Landscape Ecol (2020) 35:893–906
https://doi.org/10.1007/s10980-020-00986-x

RESEARCH ARTICLE

Thermal performance curves based on field movements reveal context-dependence of thermal traits in a desert ectotherm

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Received: 26 June 2019 / Accepted: 26 February 2020 / Published online: 9 March 2020

Abstract

Context Thermal traits likely mediate organismal responses to changing thermal environments. As temperatures increase, predicting species responses will depend on understanding how thermal traits vary within and among individuals and across time and space.

Objectives We evaluated variation in thermal traits within and among individual Mojave Desert Tortoises, using GPS telemetry to quantify movement performance and animal-mounted sensors to measure carapace temperatures.

Methods We constructed thermal performance curves (TPCs) based on movement velocity and assessed variation in associated thermal traits by sex, season, and proximity to roads. We also examined the temperature-dependence of monthly home ranges and the frequency of high-displacement movements.

Results Individuals exhibited lower variation in upper critical temperatures (CT_{maxE}) than in other traits, such as optimum temperatures and lower critical temperatures for movement. All thermal traits varied within individuals, either by season or proximity to roads. We also found that monthly home range size and the frequency of high-displacement movements increased with the time individuals spent within their optimal temperature range; however, this effect was only apparent during months with greater rainfall.

Conclusions Low standing variation in CT_{maxE} suggests that this trait may be constrained, limiting potential changes through acclimation or selection in warming environments. Our results demonstrate the

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-020-00986-x) contains supplementary material, which is available to authorized users.

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modifying effect of rainfall on temperature-space use relationships and highlight the dependence of thermal traits on ecological and landscape contexts. Field-based TPCs derived from GPS movement tracks provided ecologically-relevant estimates of thermal traits and suggest an informative framework for unifying elements of thermal biology and spatial ecology.

Keywords Thermal ecology · Mojave desert tortoise · GPS telemetry · Thermal optimum · CT_{max} · Body temperature · Space use · Roads

Introduction

For ectotherms, activity in space and time is often limited by temperature. Temperature affects hours of activity, speed of movement, efficiency of predator escape and foraging, and reproductive effort, factors that can affect population growth (Porter et al. 1973; Huey and Stevenson 1979; Deutsch et al. 2008; Navas et al. 2008; Sinervo et al. 2010). Recent work also shows that species' thermal biology is associated with their responses to drivers of global change, such as habitat loss, climate change, and disease (Huey et al. 2012; Valladares et al. 2014; Frishkoff et al. 2015; Nowakowski et al. 2016, 2017, 2018b; Hamblin et al. 2017). To fully assess organismal-temperature relationships and species' vulnerability to changing thermal environments, however, requires detailed information on (1) temperature exposure at fine scales, (2) variation in thermal traits among individuals, and (3) the context-dependence of thermal trait measurements, information that is unavailable for most species (Valladares et al. 2014; Sinclair et al. 2016; Nowakowski et al. 2018a). Furthermore, any comprehensive assessment of temperature sensitivity must account for the ability of ectotherms to behaviorally moderate their exposure to environmental temperatures and, therefore, their realized body temperatures (Porter et al. 1973; Kearney et al. 2009; Sears et al. 2016; Pincebourde and Casas 2019).

Thermal performance curves (TPCs) provide a useful framework for understanding organism-temperature relationships and for deriving multiple thermal traits (Huey and Stevenson 1979). TPCs are models or equations that describe the relationship between some measure of organismal performance (or fitness) and temperature. Typically, performance increases slowly with temperature until it is maximized at the thermal optimum temperature (T_{opt}). Beyond T_{opt}, performance often decreases precipitously with further increase in temperature, giving rise to the classically left-skewed, empirical TPC (Navas et al. 2008; Sinclair et al. 2016). Though not universal, this common TPC form may arise as emergent outcomes of biochemical reactions that are temperature-dependent; for example, during acute exposure to high temperatures, blood-oxygen concentrations typically decrease quickly while demand increases (Angilletta Jr and Angilletta 2009; MacMillan 2019). TPCs are bounded by critical lower and upper thermal tolerances—temperatures beyond which performance (or fitness) is zero and animals cannot function physiologically or ecologically. One can fit TPCs to a plethora of performance variables, which can all vary in form (Angilletta Jr and Angilletta 2009; Sinclair et al. 2016). However, TPCs are commonly based on movement performance, likely because temperature-dependent movement is relatively easy to measure in the laboratory using experiments and is linked to proximate determinants of fitness (Miles et al. 2004).

Although typically measured in a laboratory setting, TPCs can also be constructed from field data (Payne et al. 2016; Childress and Letcher 2017), including GPS tracking data. Field-derived TPCs should provide more ecologically-relevant estimates of thermal traits than lab-based assays, in which organisms are prompted to move, because study organisms can behave under natural conditions, seeking refuge to avoid extreme temperatures while experiencing additional constraints on performance, such as food or water limitation. For these reasons, it is also important to examine the influence of ecological context, such as season and anthropogenic stressors, on field-derived thermal traits. Here, we propose using GPS telemetry data and animal-mounted temperature sensors to examine field-based TPCs; this method has the potential to provide information with very high spatiotemporal resolution on organismal-temperature relationships and that integrates behavior and performance across a range of ecological conditions into estimates of thermal traits.

Examining the thermal-dependence of movement performance in the field can be informative for a range of ecological and conservation applications because movement is a fundamental process that is linked to fitness and that shapes the spatial distributions of individuals. Constrained by both environmental conditions and evolved, niche-related traits, organisms presumably optimize their fitness through movement behavior in heterogeneous landscapes, balancing predator avoidance and energetic costs with the search for food, water, and mates (Cushman and Huettmann 2010). Temperature likely plays a key role in modulating these movement behaviors by affecting the internal state of the organism—e.g., the motivation for movement—and the biomechanical capacity for movement (Nathan et al. 2008). By serving as a link between local-scale behaviors and landscape-scale distributions, TPCs based on large-scale movement datasets can serve as a framework for integrating elements of thermal biology and spatial ecology.

In this study, we used GPS tracking data for a desert ectotherm, the Mojave Desert Tortoise (*Gopherus agassizii*), to examine temperature thresholds and optima for movement behavior. Specifically, we generated TPCs based on the relationships between individual tortoise velocity and external carapace temperature. We then defined parameters of these curves, including ecologically optimal temperatures (T_{optE}) for movement (Payne et al. 2016; Sinclair et al. 2016); the optimal temperature range or B80—defined here as the range of temperatures at which performance is at least 80% of the maximum (Crowley 1985); and the lower (CT_{minE}) and upper (CT_{maxE}) ecological limits of the thermal performance range—defined here as the temperature thresholds between which velocity is effectively > 0, while accounting for GPS error. We used an altered notation for field-derived TPC parameters – T_{optE}, CT_{minE}, and CT_{maxE}—to distinguish these thermal traits measured under natural environmental conditions (following Payne et al. 2016) from analogous thermal traits that are typically measured under laboratory conditions (Sinclair et al. 2016). We then examined the degree of variation in TPC parameters within and among individuals, determining whether parameters varied between sexes, seasons, or when in proximity to anthropogenic structures (here, roads or road fencing). Finally, we examined the relationship between frequency of carapace temperatures within the B80 range and the size of monthly home ranges or the frequency of high-displacement movement paths. By understanding individual variation in temperature-dependent movement in the field, we may gain new insights into the responses of species to changing temperature regimes under habitat alteration and climate change.

Methods

Study system

The Mojave Desert Tortoise occurs in the Mojave and Sonoran Deserts of the southwestern United States and is listed as threatened under the U.S. Endangered Species Act (Federal Register 1990). The species has declined in much of its range due to a combination of threats, including widespread habitat loss from urbanization and renewable energy development, road mortality, and disease. We collected movement data on desert tortoises in the southern Ivanpah Valley of the Mojave Desert in California. Tortoises were tracked at two sites within the valley that were separated by approximately 11 km (Peaden et al. 2017). One site was within the Mojave National Preserve and included a two-lane, unfenced road with low traffic volume. The second site was just west of Interstate 15, a high traffic volume highway along which mitigation fencing had been recently installed to exclude tortoises from roads and construction areas.

GPS telemetry and temperature measurements

During 2013–2015, we tracked a total of 15 individuals (9 males and 6 females) using GPS-loggers, resulting in 89,068 total locations. All individuals were initially captured within 1 km of a road and were fitted with VHF radios, GPS loggers (G30L, Advanced Telemetry Systems Inc. Isanti, MN), and iButton temperature loggers (1922L, Maxim Integrated, San Jose, CA). We only outfitted adult tortoises (midline carapace length > 210 mm) with GPS transmitters and temperature sensors so that the total weight of affixed equipment did not exceed 6% of the body mass of each tortoise. The location error of GPS transmitters was assessed by examining variation in position fixes at a stationary point. The iButton sensors were affixed to the first left or right costal scute of each tortoise using epoxy putty (J-B Weld SteelStik). We covered sensors with a thin (approx. 2.5 mm) layer of epoxy, thereby shielding the sensor from direct solar radiation that could result in biased temperature measurements. Because sensors were insulated and affixed to the carapace, measurements approximate temperatures of the carapace surface, shielded from direct sun exposure. We also examined the relationship between temperatures from externally mounted sensors to operative temperatures using physical models (see below and supplemental methods). We programmed the GPS and temperature data loggers to record tortoise locations and carapace temperatures, respectively, at 15 min intervals for the duration of the tracking period of each animal (for additional details of tracking methods, see Peaden et al. 2017). Tortoises were re-sighted every 1–2 months over the course of the study to download GPS and temperature data and to replace batteries of GPS transmitters.

Statistical analyses

To examine variation in thermal traits (i.e., TPC parameters) and their associations with measures of movement and space use, we conducted two sets of analyses: (1) We analyzed variation in thermal traits in relation to sex, season, and proximity to roads, and (2) we examined the relationships between the amount of time tortoises spent within their optimal temperature range and space use patterns measured as monthly home range size and the number of days with high-displacement movement bouts.

We first calculated derived variables from GPS tracking data to be used in downstream analyses. These variables included velocity, change in net-squared displacement (ΔNSD) for each step, categorical variables representing proximity to roads and behavioral movement modes based on daily ΔNSD, and monthly home range size. Velocity was calculated as the step length between GPS fixes divided by the time interval between fixes; often, this interval was 15 min but was longer in cases when GPS loggers failed to acquire a fix (e.g., when tortoises were in burrows). We calculated net-squared displacement as the squared straight-line distance between the starting point of an individual's movement track—a track is the entire sequence of locations obtained from the GPS transmitter—and each consecutive location on the landscape (Fig. 1a) (Börger and Fryxell 2012). Net-squared displacement provides a measure of roaming behavior because it represents the spatial diffusion of an individual from a fixed starting location. Because NSD values are relative to an arbitrary starting point (here the first point of each track), we calculated absolute differences in NSD between serial locations—ΔNSD—for further analyses of high-displacement movements. We then classified movement tracks into three segment types representing different movement modes: sedentary activity, normal movement, and bouts of directed, high-displacement movement. To categorize sedentary activity and bouts of directed movement, we used simple thresholds corresponding to the 10th (= low displacement) and 90th (= high displacement) percentiles of summed daily ΔNSD to identify path segments (Fig. 1b) (Edelhoff et al. 2016). We also derived categorical predictor variables representing season based on rainfall—Spring/Summer (March–June) versus Monsoon season (July to November)—and a binary categorical variable representing proximity to a road—tortoise locations $\leq$ 20 m of a road (or road fence) were classified as being in close proximity to a road (as in Peaden et al. 2017). For analysis of variation in monthly home range size, we calculated 100% minimum convex polygons (MCPs) for each individual tortoise, for each month, using the adehabitatHR package in R (Fig. 1c; R Core Team 2018; Calenge 2019).

To estimate TPC parameters for each tortoise, we fit general additive models (GAMs) with loess smoother functions in which carapace temperature was the predictor and the 95th percentile of velocity at each 1-degree Celsius carapace temperature was the response variable. We fit curves to the 95th percentile of velocity at each temperature because we wanted to characterize the upper capacity for movement performance (here velocity) while avoiding the influence of outliers. We did not fit curves to all points because this includes many points during sedentary periods in which the animal was not motivated to move. We used GAMs, as opposed to comparing alternative parametric functions (e.g., Gaussian vs quadratic; Angilletta Jr. 2006), because this approach allows us to flexibly model nonlinear relationships, asymmetries in curves, and variation and irregularities among individuals (Zajitschek et al. 2012; Gilbert and Lattanzio 2016). We defined the optimum temperature for movement (T_{opt}) as the temperature associated with the maximum predicted velocity from GAMs fit for each individual tortoise. The optimal temperature range (B80) was then identified from the lower and upper temperatures

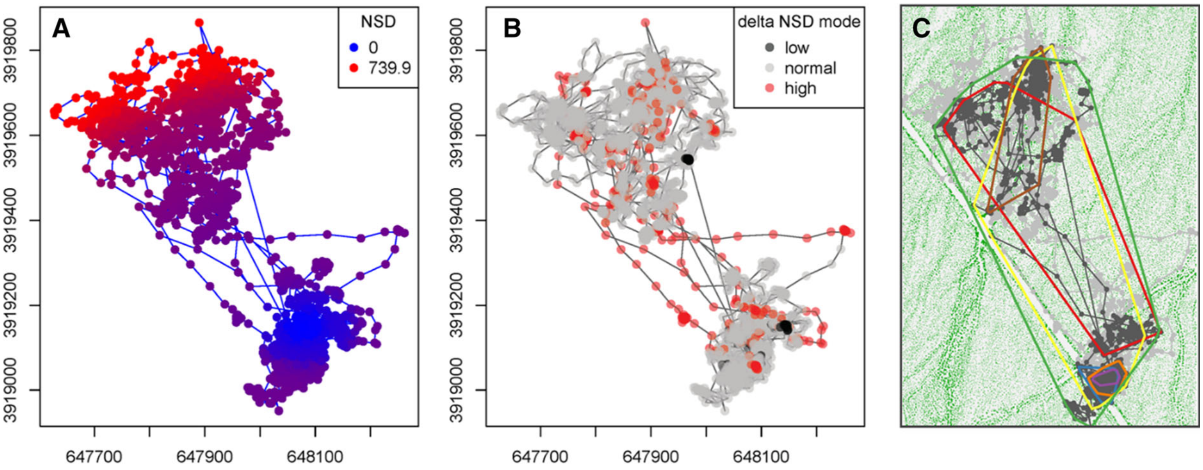

Fig. 1 **a** An example movement track for an individual tortoise with points colored by net squared displacement (NSD). **b** Segmentation of movement track for an individual tortoise with points colored by movement mode, calculated as the 10th (= low) and 90th (= high) percentiles of daily summed ΔNSD. **c** Monthly home ranges, measured as 100% minimum convex polygons (MCPs) for an individual tortoise. Light grey points and lines depict movement track from 2013 and dark grey depicts movement track from 2014. Only monthly MCPs from 2014 are shown

at which velocity was 80% of the maximum predicted value (Crowley 1985). We defined the ecological lower (CT_{minE}) and upper (CT_{maxE}) limits of the thermal performance range as the lower and upper temperatures thresholds at which predicted velocity is indistinguishable from zero (Sinclair et al. 2016), after accounting for GPS error. Rather than defining CT_{minE} and CT_{maxE} where velocity intersects with 0, we used a threshold of 0.56 m/min that accounts for the mean GPS position error for the study. We fit individual TPCs for the entire study period as well as by season and by whether tortoises were in close proximity to roads. We also fit a TPC to the 95th percentile of mean monthly home range size (across individuals) with each 1-degree Celsius change in mean monthly carapace temperature.

We determined whether TPC parameters varied by sex, season, and proximity to roads by fitting linear mixed models (LMMs) with individual ID as a varying intercept. To examine the effect of season on each parameter, including T_{optE}, B80, CT_{minE}, and CT_{maxE}, we fit an intercept-only model, a model with season, and both additive and interactive models with season and sex as fixed effects. We then compared these models using Akaike's Information Criterion corrected for small sample sizes (AICc). To examine the effect of road proximity on each parameter, we again fit an intercept-only model, a model with road proximity, a model with sex, and both additive and interactive models with road proximity and sex as fixed effects and compared these models using AICc. We also examined whether using estimates of core, operative temperatures might alter model selection. Specifically, we estimated the mean relationship between external carapace and internal operative temperatures using measurements of physical models (Hertz et al. 1993; Sieg et al. 2015) and then re-fit LMMs as described above but with each physical model as a random intercept (see SI methods; Fig S1). The objective of this supplemental analysis was not to precisely estimate core body temperatures but to examine the potential sensitivity of our main results—using external, carapace temperatures—to other temperature measurements, such as operative temperatures.

We then analyzed variation in monthly home range size using LMMs with individual ID as a varying intercept. To normalize home range size, we calculated the square root of this variable. To ask whether carapace temperatures within B80 range affect space-use at larger scales and whether this effect depends on season or sex, we first fit an intercept-only model; then, we fit models individually with season, sex, and the proportion of monthly GPS fixes that were associated with temperatures within the mean B80 range across all individuals (29–40 °C; hereafter, 'time at B80'), as well as the interaction between season and time at B80 and sex and time at B80. We also fit an ad hoc model to examine the relationship between mean monthly velocity, using all data points, and time at B80. Last, we analyzed the frequency of days during each month in which tortoises made long-distance, directed movements (as determined by path segmentation described above) using generalized linear mixed models (GLMMs) with a Poisson probability distribution and individual ID as a varying intercept. We fit the same set of models, in terms of fixed effects and random effects, as in the analysis of home range size described above and again compared competing models using AICc.

Results

The final dataset used to develop TPCs and analyze space use patterns included a mean of 5,938 locations per tortoise. The frequency of GPS fixes on tortoise locations varied across months, with highest frequencies in early spring and during the Monsoon season (Fig S2). We obtained lowest frequencies of fixes during June and November when tortoises were likely seeking refuge in burrows during dry periods and low temperatures, respectively. There was a seasonal shift in movement mode, from increased frequency of low displacement (or sedentary) movement activity in the spring to increased frequency of high displacement (or long-distance, directed) movements in the Monsoon season (Fig S2). Mean home range size also varied considerably across months and between seasons (Fig. S3), ranging from 0.02 to 133.9 ha (mean = 20.3 ha).

We found that TPCs for most individuals exhibited a characteristic left-skewed form (Fig. 2a). Notably, CT_{maxE} was quite consistent among individuals (mean = 42.8 °C; SD = 1.4); other TPC parameters, however, exhibited greater intraspecific variation, including the B80 range (mean = 11.2 °C; SD = 4.0), T_{optE} (mean = 36.0 °C; SD = 3.3), and CT_{minE} (mean = 12.4 °C; SD = 4.5). We found that TPCs for the 95th percentile of monthly home range size also exhibited a characteristic left-skewed form (Fig. 2b). Based on LMMs, we found statistical support for context-dependence of TPC parameters based on step velocity with respect to season, sex, or proximity to roads (Tables 1 and 2). For T_{optE}, the best supported models indicated that this parameter was lower in the Spring/Summer than during the Monsoon season ($\beta = -3.23$, SE = 1.26, $P = 0.010$) and was also lower when animals were in close proximity to roads ($\beta = -4.161$, SE = 1.16, $P < 0.001$). The best supported model with B80 as the response indicated that the optimal temperature range, B80, was significantly narrower during the Spring/Summer than the Monsoon season ($\beta = -2.62$, SE = 1.18, $P = 0.026$) and was also narrower in male than in female tortoises ($\beta = -3.17$, SE = 1.19, $P = 0.008$); B80 was not affected by proximity to roads. CT_{minE} did not differ between seasons but was significantly greater when animals were in close proximity to roads ($\beta = 6.65$, SE = 1.59, $P < 0.001$; Fig. 3). When examining the effect of season on the upper thermal tolerance based on velocity, the best supported model included additive effects of season and sex, showing that CT_{maxE} for movement activity was lower in the

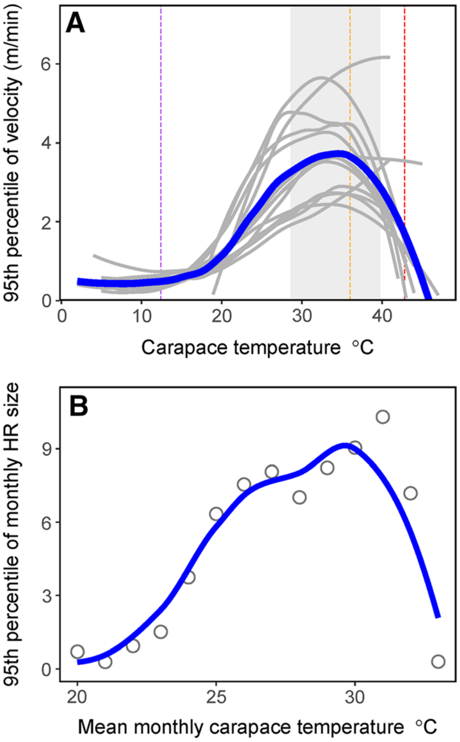

Fig. 2 Left-skewed thermal performance curves (TPCs) are apparent at two spatio-temporal scales. **a** TPCs fit to the 95th percentile of step velocity across temperatures using GPS tracking data and animal mounted temperature sensors. Grey lines show individual tortoise TPCs and the blue line shows the mean TPC fit to data for all tortoises. Vertical dashed lines indicate the mean CT_{minE} (purple), CT_{maxE} (red), T_{optE} (orange), and B80 range (grey). **b** TPC fit to the 95th percentile of monthly home range size—calculated here as the square root of the 100% MCP (ha)

Table 1 Comparisons of linear mixed models evaluating the effects of season and sex on thermal traits of the Mojave Desert Tortoise

Trait	Seasonal effects on thermal traits			ΔAICc	*P*
	Model	df	AICc		
T_{optE}	~ Intercept	3	159.6462	3.187	
T_{optE}	**~ Season**	**4**	**156.4593**	**0.000**	**0.015**
T_{optE}	~ Season + Sex	5	159.4473	2.988	0.052
T_{optE}	~ Season * Sex	6	162.6933	6.234	0.114
B80	~ Intercept	3	160.151	4.259	
B80	~ Season	4	159.1986	3.306	0.011
B80	**~ Season + Sex**	**5**	**155.8924**	**0.000**	**0.007**
B80	~ Season * Sex	6	158.7762	2.884	0.016
CT_{minE}	**~ Intercept**	**3**	**171.145**	**0.000**	
CT_{minE}	~ Season	4	172.449	1.304	0.231
CT_{minE}	~ Season + Sex	5	175.392	4.247	0.477
CT_{minE}	~ Season * Sex	6	178.560	7.415	0.663
CT_{maxE}	~ Intercept	3	112.085	6.515	
CT_{maxE}	~ Season	4	107.658	2.088	0.007
CT_{maxE}	**~ Season + Sex**	**5**	**105.570**	**0.000**	**0.002**
CT_{maxE}	~ Season * Sex	6	105.879	0.309	0.002

Thermal traits were derived from thermal performance curves based on desert tortoise field movements and include ecologically optimal temperature (T_{optE}), optimal temperature range (B80), ecologically critical thermal minimum (CT_{minE}), and critical thermal maximum (CT_{maxE}) for movement activity. Some thermal traits varied according to season and sex; for example, T_{optE} and CT_{maxE} were lower in the Spring/Summer than in the Monsoon season, and CT_{maxE} was lower in males than in females. Best supported models for each trait, based on Akaike's Information Criterion corrected for small sample size (AICc), are in bold. We also report model degrees of freedom (df), change in AICc from lowest AICc value (ΔAICc), and *P*-values

Spring/Summer than in the Monsoon season ($\beta = -1.31$, SE = 0.43, $P = 0.002$) and was also lower in males than females ($\beta = -1.35$, SE = 0.54, $P = 0.013$). When examining the effect of roads, CT_{maxE} was lower when tortoises were in close proximity to roads ($\beta = -2.15$, SE = 0.54, $P < 0.001$) and again, was lower for males than females ($\beta = -1.56$, SE = 0.63, $P = 0.013$; Fig. 3). Our analyses of thermal trait variation based on predicted core body temperatures, using physical models, were consistent with those based on carapace temperatures (Tables S1 and S2).

Table 2 Comparisons of linear mixed models evaluating the effects of landscape context (road proximity) and sex on thermal traits of the Mojave Desert Tortoise

Trait	Road effects on thermal traits			ΔAIC	*P*
	Model	df	AIC		
T_{optE}	~ Intercept	3	144.5763	5.944	
T_{optE}	**~ Road**	**4**	**138.6319**	**0.000**	**0.003**
T_{optE}	~ Road + Sex	5	141.6455	3.014	0.011
T_{optE}	~ Road * Sex	6	144.5994	5.968	0.023
B80	**~ Intercept**	**3**	**150.6239**	**0.000**	
B80	~ Road	4	152.087	1.463	0.238
B80	~ Road + Sex	5	153.5251	2.901	0.211
B80	~ Road * Sex	6	155.8933	5.269	0.235
CT_{minE}	~ Intercept	3	159.3734	10.365	
CT_{minE}	**~ Road**	**4**	**149.0082**	**0.000**	**< 0.001**
CT_{minE}	~ Road + Sex	5	152.1413	3.133	0.001
CT_{minE}	~ Road * Sex	6	155.6026	6.594	0.004
CT_{maxE}	~ Intercept	3	108.3274	7.004	
CT_{maxE}	~ Road	4	103.5289	2.205	0.006
CT_{maxE}	**~ Road + Sex**	**5**	**101.3239**	**0.000**	**0.001**
CT_{maxE}	~ Road * Sex	6	104.740	3.416	0.004

Thermal traits were derived from thermal performance curves based on desert tortoise field movements and include ecologically optimal temperatures (T_{optE}), optimal temperature range (B80), ecologically critical thermal minimum (CT_{minE}), and critical thermal maximum (CT_{maxE}) for movement activity. Some thermal traits varied according to landscape context (proximity to a road) and sex; for example, tortoises exhibited greater CT_{minE} and lower CT_{maxE} when near roads, and males had lower CT_{maxE} than females, on average. Best supported models for each trait, based on Akaike's Information Criterion corrected for small sample size (AICc), are in bold. We also report model degrees of freedom (df), change in AICc from lowest AICc value (ΔAICc), and *P*-values

In our analysis of the effect of time at B80 on monthly home range size and the potential dependency of this effect on sex or season, the best supported model included the interaction between time at B80 and season ($\beta_{B80} = 7.88$, SE = 1.48, $P < 0.001$, $\beta_{Season} = 1.26$, SE = 1.23, $P < 0.001$, $\beta_{B80\ xSeason} = -5.67$, SE = 2.24, $P < 0.001$, $R_{LR}^{2-} = 0.25$; Table 3). Monthly home range size (100% MCP) increased with increasing time that each tortoise spent within the optimal temperature range, B80; however, the slope of the B80 effect was significantly greater during the Monsoon season than during the

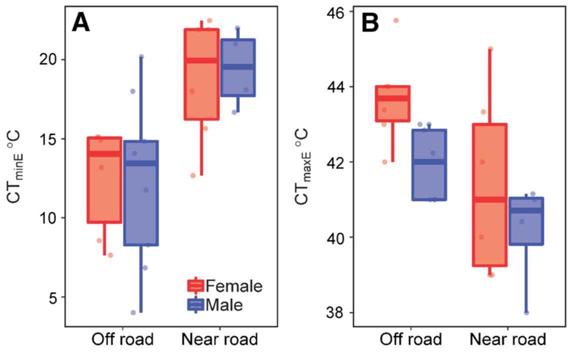

Fig. 3 Results indicate that thermal traits are dependent upon ecological context, here proximity to roads. When near roads, tortoises tend to exhibit greater CT_{minE} (**a**) and lower CT_{maxE} (**b**). On average, females had greater CT_{maxE} than males while CT_{minE} did not differ between sexes

Spring/Summer (low-rainfall months; Fig. 4a). In our analysis of the effect of time at B80 on frequency of high-displacement movements and the potential dependency of this effect on sex or season, the best supported model again included the interaction between time at B80 and season (β_{B80} = 4.16, SE = 0.76, $P < 0.001$, β_{Season} = 0.228, SE = 0.733, P = 0.756, $\beta_{B80\quad xSeason}$ = −.27, SE = 1.23, P = 0.065, R_{LR}^2 = 0.42; Table 3). The number of days each month during which tortoises made high-displacement movements increased with increasing proportion of fixes that were within the optimal temperature range (B80). Again, however, this effect depended on season, though the interaction was marginally non-significant, with temperature effects on movement being greater during the Monsoon season when water from rainfall is less limited in this part of the Mojave Desert (Fig. 4b).

Discussion

As climate change and habitat alteration create novel thermal environments, predicting species responses to these threats will hinge on understanding temperature exposure at fine spatial and temporal scales, variation among individuals in key thermal traits, and the dependence of intraspecific trait variation on environmental factors. This intraspecific variation may indicate both plasticity of thermal traits and the amount of raw material for natural selection, serving as a foundation for studies of adaptive capacity and for

Table 3 Comparisons of models evaluating the effects of time spent within the optimal temperature range (B80), and interactions of B80 with season and sex, on space use variables for the Mojave Desert Tortoise

Space-use variable	Model	df	AIC	ΔAIC	P
HR size (100% MCP)	∼ Intercept	3	710.0025	36.931	
HR size (100% MCP)	∼ Sex	4	707.230	34.158	0.027
HR size (100% MCP)	∼ Season	4	696.0843	23.012	< 0.001
HR size (100% MCP)	∼ B80	4	698.1612	25.089	< 0.001
HR size (100% MCP)	∼ B80*Sex	6	694.7559	21.684	< 0.001
HR size (100% MCP)	**~ B80*Season**	**6**	**673.072**	**0.000**	**< 0.001**
Days with long-distance movements	∼ Intercept	3	538.0114	73.510	
Days with long-distance movements	∼ Sex	4	538.3261	73.825	0.184
Days with long-distance movements	∼ Season	4	501.697	37.195	< 0.001
Days with long-distance movements	∼ B80	4	512.629	48.127	< 0.001
Days with long-distance movements	∼ B80*Sex	6	505.864	41.363	< 0.001
Days with long-distance movements	**~ B80*Season**	**6**	**464.501**	**0.000**	**< 0.001**

The interaction between time spent at B80 and season best explained both monthly variation in home range size and frequency of days with long-distance movements (also see Fig. 4). To evaluate variation in monthly home range size (100% MCP), we fit linear mixed models with tortoise ID as a varying intercept. To evaluate frequency of days with high-displacement movements, we fit generalized linear mixed models with a Poisson probability distribution and tortoise ID as a varying intercept. Best supported models for each space-use variable, based on Akaike's Information Criterion corrected for small sample size (AICc), are in bold. We also report model degrees of freedom (df), change in AICc from lowest AICc value (ΔAICc), and P-values

FIGURES

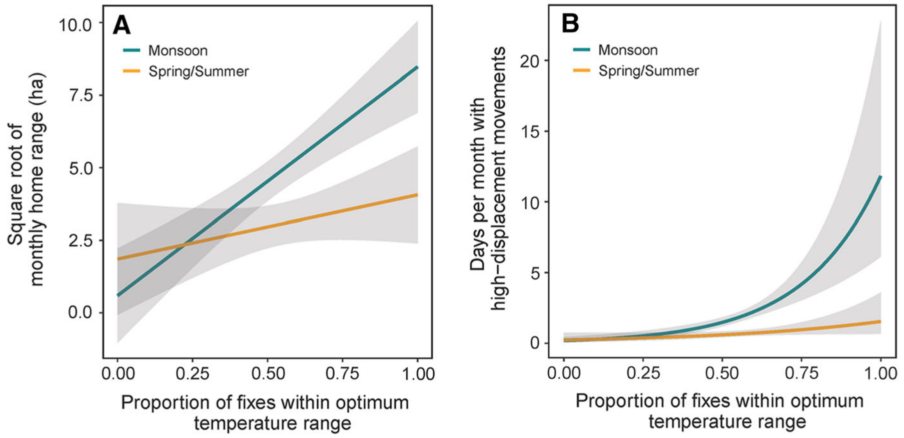

Fig. 4 Measures of space use increased with the amount of time tortoises spent within their optimum temperature range; the rate of increase was greater during the Monsoon season, indicating that rainfall is a limiting factor that modifies temperature-space use relationships. **a** Predicted monthly home range size (100% MCP) with increasing amount of time tortoises spent within the optimal temperature range (B80). Model predictions are from a linear mixed model with tortoise ID as a varying intercept. **b** Predicted frequency of high-displacement movements with increasing amount of time tortoises spent within the B80 range. Model predictions are from a generalize linear mixed model with Poisson probability distribution and tortoise ID as a varying intercept

predicting species responses under changing thermal environments. Here we show that GPS tracking data and animal-mounted temperature sensors generate data with high-spatiotemporal resolution from which we can readily characterize individual TPCs based on movements in the field. These TPCs allow us to characterize thermal trait variation among individuals and ecological contexts, and therefore, will be useful for management and conservation under changing thermal environments.

There are several advantages and limitations of field-derived TPCs from GPS data. The high-resolution data obtained through GPS transmitters and animal-mounted temperature sensors enable us to characterize (1) an organism's T_{optE}—an important thermal trait for assessing vulnerability to climate change but one that is rarely available (Huey et al. 2012), (2) intraspecific variation of thermal traits, and (3) dependence of thermal traits on individual and ecological covariates. This level of detail allows us to readily address questions, such as how thermal traits vary within or among individuals, across seasons, years, and habitats, that are not as easily studied with laboratory-measured TPCs or those based on population parameters (Sinclair et al. 2016). For example, addressing questions about how thermal traits of individuals vary across seasons, years, and habitats in the lab would require recapturing, transporting, and housing individuals multiple times and measuring traits under laboratory conditions, where their behavior is likely to differ from that in natural environments. Moreover, TPCs from GPS telemetry can produce estimates of thermal traits that are more ecologically-relevant than many experimental approaches; experimentally-measured TPCs may underestimate species' thermal sensitivity because they typically do not integrate constraints on movement performance imposed by animal behavior and other limiting factors (e.g., food availability, precipitation, and biotic interactions), which can vary across time and space. Parameters of field derived TPCs, therefore, can be considered more conceptually aligned with the realized thermal niche (Araújo et al. 2013; Gvoždík 2018). In contrast, TPCs from laboratory assays usually control for motivation—for example, by prodding animals—and external factors to measure maximum potential movement performance at each temperature; estimates from laboratory assays are, therefore, conceptually aligned with the fundamental thermal niche (Kearney & Porter 2004; Araújo et al. 2013; Gvoždík 2018; Nowakowski et al. 2018a). Conversely, some of the advantages of field-derived TPCs may also be considered limitations under certain research contexts, such as when it is important to control for or manipulate movement stimuli and ecological factors to isolate causal mechanisms. As with all applications of GPS tracking, development of TPCs is limited to animals that are large enough to accommodate the size of GPS transmitters or similar high-resolution tracking devices, which currently may exclude many small-bodied species. Field-derived TPCs can, however, facilitate measurements of thermal traits for species that are difficult to work with in a laboratory setting, such as very large-bodied species, or for species under strict use regulations, such as threatened and endangered species like the Mojave Desert Tortoise.

Using field-derived TPCs for the Mojave Desert Tortoise, we quantified individual-level variation in multiple thermal traits, with some traits exhibiting a high level of concordance among tortoises while others exhibited greater intraspecific variation. We found that, across the entire tracking period, desert tortoises had characteristic, left-skewed TPCs with a mean T_{optE} for movement of 36.0 °C and a SD of 3.26 °C; as carapace temperatures decreased from mean T_{optE}, movement performance gradually decreased toward zero (plus mean GPS error), reaching a mean CT_{minE} of 12.4 °C (SD = 4.5 °C). As carapace temperatures exceeded T_{optE}, movement performance decreased precipitously until reaching a CT_{maxE} of 42.8 °C (SD = 1.35 °C; Table 1, Fig. 2a). Our field-derived measure of CT_{maxE} from GPS data is similar to previous estimates for the Mojave Desert Tortoise (43.1 °C) and other tortoise species (42.5–44.0 °C) based on laboratory assays (Hutchison et al. 1966). A key difference in these measurements, however, is that CT_{maxE} in this study reflects the carapace temperature at the upper limit of movement performance in the field; whereas, laboratory estimates reflected the core body temperatures at which tortoises exhibited the onset of spasms and, therefore, these measurements have different ecological interpretations. For example, our CT_{maxE} estimate represents a behavioral threshold with ecological consequences because it limits opportunities to forage and reproduce. This cessation of activity is likely a behavioral mechanism for avoiding physiological consequences of acute thermal stress that can result from core temperatures reaching $\sim$ 43 °C (Hutchison et al. 1966)—core body temperatures of large-bodied tortoises increase more slowly than carapace temperatures due to thermal inertia (Fig. S1).

Our estimate of CT_{maxE} also exhibited lower variation among individuals compared to other thermal traits like CT_{minE}, a pattern that is generally consistent with multiple ectothermic vertebrates for which CT_{min} and CT_{max} have been measured in the lab (Araújo et al. 2013; Muñoz and Bodensteiner 2019). Low overall standing variation in CT_{maxE} suggests that there is limited potential for directional selection to increase CT_{maxE} under warming climatic conditions (Grigg and Buckley 2013; Hoffmann et al. 2013; Muñoz and Bodensteiner 2019). Additional molecular studies are needed, however, to further evaluate this inference. Other thermal traits, including T_{optE}, B80 range, and CT_{minE} were more variable among individuals. These traits, therefore, appear to be more labile, potentially because they are governed by different physiological mechanisms (MacMillan 2019), and are possibly subject to greater shifts due to acclimation or selection (Clusella-Trullas and Chown 2014; von May et al. 2017; Muñoz and Bodensteiner 2019).

The parameters of individual TPCs varied by sex, season, and when in close proximity to roads (Tables 1, 2; Fig. 3). For example, the optimal temperature range of individual tortoises, B80, was narrower and T_{optE} was lower during the dry season than the monsoon season. During months when precipitation is scarce and thus water is limiting, tortoises may move less and under cooler conditions to maintain lower metabolic rates (i.e., expend less energy) and conserve water during months when precipitation is scarce. Desert tortoises experience a net loss of energy and negative water balance during much of the dry season, which is recouped only after heavy rains and increased foraging in the fall months (Nagy and Medica 1986; Peterson 1996). We also found that the CT_{minE} and CT_{maxE} for movement performance were higher and lower, respectively, when tortoises were in close proximity to roads, decreasing the overall performance breadth of tortoises. This result may be due to changes in behavioral motivation for movement when tortoises are near roads. Our working hypotheses, based on field observations, are that (1) tortoises use roads and road margins for thermoregulation, (2) to drink water that collects on roads after rains, or (3) to forage along road margins where vegetation is often dense (Peaden et al. 2017), all of which are behaviors that involve reduced movement. Alternatively, tortoises may reduce activity near roads to avoid risks associated with roads, such as thermal stress, vehicles, and predators. More broadly, the context-dependence of the thermal traits reported here underscores the need to evaluate simplifying assumptions that are frequently made when using thermal traits to predict species responses to climate change (Sinclair et al. 2016). Studies often assume, for example, that thermal traits vary little within species, are independent of organismal state (e.g., disease or nutrition status), or are invariant across environmental gradients (Deutsch et al. 2008; Sunday et al. 2014; Nowakowski et al. 2017; see assumptions 2, 3, 10 and 11 of Sinclair et al. 2016). This study and other studies have shown that these assumptions often do not hold (Richter-Boix et al. 2015; Llewelyn et al. 2016; Rivera-Ordonez et al. 2019).

We found that temperature-dependence of fine-scale movement behavior—velocity of individual steps—scales to predict space use and movement patterns at larger spatial extents. Specifically, the relative amount of time tortoises spent within their B80 range was positively associated with both monthly home range size and frequency of high-displacement movement paths. Interestingly, there was not a strong relationship between mean monthly velocity (using all data points) and time at B80 (R_{LR}^{2} = 0.11), suggesting that large-scale space use and movement patterns emerge from other movement characteristics in addition to high velocity; for example, roaming behavior may be temperature-dependent and occur at moderate or low velocities. However, the effect of time at B80 depended on a second limiting factor, precipitation, such that both home range size and frequency of high-displacement movements increased at a greater rate during months with more rainfall. Previous work shows that field metabolic rate, foraging rates, activity, and home range size of desert tortoises are seasonally variable and appear to be limited, at least in part, by water availability (Peterson 1996; Duda et al. 1999; Agha et al. 2015; Peaden et al. 2017). Finally, the relationship between the 95th percentile of monthly home range size and mean monthly carapace temperature also produced a characteristic, left-skewed TPC (Fig. 2b). This result adds to other empirical examples that suggest temperature-dependent biophysical mechanisms often generate left-skewed performance curves at several biological scales, ranging from an ectotherm's heart rate (Sinclair et al. 2016), to whole-organism movement performance (Navas et al. 2008), to space use patterns across an entire year (this study), to population growth rates (Huey and Berrigan 2001; Deutsch et al. 2008).

Temperature determines the rates of biochemical reactions, serves as a metabolic constraint, and often has an outsized effect on ecological parameters for both ectotherms and endotherms, including movement (Huey and Stevenson 1979; Angilletta Jr. et al. 2007; Angilletta Jr. and Angilletta 2009; Dillon et al. 2010; Nowakowski et al. 2013; Nowakowski et al. 2015; Frishkoff et al. 2019). The responses of animal populations to rapidly changing thermal environments will be shaped by their temperature exposure, which is determined by local microclimates and behavior, and their temperature sensitivity, which is governed by evolved thermal traits (Todd and Andrews 2008; Kearney et al. 2009; Huey et al. 2012; Scheffers et al. 2014). TPCs based on GPS telemetry provide a useful means for measuring thermal traits in the field, generating fine-scale data with which to assess intraspecific variation and the dependence of traits on ecological context. Here, for example, we found that the home range size and frequency of high-displacement movements of Mojave Desert Tortoises increased with the amount of time tortoises spent at optimal temperatures; however, this effect was only apparent during months when rainfall was more abundant. We also observed that tortoises had lower variation in $\mathrm{CT}_{\mathrm{maxE}}$ than other thermal traits, suggesting that there may be limited potential for tortoises to adapt to warming climate conditions through selective shifts in thermal tolerances. Other factors, however, such as changes in behaviors like activity timing or migration to cooler habitats may represent additional adaptive pathways in response to warming climate. Notably, field estimates of thermal traits integrate the animal's ability to behaviorally thermoregulate, their prior temperature exposure (i.e., acclimation history), and their state-dependent motivation for movement under natural conditions. Laboratory-based methods may underestimate thermal sensitivity if conducted under idealized conditions (e.g., ad libitum feeding) and do not test for effects of other limiting factors on traits, such as the nutrition, hydration, infection status, and heat-avoidance behavior of animals (Sinclair et al. 2016; Greenspan et al. 2017). Field-derived TPCs should be useful in future studies for understanding the capacity of organisms to locally adapt to changing microclimates (especially when combined with molecular methods) (Llewelyn et al. 2016), for assessing connectivity in heterogeneous thermal landscapes (Rothermel and Semlitsch 2002; Nowakowski et al. 2015; Watling and Braga 2015), and by extension, for predicting the ability of organisms to track their climatic niche and shift their distributions under climate change (Bonebrake et al. 2017; Nowakowski et al. 2018a). Because movement contributes to the spatial distributions of genes, individuals, and species, TPCs based on movements in changing thermal landscapes can serve as a framework for integrating concepts across disciplines and for improving management of populations under climate change.

Acknowledgements We thank K. Drake and R. Tracy for providing physical models. This study was supported by the US Department of the Interior, Bureau of Land Management, through an agreement (L11AC20333) with UC Davis, by a California Energy Commission agreement 500-10-020 with UC Davis, and through a US Department of the Interior, National Park Service agreement P08AC00193 with University of Georgia. Additional funding was provided by the USDA National Institute of Food and Agriculture, Hatch project CAD-WFB-2097-H and by the Department of Energy through award number DE-EM0004391 to the University of Georgia Research Foundation.

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