. 4d). Similar trends are predicted for nearby rangelands, in which operative temperatures of >50 °C are uniformly predicted to occur across the landscape (Carroll *et al.*, 2016). Behavioral adaptations such as selection of fine-scale microclimates can be crucial in buffering organisms against environmental extremes (Scheffers *et al.*, 2014) and such adaptations may have precluded any relationship with adult survival and extreme heat events in our study. Variation in operative temperatures within similar systems can be as great as 40 °C under the same ambient temperature across the landscape (Carroll *et al.*, 2015a,b). This suggests that thermal conditions available to individuals across a landscape are highly variable during periods of high ambient temperatures and that microclimates may be playing an important role in buffering thermal stress and providing refugia. Furthermore, decreases in survival associated with extreme cold events may have been related to decreased food availability. These periods of extreme cold coincide with an increased need for food to maintain metabolic rates (Elkins, 2004), yet food availability is most limiting during the late winter period for *Colinus virginianus* (Errington, 1939). Conversely, a shift in diets (arthropods and seeds) during the summer (Stoddard, 1931) could have precluded decreases in survival related to extreme heat events, as food resources are typically more abundant during this period when compared to the winter period.

Model complexity and variable selection can affect MAXENT performance during the model building process (Warren & Seifert, 2011). Model complexity was a concern when incorporating FRAGSTATS metrics and vegetation variables into our MAXENT modeling approach, as the number of variables that could be included can easily exceed 100 unique variables (Lustig *et al.*, 2015). However, we used previous published literature and detailed knowledge of *Colinus virginianus* ecology to help narrow the breadth of variables to decrease our model complexity. There may have inevitably been variables that could have contributed better to our models; however even with our *a priori*, correlated reduction (Dormann *et al.*, 2013) and variable contribution approach, all of our models gave reasonable predictions based on AUC values (Swets, 1988) and test

omission errors. Only our two thermal extreme categories had test omission errors >0.20 (0.25 and 0.29); however, these models also had the highest AUC values and still performed with reasonable predictions of space use.

A consideration regarding the results of our study is how long-term drought may have influenced the response of *Colinus virginianus* to thermal extremes. As mentioned before, at no time during the study was our study area out of drought conditions. *Colinus virginianus* have been shown to decrease in abundance (Bridges *et al.*, 2001) and may have lower vital rates during periods of drought when vegetation cover and food availability are potentially limited (Hernández *et al.*, 2005; Rader *et al.*, 2007). Prolonged drought conditions can influence individual's fitness levels which can cause long-term population declines (Cruz-McDonnell & Wolf, 2016). Although some species may moderate their behavior and space use in response to drought conditions to buffer negative impacts on fitness levels, these behavioral responses may not be enough to maintain population persistence (Gibson *et al.*, 2016). Projected increases in ambient temperatures coupled with increased frequency and intensity in drought conditions (Cook *et al.*, 2015) will likely lead to significant declines in many avifaunal species because of increased water requirements (McKechnie & Wolf, 2010). Although we do not discredit that long-term drought on our study site may have influenced the population of *Colinus virginianus*, our research was focused on the effects of short-term weather rather than long-term events such as drought or changes in climate. Furthermore, our focus on short events may have precluded any detection of lag effects of ECEs on *Colinus virginianus*. Lag effects can have important implications on how populations respond to ECEs across the annual cycle (Harrison *et al.*, 2011) and have been shown to exist in other Galliformes (Anthony & Willis, 2009; Blomberg *et al.*, 2014). Our survival analysis, which was focused on weekly responses to thermal conditions, would not have detected long-term lag effects in the population. However, if *Colinus virginianus* were responding at the temporal scale of a week with regard to these ambient temperature events (which ranged from 0.08 to 12.8 h in length), our analysis would have accounted for these responses. Inherently our survival results are likely a best case scenario, and survival responses to long-term extreme events could be greater than the relationships we present here (Dunbar *et al.*, 2009). Yet, accounting for longer time lags from chronic stress would inherently mask the discrete and acute responses we tested for. We argue that given future predictions on climate change (Kjellström *et al.*, 2007), these acute effects will be more likely to occur for many organisms.

Disparity in the range overlap value between our hottest and coldest ambient temperature categories (0.38) helps emphasize the importance of heterogeneity in vegetation to facilitate tolerance of extreme thermal conditions. Furthermore, the greater range overlap values of the intermediate ambient temperature categories (range: 0.76–0.89) indicate that these areas potentially act as 'thermally neutral' areas when birds are not thermally stressed. However, our data suggest that under periods of potential thermal stress, space use of organisms can be restricted idiosyncratically at either ends of a temperature gradient. This illustrates that cover should not be viewed as a stable or stagnant component of an organism's habitat and that the variance in space use related to environmental gradients should not be ignored. Instead, our perception of habitat for each species should account for the spatiotemporal variation in behavioral patterns and how these patterns are likely to change in the future.

We argue that traditional methods of assessing space use and survival across averaged conditions and/or resources (e.g., season, year) are likely not adequate particularly given the nonequilibrium nature of these systems, and that the variability within these systems is important for species persistence. For example, ambient temperatures within the coldest (<-15 °C) and hottest (>35 °C) categories occurred 1% and 3.7% of the time during our study, respectively (Fig. 4). This was associated with persistent events with thermal extreme conditions lasting for a maximum of 12.8 hours and 11.6 hours for the coldest and hottest ambient temperature categories, respectively. However, it was these discrete events that constrained space use and/or survival. An increased emphasis on viewing cover for thermal refugia should be considered within the context of both weather variability and global climate change. Ambient temperatures within and beyond the hottest thermal category are predicted to become more common within much of the world. Furthermore, there is uncertainty in predictions of daily temperature extremes based on climate change models (Kjellström *et al.*, 2007). Daily maximum temperatures are typically underestimated and daily minimum temperatures are overestimated (Kjellström *et al.*, 2007), and more profound changes in future daily extremes will likely have important implications on the prevalence of ecological constraints if species are unable to adapt.

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References

Albright TP, Pidgeon AM, Rittenhouse CD *et al.* (2010) Effects of drought on avian community structure. *Global Change Biology*, **16**, 2158–2170.

Andersen PK, Gill RD (1982) Cox's regression model for counting processes: a large sample study. *Annals of Statistics*, **10**, 1100–1120.

Angilletta MJ, Sears MW, Pringle RM (2009) Spatial dynamics of nesting behavior: lizards shift microhabitats to construct nests with beneficial thermal properties. *Ecology*, **90**, 2933–2939.

Anthony RG, Willis MJ (2009) Survival rates of female greater sage-grouse in autumn and winter in southeastern Oregon. *Journal of Wildlife Management*, **73**, 538–545.

Araújo CB, Marcondes-Machado LO, Costa GC (2014) The importance of biotic interactions in species distribution models: a test of the Eltonian noise hypothesis using parrots. *Journal of Biogeography*, **41**, 513–523.

Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *Journal Wildlife Management*, **74**, 1175–1178.

Baasch DM, Tyre AJ, Millspaugh JJ, Hygnstrom SE, Vercauteren KC (2010) An evaluation of three statistical methods used to model resource selection. *Ecological Modelling*, **221**, 565–574.

Bahn V, McGill BJ (2012) Testing the predictive performance of distribution models. *Oikos*, **122**, 321–331.

Bailey L, van de Pol M (2016) Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology*, **85**, 85–96.

Beerens JM, Frederick PC, Noonburg EG, Gawlik DE (2015) Determining habitat quality for species that demonstrate dynamic habitat selection. *Ecology and Evolution*, **5**, 5685–5697.

Begon M, Townsend CR, Harper JL (2006) *Ecology: From Individuals to Ecosystems* (4th edn). Blackwell, Malden, MA, USA.

Bestion E, Clobert J, Cote J (2015) Dispersal response to climate change: scaling down to intraspecific variation. *Ecology Letters*, **18**, 1226–1233.

Block WM, Brennan LA (1993) The habitat concept in ornithology: theory and applications. *Current Ornithology*, **11**, 35–91.

Blomberg EJ, Sedinger JS, Gibson D, Coates PS, Casazza ML (2014) Carryover effects and climatic conditions influence the postfledging survival of greater sage-grouse. *Ecology and Evolution*, **4**, 4488–4499.

Boer GJ (2009) Changes in interannual variability and decadal potential predictability under global warming. *Journal of Climate*, **22**, 3098–3109.

Bridges AS, Peterson MJ, Silvy NJ, Smeins FE, Wu XB (2001) Differential influence of weather on regional quail abundance in Texas. *Journal of Wildlife Management*, **65**, 10–18.

Briscoe NJ, Handasyde KA, Griffiths SR, Porter WP, Krockenberger A, Kearney MR (2014) Tree-hugging koalas demonstrate a novel thermoregulatory mechanism for arboreal mammals. *Biology Letters*, **10**, 20140235.

Brock FV, Crawford KC, Elliott RL, Cuperus GW, Stadler SJ, Johnson HL, Eilts MD (1995) The Oklahoma Mesonet, a technical overview. *Journal of Atmospheric and Oceanic Technology*, **12**, 5–19.

Brooke JM, Peters DC, Unger AM *et al.* (2015) Habitat manipulation influences northern bobwhite resource selection on a reclaimed surface mine. *Journal of Wildlife Management*, **79**, 1264–1276.

Brown CR, Brown MB (1998) Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution*, **52**, 1461–1475.

Burnham KP, Anderson DR (2002) *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY, USA.

Cadarso-Suárez C-S, Meira-Machado L, Kneib T, Gude F (2010) Flexible hazard ratio curves for continuous predictors in multi-state models: an application to breast cancer data. *Statistical Modelling*, **10**, 291–314.

Carr JM, Lima SL (2014) Wintering birds avoid warm sunshine: predation and the costs of foraging in sunlight. *Oecologia*, **174**, 713–721.

Carrascal LM, Díaz JD, Huertas DL, Mozetich I (2001) Behavioral thermoregulation by treecreepers: trade-off between saving energy and reducing crypsis. *Ecology*, **82**, 1642–1654.

Carroll JM, Davis CA, Elmore RD, Fuhlendorf SD, Thacker ET (2015a) Thermal patterns constrain diurnal behavior of a ground-dwelling bird. *Ecosphere*, **6**, art222.

Carroll JM, Davis CA, Elmore RD, Fuhlendorf SD (2015b) A ground-nesting Galliform's response to thermal heterogeneity: implications for ground-dwelling birds. *PLoS ONE*, **10**, e0143676.

Carroll JM, Davis CA, Fuhlendorf SD, Elmore RD (2016) Landscape pattern is critical for the moderation of thermal extremes. *Ecosphere*, **7**, e01403.

Chen J, Saunders SC, Crow TR *et al.* (1999) Microclimate in forest ecosystem and landscape ecology. *BioScience*, **49**, 288–297.

Cook BI, Ault TR, Smerdon JE (2015) Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*, **1**, e1400082.

Cruz-McDonnell KK, Wolf BO (2016) Rapid warming and drought negatively impact population size and reproductive dynamics of avian predator in the arid southwest. *Global Change Biology*, **22**, 237–253.

Dormann CF, Elith J, Bacher S *et al.* (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27–46.

Dunbar RIM, Korstjens AH, Lehmann J (2009) Time as an ecological constraint. *Biological Reviews*, **84**, 413–429.

Easterling DR, Evans JL, Ya Groisman P, Kal TR, Kunkel KE, Ambenje P (2000) Observed variability and trends in extreme climate events: a brief review. *Bulletin of the American Meteorological Society*, **81**, 417–425.

Elith J, Phillips SJ, Hastie T, Dudik M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.

Elkins N (2004) *Weather and Bird Behavior*. T and A. D. Poyser, London, UK.

Errington PL (1939) The comparative ability of the bob-white and the ring-necked pheasant to withstand cold and hunger. *The Wilson Bulletin*, **51**, 22–37.

ESRI. (2011) *ArcGIS Desktop: Release 10.2*. Environmental Systems Research Institute, Redlands, CA, USA.

Finlayson HH (1932) Heat in the interior of South Australia: holocaust of bird-life. *South Australian Ornithologist*, **11**, 158–160.

Foley DH, Rueda LM, Peterson AT, Wilkerson RC (2008) Potential distribution of two species in the medically important *Anopheles minimus* complex (Diptera: Culicidae). *Journal of Medical Entomology*, **45**, 852–860.

Forrester ND, Guthery FS, Kopp SD, Cohen WE (1998) Operative temperature reduces habitat space for northern bobwhites. *Journal of Wildlife Management*, **62**, 1506–1511.

Fox J (2002) Cox proportional-hazards regression for survival data. In: *An R and S-Plus Companion to Applied Regression* (ed. Fox J), pp. 1–312. Sage Publication Inc, Thousand Oaks, CA, USA.

Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, **77**, 1020–1029.

Fuhlendorf SD, Woodward AJW, Leslie DM, Shackford JS (2002) Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landscape Ecology*, **17**, 617–628.

Gibson D, Blomberg EJ, Atamian MT, Sedinger JS (2016) Weather, habitat composition, and female behavior interact to modify offspring survival in greater sage-grouse. *Ecological Applications*, **27**, 168–181.

Girvetz EH, Zganjar C, Raber GT, Maurer EP, Kareiva P, Lawler JJ (2009) Applied climate-change analysis: the Climate Wizard tool. *PLoS ONE*, **4**, e8320.

Grubb TC (1978) Winter-dependent foraging rates of wintering woodland birds. *Auk*, **95**, 370–376.

Guthery FS (2000) *On Bobwhites*. Texas A & M University Press, College Station, TX, USA.

Guthery FS, Lusk JM, Synatzske DR, Gallagher J, DeMaso SJ, George RR, Peterson MJ (2002) Weather and age ratios of northern bobwhites in South Texas. *Proceedings of the National Quail Symposium*, **5**, 99–105.

Guthery FS, Rybak AR, Fuhlendorf SD, Hiller TL, Smith SG, Puckett WH Jr, Baker RA (2005) Aspects of thermal ecology of bobwhites in North Texas. *Wildlife Monographs*, **159**, 1–36.

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Harrell FE, Califf RM, Pryor DB, Lee KL, Rosati RA (1982) Evaluating the yield of medical tests. *Journal of the American Medical Association*, **247**, 2543–2546.

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, **80**, 4–18.

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29**, 773–785.

Hernández F, Hernández F, Arredondo JA, Bryant FC, Brennan LA, Bingham RL (2005) Influence of precipitation on demographics of northern bobwhites in southern Texas. *Wildlife Society Bulletin*, **33**, 1071–1079.

Hernández F, Brennon LA, DeMaso SJ, Sands JP, Webster DB (2013) On reversing the northern bobwhite population decline: 20 years later. *Wildlife Society Bulletin*, **37**, 177–188.

Hiller TL, Guthery FS (2005) Microclimate vs. predation risk in roost and covert selection by bobwhites. *Journal of Wildlife Management*, **69**, 140–149.

Hovick TJ, Elmore RD, Allred BW, Fuhlendorf SD, Dahlgren DK (2014) Landscapes as a moderator of thermal extremes: a case study from an imperiled grouse. *Ecosphere*, **5**, 35.

Hovick TJ, Elmore RD, Fuhlendorf SD, Engle DM, Hamilton RG (2015) Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecological Applications*, **25**, 662–672.

Huey RB (1982) Temperature, physiology, and the ecology of reptiles. *Biology of the Reptilia*, **12**, 25–91.

Huey RB, Slatkin M (1976) Costs and benefits of lizard thermoregulation. *Quarterly Review of Biology*, **51**, 363–384.

IPCC (2007) Climate change 2007: mitigation of climate change. IPCC Fourth Assessment Report, Working Group III. Geneva: International Panel on Climate Change.

IPCC (2014) Summary for policymakers in climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. In: *Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Field CB, Barros VR, Dokken DJ *et al.*), pp. 1–32. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Janke AK, Gates RJ, Terhune TM II (2015) Habitat influences northern bobwhite survival at fine spatiotemporal scales. *Condor*, **117**, 41–52.

Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer cold-blooded animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 3835–3840.

Kjellström E, Bärring L, Jacob D, Jones R, Lenderink G, Schär C (2007) Modelling daily temperature extremes: recent climate and future changes over Europe. *Climate Change*, **81**, 249–265.

Krebs CJ (1988) *The Message of Ecology*. Harper and Row, New York, NY, USA.

Lawler JJ, Shafer SL, White D, Kareiva P, Maurer EP, Blaustein AR, Bartlein PJ (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, **90**, 588–597.

Lima SL (1990) Protective cover and the use of space: different strategies in finches. *Oikos*, **58**, 151–158.

Lohr M, Collins BM, Castelli PM, Williams CK (2011) Life on the edge: northern bobwhite ecology at the northern periphery of their range. *Journal of Wildlife Management*, **75**, 52–60.

Lusk JJ, Guthery FS, DeMaso SJ (2001) Northern bobwhite (*Colinus virginianus*) abundance in relation to yearly weather and long-term climate patterns. *Ecological Modelling*, **146**, 3–15.

Lusk JJ, Guthery FS, George RR, Peterson MJ, DeMaso SJ (2002) Relative abundance of bobwhites in relation to weather and land use. *Journal of Wildlife Management*, **66**, 1040–1051.

Lustig A, Stouffer DB, Roigé M, Worner SP (2015) Towards more predictable and consistent landscape metrics across spatial scales. *Ecological Indicators*, **57**, 11–21.

Marchand P, Garel M, Bourgoin G, Dubray D, Maillard D, Loison A (2015) Sex-specific adjustments in habitat selection contribute to buffer mouflon against summer conditions. *Behavioral Ecology*, **26**, 472–482.

Maron M, McAlpine CA, Watson JEM, Maxwell S, Barnard P (2015) Climate-induced resource bottlenecks exacerbate species vulnerability: a review. *Diversity and Distributions*, **21**, 731–743.

Martin RO, Cunningham SJ, Hockey PAR (2015) Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. *Ostrich*, **86**, 127–135.

Maurer EP, Brekke L, Pruitt T, Duffy PB (2007) Fine-resolution climate projections enhance regional climate change impact studies. *Eos Transactions American Geophysical Union*, **88**, 504.

McGarigal K, Cushman SA, Ene E (2012) *FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst*. Available at: http://ww.umass.edu/landeco/research/fragstats/fragstats/html. (accessed 1 September 2015).

McKechnie AE, Wolf BO (2010) Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, **6**, 253–256.

McPherson RA, Fiebrich C, Crawford KC *et al.* (2007) Statewide monitoring of the mesoscale environment: a technical update on the Oklahoma Mesonet. *Journal of Atmospheric and Oceanic Technology*, **24**, 301–321.

Meehl GA, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. *Science*, **305**, 994–997.

Meehl GA, Zwiers F, Evans J *et al.* (2000) Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. *Bulletin of the American Meteorological Society*, **81**, 427–436.

Meira-Machado L, Cadarso-Suárez C, Gude F, AraájoA A (2013) smoothHR: an R package for pointwise nonparametric estimation of hazard ratio curves of continuous predictors. *Computational and Mathematical Methods in Medicine*, **2013**, 745742.

Melin M, Matala J, Mehtatalo L *et al.* (2014) Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelter in boreal forests-an analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biology*, **20**, 1115–1125.

Mooij WM, Bennetts RE, Kitchens WM, DeAngelis DL (2002) Exploring the effect of drought extent and interval on the Florida snail kite: interplay between spatial and temporal scales. *Ecological Modelling*, **149**, 25–39.

Moynahan BJ, Lindberg MS, Thomas JW (2006) Factors contributing to process variance in annual survival of female greater sage-grouse in Montana. *Ecological Applications*, **16**, 1529–1538.

Mysterud A, Østbye E (1999) Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin*, **27**, 385–394.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics*, **37**, 637–669.

Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, **81**, 443–450.

Perez RM, Gallagher JF, Frisbie MC (2002) Fine scale influence of weather on northern bobwhite abundance, breeding success, and harvest. *Proceedings of the National Quail Symposium*, **5**, 106–110.

Phillips SJ, Dudik M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.

Rader MJ, Teinert TW, Brenna LA, Hernández F, Silvy NJ, Wu XB (2007) Identifying predators and nest fates of bobwhites in southern Texas. *Journal of Wildlife Management*, **71**, 1626–1630.

Ritters KH, O'Neill RV, Hunsaker CT *et al.* (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecology*, **10**, 23–39.

Ryder TB, Sillet TS (2016) Climate, demography and lek stability in an Amazonian bird. *Proceedings of the Royal Society B*, **283**, 20152314.

Sahlean TC, Gherghel I, Papeş M, Strugariu A, Zamfirescu ŞR (2014) Refining climate change projections for organisms with low dispersal abilities: a case study of the Caspian whip snake. *PLoS ONE*, **9**, e91994.

Sanz-Aguilar A, Bechet A, Germain C, Johnson AR, Pradel R (2012) To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo. *Journal of Animal Ecology*, **81**, 1171–1182.

Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski DJ Jr, Link WA (2014) The North American Breeding Bird Survey, results and Analysis 1966–2012. *Version 02.19.2014*. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Scheffers BR, Edward DP, Diesmos A, William SE, Evans TA (2014) Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, **20**, 495–503.

Sears MW, Raskin E, Angilletta MJ (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*, **51**, 666–675.

Selwood KE, McGeoch MA, Mac Nally R (2015) The effects of climate change and land-use change on demographic rates and population viability. *Biological Reviews*, **90**, 837–853.

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, **4**, 367–387.

Skelly DK, Freidenburg LK (2010) *Evolutionary Responses to Climate Change. Encyclopedia of Life Sciences (ELS)*. John Wiley and Sons Ltd, Chichester.

Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology*, **99**, 656–663.

Sohl TL (2014) The relative impacts of climate and land-use change on conterminous United States bird species from 2001 to 2075. *PLoS ONE*, **9**, e112251.

Stoddard HL (1931) *The Bobwhite Quail: Its Habits, Preservation, and Increase*, pp. 113–166. Charles Scibner's Sons, New York, NY, USA.

Swanson DL (2010) Seasonal metabolic variation in birds: functional and mechanistic correlates. *Current Ornithology*, **17**, 75–129.

Swets JA (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285–1293.

Tanner EP, Elmore RD, Fuhlendorf SD, Davis CA, Thacker ET, Dahlgren DK (2015) Behavioral responses at distribution extremes: how artificial surface water can affect quail movement patterns. *Rangeland Ecology and Management*, **68**, 476–484.

Tanner EP, Elmore RD, Davis CA, Fuhlendorf SD, Dahlgren DK, Thacker ET, Orange JP (2016) Does the presence of oil and gas infrastructure potentially increase risk of harvest in northern bobwhite? *Wildlife Biology*, **22**, 294–304.

Therneau TM, Grambsch PM, Fleming TR (1990) Martingale-based residuals for survival models. *Biometrika*, **77**, 147–160.

Thomas CD (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488–495.

Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, **20**, 171–197.

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342.

Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, **33**, 607–611.

Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B*, **275**, 419–425.

Wiens JJ, Ackerly DD, Allen AP *et al.* (2012) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, NCEAS Predicting Species Distributions Working Group (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14**, 763–773.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Descriptive data on long term and study period weather conditions.
Table S2. Number of training and testing locations used for MAXENT analysis of *Colinus virginianus* space use across 12 ambient temperature categories.
Table S3. List of variables used in MAXENT analysis for *Colinus virginianus* locations.
Table S4. Percent variable contribution of variables used to estimate *Colinus virginianus* space use across ambient temperature categories using MAXENT and 30 m resolution data.
Table S5. All pairwise comparisons of range overlap analyses for predicted usable space for *Colinus virginianus* across 12 ambient temperature categories.
Figure S1. Percent usable space (± 1 standard error) for *Colinus virginianus* across a temperature gradient (°C)[1] as determined through MAXENT.
Figure S2. Histogram of predicted usable space of *Colinus virginianus* during ambient temperatures of −20 to −15 °C (blue) and 15–20 °C (black) when corrected for sample size.
Figure S3. Percent time (minutes/month) occurring within ambient temperature categories (°C) during 2012–2015 compared to future climate conditions as predicted by five general circulation models under a medium emission scenario (A1B) and projected to the year 2080 at Beaver River WMA, Beaver County, OK, USA.
Figure S4. Percent time (minutes/month) occurring within ambient temperature categories (°C) during 2012–2015 compared to future climate conditions as predicted by five general circulation models under a low emission scenario (B1) and projected to the year 2080 at Beaver River WMA, Beaver County, OK, USA.
Figure S5. Percent time (minutes/month) occurring within ambient temperature categories (°C) during 2012–2015 compared to future climate conditions as predicted by five general circulation models under a high emission scenario (A2) and projected to the year 2050 at Beaver River WMA, Beaver County, OK, USA.
Figure S6. Percent time (minutes/month) occurring within ambient temperature categories (°C) during 2012–2015 compared to future climate conditions as predicted by five general circulation models under a medium emission scenario (A1B) and projected to the year 2050 at Beaver River WMA, Beaver County, OK, USA.
Figure S7. Percent time (min month^{-1}) occurring within ambient temperature categories (°C) during 2012–2015 compared to future climate conditions as predicted by five general circulation models under a low emission scenario (B1) and projected to the year 2080 at Beaver River WMA, Beaver County, OK, USA.