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Using motion-sensor camera technology to infer seasonal activity and thermal niche of the desert tortoise (*Gopherus agassizii*)

Mickey Agha [a], Benjamin Augustine [b], Jeffrey E. Lovich [c], David Delaney [d], Barry Sinervo [e], Mason O. Murphy [f], Joshua R. Ennen [g], Jessica R. Briggs [h], Robert Cooper [e], Steven J. Price [a,*]

[a] *Department of Forestry, University of Kentucky, Lexington, KY 40546, USA*
[b] *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*
[c] *US Geological Survey, Southwest Biological Science Center, MS-9394, Flagstaff, AZ 86001, USA*
[d] *US Army Construction Engineering Research Laboratory, P.O. Box 9005, Champaign, IL 61826-9005, USA*
[e] *Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95064, USA*
[f] *Department of Biology, University of Kentucky, Lexington, KY 40546, USA*
[g] *Tennessee Aquarium Conservation Institute, 201 Chestnut Street, Chattanooga, TN 37402, USA*
[h] *Warner College of Natural Resources, Colorado State University, Fort Collins, CO 80523, USA*

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ABSTRACT

Understanding the relationships between environmental variables and wildlife activity is an important part of effective management. The desert tortoise (*Gopherus agassizii*), an imperiled species of arid environments in the southwest US, may have increasingly restricted windows for activity due to current warming trends. In summer 2013, we deployed 48 motion sensor cameras at the entrances of tortoise burrows to investigate the effects of temperature, sex, and day of the year on the activity of desert tortoises. Using generalized estimating equations, we found that the relative probability of activity was associated with temperature (linear and quadratic), sex, and day of the year. Sex effects showed that male tortoises are generally more active than female tortoises. Temperature had a quadratic effect, indicating that tortoise activity was heightened at a range of temperatures. In addition, we found significant support for interactions between sex and day of the year, and sex and temperature as predictors of the probability of activity. Using our models, we were able to estimate air temperatures and times (days and hours) that were associated with maximum activity during the study. Because tortoise activity is constrained by environmental conditions such as temperature, it is increasingly vital to conduct studies on how tortoises vary their activity throughout the Sonoran Desert to better understand the effects of a changing climate.

1. Introduction

Understanding the thermal sensitivity of wildlife (e.g., optimal temperature range) is fundamental to effective wildlife and habitat management, as climate shifts can alter thermal niches and cause species extinctions (Sinervo et al., 2010). Knowledge about the interactions between abiotic attributes and the ecology of wildlife once remained obscure, in part due to difficulty collecting unbiased, empirical data required to document physiological sensitivities of species and their respective ecological critical thresholds (Huey and Stevenson, 1979). Recently, however, estimating and comparing thermal performance of animals has become a major focal point of research programs, especially for ectotherms, as their behavior and physiological stability are uniquely tied to their ability to regulate exposure to thermal stimuli (Angilletta et al., 2002, 2010; Hertz et al., 1982; Huey et al., 2012). Because ectotherms produce minimal metabolic heat, they must employ various behaviors (e.g., basking, foraging, restricted activity, shade seeking) and select suitable habitat to maintain ecological and physiological performance (Bulte and Blouin-Demers, 2010).

Accurately assessing ectotherm activity and behavior can be difficult using direct methods. For instance, direct observations by investigators during research activities (i.e., active surveys) can provide biased information as the study subject may alter its behavior or activity when followed by the researcher (Bridges and

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* Corresponding author. Fax: +1 859 323 1031.
E-mail addresses: mickey.agha@uky.edu (M. Agha), ben.augustine@uky.edu (B. Augustine), jeffrey_lovich@usgs.gov (J.E. Lovich), David.Delaney@usace.army.mil (D. Delaney), lizardrps@gmail.com (B. Sinervo), mason.murphy@uky.edu (M.O. Murphy), jre@tnaqua.org (J.R. Ennen), jessiebriggs13@gmail.com (J.R. Briggs), rdcooper408@gmail.com (R. Cooper), steven.price@uky.edu (S.J. Price).

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Noss, 2011; Cutler and Swann, 1999; Horne et al., 2007; Johnson, 2002). Thus, researchers have increasingly used indirect methods to document wildlife activity, such as motion-sensor camera traps (see O'Connell et al., 2010 for a review). Researchers suggest that camera traps provide a more accurate empirical documentation and quantification of wildlife behavior and activity patterns than historical trapping and observational methods (Dillon and Kelly, 2007; Meek et al., 2012). For example, camera traps provided a rare insight into specific partitioning of activity timing in small mammals that was previously unknown (Meek et al., 2012), of extended activity in amphibians (Hoffman et al., 2010), and of the first known evidence of nocturnal activity in a presumptive diurnal primate (Tan et al., 2013).

Documenting activity and behavior in desert wildlife via camera traps may be particularly beneficial to further understanding enigmatic species. Due to the harsh desert climate, activity periods of most desert wildlife are temporally and spatially limited both seasonally and daily (Porter et al., 1973; Grant and Dunham, 1988; Huey et al., 1977). Thus, researchers studying desert wildlife often restrict their research efforts to times when their study organisms are presumed active. Additionally, climate change is expected to result in restricted activity windows, population declines and extinction of many desert species (Sinervo et al., 2010), including the desert tortoise (*Gopherus agassizii*; Lovich et al., 2014b), a species listed as threatened under the US Endangered Species Act (US Fish and Wildlife Service, 2011). Desert tortoises inhabit an extreme environment where ambient temperatures frequently exceed the tortoise's critical thermal maximum (43.1 °C; Hutchison et al., 1966; 38.6–45.1 °C; Naegle, 1976). Several studies of the desert tortoise have used direct observational methods to examine daily and seasonal timing of activity (Averill-Murray et al., 2002; Luckenbach, 1982; Nagy and Medica, 1986; Osorio and Bury, 1982; Ruby et al., 1994), air temperature activity ranges (Berry and Turner, 1986; Brattstrom, 1965; McGinnis and Voigt, 1971; Woodbury and Hardy, 1948; Zimmerman et al., 1994), and temperature thresholds for activity (Hutchison et al., 1966; Naegle, 1976). However, few studies use indirect methods and constant activity temperature monitoring to examine activity patterns (i.e., thermal models, ibutton sensors) (Bulova, 1994; Nussear et al., 2007; Zimmerman et al., 1994).

In this study, we used passive infrared (PIR) motion-sensor camera traps to examine activity of desert tortoises and to better define the relationship between activity and environmental temperature. We had three specific objectives: (i) to assess the daily thermal niche of a western Sonoran Desert population of desert tortoises over one field season by testing the effect on activity of air temperature, sex, time of year, and biologically relevant interactions of these parameters, (ii) to identify temporal partitioning (patterns) of activity over calendar days of the year during the activity season, and (iii) to identify patterns of activity during hours of the day over the activity season.

2. Materials and methods

2.1. Study area

Our study was conducted at a wind energy generation facility, known as Mesa, near Palm Springs in Riverside County, California, USA. This tortoise population has been studied since the early 1990s. Located at the western edge of the Sonoran Desert, the study site (approximately 6.25 km^2) is bounded on the north and west by the San Gorgonio Wilderness Area (see Lovich et al., 2011a).

Fig. 1. Motion sensor camera placed at the mouth of desert tortoise burrows at Mesa.

2.2. Field techniques

Tortoises have been studied at Mesa for over 20 years resulting in publications on growth, demography, reproduction and various other aspects of their ecology and behavior (Lovich et al., 2011a, 2011b, 2012, Ennen et al., 2012, Agha et al., 2013). When a tortoise was captured, we recorded sex (based on secondary sexual characteristics) and marked each animal with a unique identification code by cutting shallow notches into the marginal scutes of the carapace using a triangular metal file (Cagle, 1939). In addition to carapace notching, clear epoxy tags (with the corresponding identification number) were glued to the fourth left pleural scute. Lastly, tortoises were measured for straight-line carapace length (CL) with tree calipers (see Lovich et al., 2011a for detailed field methods).

From June 1 to November 14, 2013, we used 48 Reconyx and Wildgame trail cameras (models HC500, PC800 and W8E) placed at active burrows to monitor desert tortoises (Lovich et al., 2014a) (Fig. 1). All cameras were programmed to take 1-5 high definition photographs (camera trap events) when triggered (0.2 s trigger speed) by movement of wildlife (Rovero et al., 2010, 2013). For each camera trap event, sex and unique identification code of the individual were recorded (determined by carapacial notching or epoxy tag). Also, we determined whether the tortoise was alert or not alert (eyes closed), basking (based on posture), foraging, walking, copulating, digging, fighting, or nesting. We also recorded proximity of these behaviors to the tortoise burrow (see Zimmerman et al., 1994 and Ruby and Niblick, 1994 for basking posture). In the case that a tortoise on the surface was captured on camera prior to sunrise, having spent the night outside, activity was considered when the tortoise started to walk (Bulova, 2002; Zimmerman et al., 1994). Camera detection range varied, but typically we could see the entrance to the burrow and the surrounding landscape in a radius of approximately 2–4 m^2.

Cameras were monitored and checked on a weekly to monthly basis to retrieve photos. During 2013, surface air temperature readings were collected every 30 min from a Remote Automated Weather Station (RAWS) at the site and accessed via the MesoWest website (http://mesowest.utah.edu/index.html) and White Water Station (WWAC1). These temperature readings were then associated to each individual camera trap event for all 48 cameras.

2.3. Statistical analysis

Because cameras frequently took multiple pictures of the same individual during an event, the active records exhibited strong temporal correlation (a concern noted by previous camera trap investigations; Cutler and Swann, 1999; Hughson et al., 2010). To remove this pattern, we randomly subsampled active records to retain a maximum of one active record per individual per activity period (sunrise to sunset). Photos captured before sunrise and after sunset, as determined by U.S. Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/RS_OneYear.php), were removed. Nocturnal activity was not considered due to lack of data and because our study was strongly focused on quantifying daytime activity. In addition, we removed images that yielded partial views of tortoises that could not be unambiguously identified or given an activity classification.

To determine environmental factors that most influence probability of tortoise activity, we used Resource Selection Functions, which compare used to available resource units (i.e., air temperature) to produce “values proportional to the probability of use of resource units” (RSF; Manly et al., 2002). RSFs with an exponential link function are mathematically equivalent to binomial generalized linear models (GLMs) with the logit link function (McDonald, 2013). Further, binomial GLMs can be extended to account for correlation within individuals and still allow for population-level inference using Generalized Estimating Equations (GEEs, Hardin, 2005, Koper and Manseau, 2009). Therefore, we used binomial GEEs to assess the effect of covariates on the relative probability of adult desert tortoise daily activity during the warmest part of the year (June to November) at Mesa.

Models were fit in the program R (R Development Core Team, 2013), using the ‘geepack’ package (Yan, 2004). Available resource units were produced by randomly generating 300 day-hour combinations per individual, with a corresponding RAWS record during the duration camera traps were deployed. Covariates of interest in this analysis were temperature (linear and quadratic, T and T^2) and sex (SEX). Changing activity patterns or the activity budget across the active season were also of interest, but preliminary analysis revealed complex patterns that would be difficult to model completely in a regression context. However, we did include calendar days from January 1 (hereafter DOY) in the RSF models because T linearly correlated with DOY. We also accounted for variable activity levels across individuals by using an exchangeable correlation structure in the GEE models. Subsequently, we tested all possible combinations of T (linear and quadratic), SEX, and DOY (linear and quadratic). All two-way interactions were considered *a priori* plausible and so were all fit using the ‘MuMIn’ package (Barton, 2011). Models were ranked using the quasi-likelihood criterion under the independence model, QIC (I) (hereafter QIC; Pan, 2001), and any models within 7 QIC units of the top model were considered competitive (Burnham and Anderson, 2002). Within this model set, parameter estimates and standard errors were obtained by refitting the models using the exchangeable correlation structure, and then averaged following Burnham and Anderson (2002).

By applying quadratic temperature effects in the RSF, we estimated the operative temperature at which activity peaked, separating SEX in models with a temperature-by-sex interaction. To obtain confidence intervals on these maxima, we used nonparametric bootstrapping in the model fitting and averaging process. Ninety-five percent intervals were calculated from the bootstrap distributions composed of 200 resamples. Also of interest was the maximum temperature at which tortoises were observed to be active outside the burrow, which we summarized by the mean and range (separated by SEX).

2.3.1. *Mixture models*

To investigate temporal partitioning of activity across DOY, we used normal mixture models (Benaglia et al., 2009; Connette et al., in press; Owen-Smith et al., 2012). These models allowed us to parse out periods of activity during the active season for desert tortoises, and compare them between sexes. These models adequately represent multi-modal frequency distributions of activity levels across DOY that are not feasibly modeled in a regression context. Our data were not described well by available count models in which the variance depends on the mean and were therefore approximated by normal distributions. We fit sex-specific normal mixture models with 1–4 mixture components (hereafter activity periods) using the R package ‘Mixtools’ (Young et al., 2009), and subsequently selected the top models for each sex using the Akaike Information Criterion (AIC). We used parametric bootstrapping to produce 95% confidence intervals for the parameters of the top models ($B = 1000$). Because some bootstrap distributions were skewed, basic intervals were used, as they are less biased in this scenario than percentile intervals (Efron, 1979). Parameters ‘π’, ‘μ’ and ‘σ’ are provided for each activity period for both males and females. Parameters reflect different factors of the mixture model: (π) indicates the percent of total activity taking place in each activity period, (μ) corresponds to mean of the activity period, and (σ) corresponds to the temporal duration of the activity period (unit: DOY).

Lastly, to identify patterns of activity over hours of the day (HOD) in the active season, we again used normal mixture models. We fit sex-specific normal mixture models with 1–2 activity periods, as a maximum of 2 activity periods (two distinct major activity peaks) was deemed to be biologically important when assessing desert tortoise activity throughout a day. Parametric bootstrapping was used to produce 95% confidence intervals for the parameters of the top models ($B = 1000$).

3. Results

In study year 2013 at Mesa, we obtained 2754 tortoise camera trap events, of which 993 (680 male and 313 female) were randomly selected for further analysis. We identified 23 individuals (13 male and 10 female) in these pictures. Individual males averaged 52.3 (16–78), active tortoise camera trap events, and females averaged 31.3 (12–53). Active tortoises were observed above ground at surface temperatures ranging from 8.33 °C and 41.67 °C. Although above-ground ambient temperatures often appeared favorable at night, very few tortoises were active (camera trap, researcher observed) above ground past sunset during the study. Nocturnal activity was noted on 23 occasions. The daily mean maximum temperature at which individual turtles were observed to be active was 37.25 °C (range 32.77–41.67 °C).

The top RSF model included the covariates SEX, T, T^2, DOY, DOY^2, SEXxDOY, and SEXxT (Table 1). Parameter estimates within the relative probability of activity model for females was: $y = -15.39 + 0.06\text{xDOY-}0.0001\text{xDOY}^2 + 0.42\text{x}T\text{-}0.007\text{x}T^2$, and for males: $y = -15.39 + 0.08\text{xDOY-}0.0001\text{xDOY}^2 + 0.38\text{x}T\text{-}0.007\text{x}T^2$. We found strong support for models including all covariates (at least $\Delta\text{QIC} > 15.94$ for all non-competing models) except for models including the interaction between SEX and T which had

Table 1
Generalized estimating equation models of Agassiz's desert tortoise activity based on fixed effects: temperature (T), squared temperature (T^2) and gender (SEX), and random effects: identification code (ID), calendar days since January 1 (DOY), and calendar days since January 1 squared (DOY^2). Models are sorted by increasing QIC weights (W_i). Symbols and abbreviations reflect different properties of each model (K=number of parameters, Δ=Difference from best model, W=QIC weight). Models that were not judged as competing according to Arnold (2010) were not included in W_i calculation.

Activity model	K	Negative quasi-log likelihood	ΔQIC	W_i
$T+T^2+SEX+\text{SEXx}T+\text{DOY}+\text{DOY}^2+\text{DOYxSEX}$	8	2868	0.00	0.66
$T+T^2+SEX+\text{DOY}+\text{DOY}^2+\text{DOYxSEX}$	7	2870	1.36	0.34

Table 2
Averaged parameter estimates on the logit scale, and confidence intervals from the top two generalized estimating equation models. Abbreviations represent different factors including temperature (*T*), squared temperature (T^2), gender (SEX), calendar days from January 1 (DOY), intercept (INT) and calendar days from January squared (DOY), DOYxSEX interaction, SEXxT interaction. LB and UB correspond to lower bound and upper bound of 95% confidence intervals, respectively.

Parameter	Est.	95% LB	95% UB
INT*	−15.3932	−20.8287	−9.9578
DOY*	0.0647	0.0272	0.1021
DOY^2*	−0.0001	−0.0002	−0.0001
T*	0.4166	0.2533	0.5799
T*^{2}	−0.0067	−0.0095	−0.0041
SEX (male)	−1.3414	−4.0298	1.3469
DOYxSEX (male)*	0.0106	0.0018	0.0194
SEX (male)x*T*	−0.0324	−0.0797	0.0149

* Effects with 95% confidence interval (CI) not overlapping zero were significant at $P < 0.05$.

almost equal support as the second ranked model (ΔQIC=1.36) (Table 2). Relative probability of activity was higher for males than for females (Fig. 2). The temperature at which desert tortoises were estimated to have the highest relative probability of activity (>0.9) was 30.7 °C (95% CI; 28.44–33.9) for females and 29.08 °C (95% CI; 27.54–30.9) for males.

Model selection supported DOY mixture models with 3 activity periods for both males and females (Table 3), which largely matched up in timing and duration (Fig. 3). The mean (μ) and duration (σ) of each activity period overlapped between sexes for activity periods 2 and 3 (Table 4). The confidence intervals for the σ overlapped between sexes for activity period 1; however, the μ for males was significantly smaller than females, indicating a peak in activity earlier in the year for males. Females allocate significantly more activity to period 1 (non-overlapping confidence intervals for π), but no significant differences were detected in the other two activity periods. Although not significant, females in the sample tended to spend less time active later in the year relative to males.

Model selection supported HOD mixture models with 2 distinct activity periods for females (Table 5). Although model selection determined HOD mixture models with 3 distinct activity periods were best for males (Table 5), we selected 2 periods due to daily temperature trends (Fig. 4). Male and female activity periods from sunrise to sunset matched well in timing and in duration, which was supported by overlapping confidence intervals for σ, μ and π parameters (Table 6).

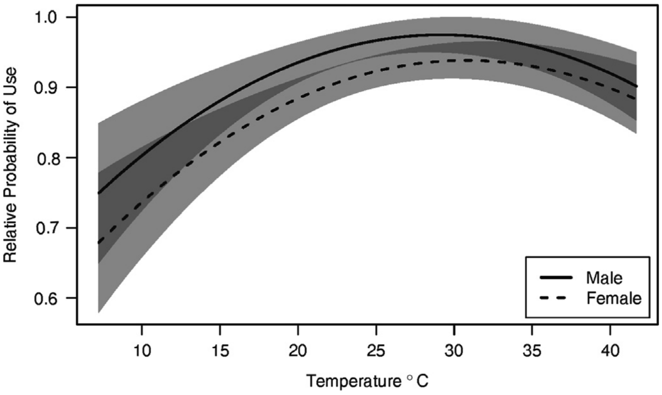

Fig. 2. Relative probability of activity in male and female Agassiz's desert tortoises using model average of top two generalized estimating equation models. Light gray shading represents unconditional standard error. Dark gray shading represents unconditional standard error overlap between males and females.

Table 3
Mixture model selection for assessing desert tortoise activity across day of the year (DOY). Symbols and abbreviations reflect different properties for each model (***K***=number of parameters, Log Lik=Log likelihood, **ΔAIC**=Akaike's information criterion difference value from best model.

Components	*K*	Female			Male		
		Log Lik	AIC	ΔAIC	Log Lik	AIC	ΔAIC
1	2	−1613	3230	68	−3465	6934	86
2	5	−1579	3168	6	−3439	6888	40
3	8	−1573	**3162**	0	−3416	**6848**	0
4	11	−1571	3164	2	−3414	6850	2

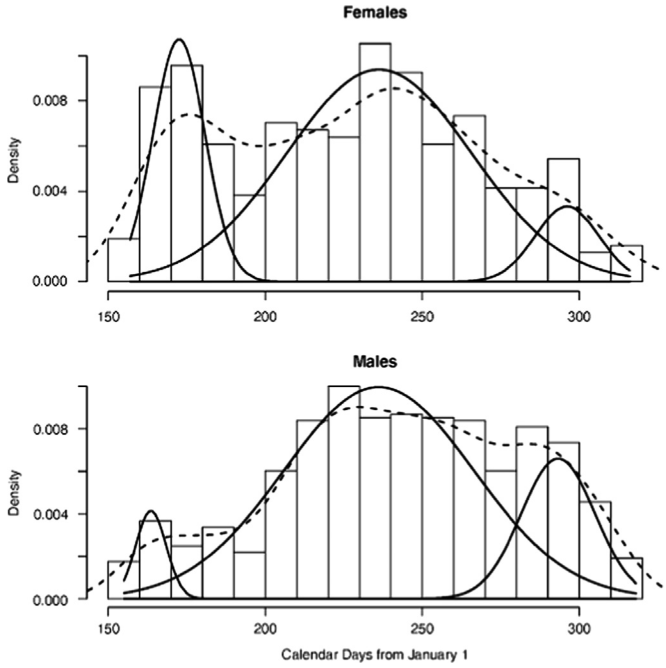

Fig. 3. Normal mixture models assessing patterns of activity in desert tortoises across calendar days from January 1 (day 150 to 318). Histogram bars represent probability density of the number of active tortoise records per day. Gaussian components (peaks in histogram) are fitted with an iterative expectation maximization algorithm. The three solid lines in each graph represent the exact density of the three-period mixture distribution. The dashed line is the nonparametric density estimate drawn from this mixture distribution.

Table 4
Mixture model parameter estimates for assessing desert tortoise activity across days of the year (DOY). Symbols and abbreviations reflect different factors: (π) indicates significance of each component (activity period), (μ) corresponds to mean peak of activity period, and (σ) is the duration of activity period (unit: DOY). LB and UB correspond to lower bound and upper bound of 95% confidence intervals, respectively.

Par	Period	Female			Male		
		Est.	95% LB	95% UB	Est.	95% LB	95% UB
π	1	0.224*	0.151	0.284	0.050*	0.026	0.069
	2	0.691*	0.612	0.868	0.755*	0.685	0.852
	3	0.085	−0.064	0.136	0.195*	0.107	0.262
μ	1	172.525	169.415	175.035	163.564	161.090	165.741
	2	236.217	230.611	245.261	236.123	231.494	241.715
	3	296.107	288.824	312.008	293.242	289.885	297.887
σ	1	8.312	5.756	10.540	4.832	2.441	6.865
	2	29.351	25.043	38.718	30.211	27.068	35.087
	3	10.166	1.045	17.028	11.762	8.234	15.242

* π estimates with 95% confidence interval (CI) not overlapping zero were significant at $P < 0.05$.

Table 5
Mixture model selection for assessing desert tortoise activity across 'hour of the day'. Symbols and abbreviations reflect different properties for each component (activity period) (***K***=number of parameters, Log Lik=Log likelihood, **ΔAIC**=Difference from best model.

Periods	*K*	Female			Male		
		Log Lik	AIC	ΔAIC	Log Lik	AIC	ΔAIC
1	2	−809.5	1623	72	−1806	3615	206
2	5	−770.6	**1551**	0	−1708	3426	17
3	8	−766.5	1549	2	−1697	**3409**	0

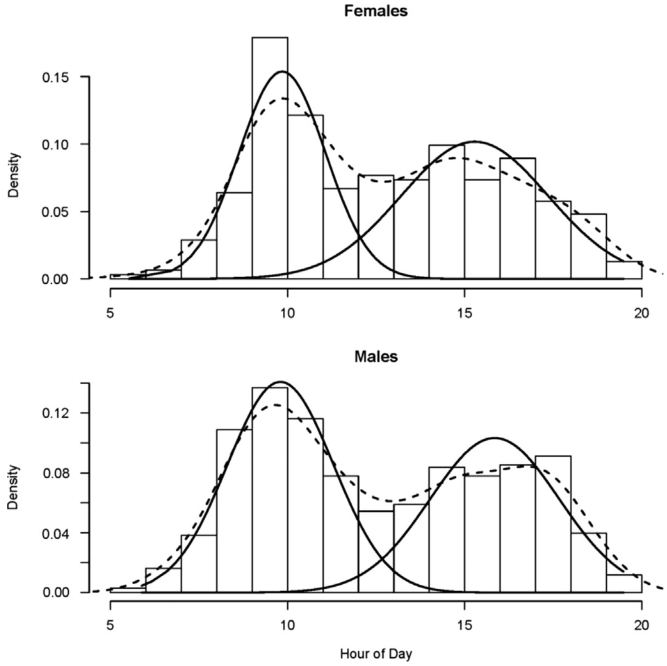

Fig. 4. Normal mixture models assessing patterns of activity in desert tortoises across hour of day (hour 0 to 24). Histogram bars represent probability density of the number of active tortoise records per hour. Gaussian components (peaks in histogram) are fitted with an iterative expectation maximization algorithm. The two solid lines in each graph represent the exact density of the two-period mixture distribution. The dashed line is the nonparametric density estimate drawn from this mixture distribution.

Table 6
Mixture model parameter estimates for assessing desert tortoise activity across 'hour of the day'. Symbols and abbreviations reflect different factors: (π) indicates significance of each component (activity period), (μ) parameter corresponds to mean peak of activity period, and (σ) is the duration of activity period (unit: hour of the day). LB and UB correspond to lower bound and upper bound of 95% confidence intervals, respectively.

Par	Period	Female			Male		
		Est.	95% LB	95% UB	Est.	95% LB	95% UB
π	1	0.472*	0.387	0.528	0.529*	0.482	0.577
	2	0.528*	0.472	0.613	0.471*	0.423	0.518
μ	1	9.850	9.554	10.164	9.800	9.595	10.011
	2	15.281	14.700	15.760	15.847	15.560	16.120
σ	1	1.225	1.008	1.442	1.499	1.344	1.662
	2	2.072	1.704	2.492	1.819	1.618	2.048

* π estimates with 95% confidence interval (CI) not overlapping zero were significant at $P < 0.05$.

4. Discussion

The behavior, physiology and fitness of ectotherms are largely determined through interactions with environmental variables (i.e., air temperature, wind speed, humidity) (Angilletta et al., 2010; Grant and Dunham, 1988; Porter et al., 1973). Consequently, it is not surprising that an ectothermic organism's performance or tolerance is highly related to thermal sensitivity as well (Huey and Stevenson, 1979). Through the application of an unbiased, enhanced field research method (i.e., camera trapping), our study supports previous research showing that abiotic variables (i.e., temperature) influence probability of activity (performance) in desert tortoises (Bulova, 2002; McGinnis and Voigt, 1971; Zimmerman et al., 1994). Our study also demonstrated that camera traps provide novel insights into *G. agassizii* ecology, such as nocturnal activity, higher than previously known activity-temperature thresholds and a tri-modal seasonal activity pattern. Furthermore, our RSF temperature activity curve follows a characteristic unimodal shape, which suggests that *G. agassizii* has a limited surface operative temperature window. Decreased activity when air temperatures exceed an average of 37.25 °C suggested that tortoises actively avoided the risk of overheating. This finding is similar to Walde et al. (2003) for desert tortoises elsewhere, and Hailey and Coulson (1996) for Speke's hinge-back tortoise (*Kinixys spekii*). In addition, daylight observations of the Mediterranean spur-thighed tortoise (*Testudo graeca*) suggested that activity is influenced linearly by air temperature, and that the interaction varies between sexes (Lambert, 1981). Temperature-influenced differences in activity between males and females have also been found in the turtles *Trachemys scripta* (Hammond et al., 1988), *Chrysemys picta* (Lefevre and Brooks, 1995), and *Emydoidea blandingii* (Millar et al., 2012). Our findings at Mesa suggest that tortoises are highly sensitive to fine-scale variation in temperature, and therefore rely on their familiarity with the micro-environment to behaviorally thermoregulate (Bulova, 2002; Chelazzi and Calzolai, 1986). When temperatures exceeded the upper thermal threshold for activity found at Mesa, tortoises were seen retreating to their burrows almost immediately, ostensibly to reduce body temperature.

Because restricted activity behaviors make this species exceedingly difficult to monitor (i.e., field survey; Freilich et al., 2000), it is most profitable and proficient to conduct investigations with indirect techniques (camera trapping) within their selected habitat, along with operative temperature models (Zimmerman et al., 1994) to capture micro-environmental variation in activity and habitat use. Although previous studies noted technological difficulties for quantitative assessments using camera traps (Cutler and Swann, 1999; Hughson et al., 2010), camera trap technology – when used correctly – provides a non-invasive tool for conservation of wildlife. Motion-sensor cameras can also allow researchers to assess how climate patterns affect the behavior of desert tortoises (e.g., foraging) based on periods that desert tortoises remain above ground. Furthermore, hatchling emergence from nests within burrows could be effectively documented via motion-sensor camera technology. Objective monitoring of the activity and thermal ecology of desert tortoises at all life history periods is critical to better understanding this imperiled species.

Our results suggested that sex of the individual plays a large role in determining probability of tortoise activity, similar to the findings of Lambert (1981) for the tortoise *T. graeca*. At Mesa, male tortoises were more active than females across the entire optimal operative temperature range. These findings may reflect sexual size dimorphism of desert tortoises, as males are significantly larger than females (Gibbons and Lovich, 1990; Lovich et al., 2011a) and thus have greater thermal inertia. We suspect that with a smaller surface to volume ratio than females, male tortoises exhibit higher activity rates (spending prolonged periods at the surface) to maintain an optimal body temperature. However, further research is needed to determine why each sex selects a unique upper temperature threshold for activity. Increased activity in males may also be linked to active searching of mates (Rostal et al., 1994) or reproduction (Morreale et al., 1984; Aresco, 2005). Strong selective forces may act upon male tortoises to increase mate searching activity (Bonnet et al., 2001). Male desert tortoises also increase burrow searching during the mating season (Bulova, 1994) and use larger home ranges (Duda et al., 1999). Increased activity in males, especially at suboptimal and supraoptimal temperatures, needs to be considered in future research monitoring of the desert tortoise, as increased anthropogenic-based hazards may occur outside of the optimal activity season in tortoises. Although males were more active than females, females had slightly higher optimal activity temperatures (Fig. 2). Females may be optimizing or displaying peak activity at temperatures identified in our study because thermoregulation is related to their reproductive physiology and clutch phenology (i.e., specifically heat unit accumulation; Lovich et al., 2012).

Mixture models allowed us to divide the activity season into early, middle and late periods of activity, as well as identify an activity gap during mid-day. These models also allowed us to quantify patterns that were not feasible in a regression context. Tortoises at Mesa displayed a tri-modal (seasonal) activity pattern over the span of the study period, as indicated by the strong effect of T and T^2 across DOY. Over the course of an activity season, tortoises budget their activity to take advantage of reproduction-related processes (i.e., mating) as well as resource availability (Medica et al., 2012). Males and females were equally active during most of the study but did differ during reproductively important periods of the year. Male tortoises at Mesa appeared to be more active during the third activity period (Table 4, Fig. 3), potentially searching for mates or taking advantage of necessary resources prior to hibernation. In contrast, females were more active during the first period (Table 4), when gravidity of several females was documented at the site through weekly X-radiography (Lovich et al., in press). Such evidence suggests that the first activity period for females may directly relate to a critical phenological stage related to first clutch appearance (Lovich et al., 2012). While not statistically significant, females allocated less activity to the last period, although further research with increased data may suggest otherwise. Desert tortoise activity modeled throughout a twenty-four hour span (Fig. 4) suggested that both male and female desert tortoises become active prior to noon (period 1), decrease activity levels at mid-day, and then subsequently become active again in the afternoon (period 2) (Fig. 4). The gap in activity during the middle of the day generally reflects restriction of activity when environmental temperatures are often extreme.

The desert tortoise evades lethal temperatures by retreating to their burrows which provide a cooler retreat (Brattstrom, 1961; Voigt, 1975; Ruby et al., 1994; Woodbury and Hardy, 1948). Motion-sensor cameras provided evidence that burrows are of critical importance to the thermal ecology of desert tortoises. Consequently, reducing anthropogenic habitat modification and disruption of soil during periods of the year when air temperatures exceed ~37.25 °C is prudent (~35 °C; Walde et al., 2003). In addition, particular attention should be paid to timing of the main activity season (Activity period 2; Fig. 3) and operative temperature thresholds (~37.25 °C) when the probability of human-caused desert tortoise mortality above and below ground may be greatest (Jacobson, 1994; Zimmerman et al., 1994).

Desert ectotherms rely on behavioral thermoregulation (e.g., basking and shade-seeking) and selection of suitable habitat to maintain their ecological and physiological performance (Bulte and Blouin-Demers, 2010; Grant and Dunham, 1988) and survival (Huey and Tewksbury, 2009). Behavior, physiological stability, and survival of desert ectotherms is uniquely tied to their ability to regulate exposure to thermal stimuli (Angilletta et al., 2002; Angilletta, 2006; Kearney et al., 2009a, 2009b) as well as time spent above ground. To critically assess these impacts, a next step in research would be to compare results of observed behavior as documented here and results from the behavior predicted from operative environmental temperature modeling (Zimmerman et al., 1994), as well as biophysical models of ectotherm activity (Kearney et al., 2009a, 2009b). Such studies could resolve the magnitude of the thermal constraints imposed on desert tortoises and potential impacts of hours of restriction in foraging on demography and extinction risks (Sinervo et al., 2010).

Our work confirms previous research demonstrating that environmental temperatures significantly affect activity in natural desert tortoise populations. However, we reexamine the subject of temperature-based activity using novel field methodology and Resource Selection Functions. From this study, we learn that desert tortoises budget their activity into three distinct periods based on preferred air temperatures, as well as timing that is congruent with their physiology and reproductive phenology. Thermal constraints and how they vary over time are fundamental to understanding impacts on reproductive success (Lovich et al., 2012; Lovich et al., In Press), temperature dependent sex-determination (Hulin et al., 2009; Spotila et al., 1994), food and water availability (Wallis et al., 1999; Zhao and Running, 2010), and energy and water relations (Henen, 1997; Henen et al., 1998; Peterson, 1996). Since climate models suggest that this region in the southwestern desert US will be subjected to warmer and more arid conditions (Cayan et al., 2010; Seager et al., 2007), optimal windows or thermal niches available to activity, as well as natural habitat, may in fact diminish, resulting in possible population declines (Lovich et al., 2014a) and species extinctions (Quintero and Wiens, 2013; Sinervo et al., 2010). Therefore directed research on climate variation, tortoise activity and habitat modification is needed to better aid in conservation of the desert tortoise.

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