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A LONG-TERM INVESTIGATION OF THE FEDERALLY THREATENED DESERT TORTOISE (*GOPHERUS AGASSIZII*) AT A WIND ENERGY FACILITY IN SOUTHERN CALIFORNIA

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A LONG-TERM INVESTIGATION OF THE FEDERALLY THREATENED DESERT TORTOISE (*GOPHERUS AGASSIZII*) AT A WIND ENERGY FACILITY IN SOUTHERN CALIFORNIA

THESIS

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Forestry in the College of Agriculture, Food, and Environment at the University of Kentucky

By

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2015

ABSTRACT OF THESIS

A LONG-TERM INVESTIGATION OF THE FEDERALLY THREATENED DESERT TORTOISE (*GOPHERUS AGASSIZII*) AT A WIND ENERGY FACILITY IN SOUTHERN CALIFORNIA

With the recent increase in utility-scale wind energy development and current climate variation in the desert southwest US, researchers have become increasingly concerned with the reaction of wildlife and critical habitat. Understanding the relationships among monitoring efforts, climate, industrial landscapes and wildlife is critical to effective management. Given the need for information available on how these potential stressors affect terrestrial wildlife, my objective was to determine how climate variation, wind energy facilities (WEF) and monitoring efforts by researchers influence behavior and survivorship in a population of the federally threatened desert tortoise (*Gopherus agassizii*). Data were collected via surveys, motion-sensor camera trapping and radio-telemetry during the span of two decades at a WEF in California. Using capture-mark-recapture survivorship analysis and generalized linear mixed-effects models, I acquired long-term estimates of survivorship, activity, and levels of stress response to researchers and climate. From this study I found that researchers as well as abiotic effects influence the probability of voiding, a possible stress induced behavior in desert tortoises. Additionally, we found that tortoise activity and survival is constrained by winter precipitation and habitat types. Further research is needed on proximate mechanisms of wind turbines (noise and vibration) and their effects on desert tortoise behavior.

KEYWORDS: desert tortoise; *Gopherus agassizii*; wildlife management; renewable energy, climate change

Mirza (Mickey) Agha

April 28, 2015

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CHAPTER ONE

GENERAL INTRODUCTION

It is well established that overexploitation and habitat loss are the primary causes for declines of reptile biodiversity (Gibbons et al., 2000; Ilhow et al., 2012). However, anthropogenic-driven global climate change and renewable energy development have the potential to create new conservation challenges and lead to species extinctions (Lovich et al., 2011a,b). Although extinction is part of a “natural order,” scientific evidence indicates that the current rate of extinction is occurring at a higher rate than in the past (Ihlow et al., 2012). Turtles are considered among the most imperiled vertebrate taxa; approximately half (58%) of the 335 species are threatened with extinction (Turtle Taxonomy Working Group, 2014). Of the 31 tortoise species known globally, 13 are vulnerable, 7 are near threatened and 11 are critically endangered (IUCN, 2013). Thus, understanding how climate variability, researchers, and anthropogenic disturbance (wind energy development) are explicitly related to survivorship of the desert tortoise has broad implications for population persistence, and ultimately, species extinction.

The desert tortoise

Native to the southwestern U.S., Agassiz’s desert tortoise (*Gopherus agassizii*) (Cooper, 1863) is a long lived herbivore that inhabits a region where surface air temperatures frequently exceed 38° Celsius (McGinnis and Voigt, 1971; Woodbury and Hardy, 1948), and resources are temporally and spatially variable (Lovich et al., 2012). Geographically, *G. agassizii* is found north and west of the Colorado River (Murphy et al., 2011), inhabiting both the Mojave and Sonoran deserts. Due to its diminished populations and range, it is protected under the federal Endangered Species Act and

California's Endangered Species Act (U.S. Fish and Wildlife Service, 1994), and is listed as vulnerable by the IUCN, 2013. Declines in desert tortoise populations have been attributed to climatic variation (Barrows, 2011; Lovich et al., 2013; Zylstra et al., 2012), drought and disease (Peterson, 1994; Turner et al., 1984), and a variety of anthropogenic influences (Lovich et. al, 2011a, b; U.S. Fish and Wildlife Service, 1994).

Effects of long-term research

In a 6 year study conducted on species closely related to *G. agassizii,* Morafka's Desert tortoise (*Gopherus morafkai*) (Murphy et al., 2011), it was found that there is limited empirical information available on the effects of long-term research on desert tortoises, and that consideration of investigator effects is critical part to the enigma when assessing survivorship in desert tortoises (Averill-Murray, 2002). It is also suggested that researchers could potentially compromise tortoise survival with standard handling and research manipulation techniques (Averill-Murray, 2002), such as the measuring, weighing and restraint of individuals. Berry et al. (2002) also noted that during drought-like conditions (below average precipitation), handling tortoises during field research could lead to death.

During handling and research manipulation of tortoises, voiding is a behavior exhibited by some individuals (Jacobson et al., 1993; Longshore et. al, 2003; Peterson, 1996a, b), where the contents of a tortoise's bladder (urea, uric acid, and/or feces) are excreted, potentially placing the animal at risk of dehydration and possible death. This may be a predator-deterrent behavior, as Bjurlin and Bissonette (2004) witnessed female tortoises voiding on nests, and Patterson (1971) reported it puckered the mouth of a kit fox.

For desert animals, efficient water regulation is essential to life (Vorhies, 1945). The desert tortoise conserves water efficiently by controlling its energy metabolism and remaining inactive in burrows. In stressful climate conditions such as drought, Agassiz's desert tortoise may utilize its urinary bladder as a water reservoir by concentrating waste and subsequently reabsorbing the remaining water (Nagy and Medica, 1986). Some studies have documented that protracted drought periods have been linked to dehydration and starvation, resulting in declines of desert tortoise populations (Peterson, 1994; Longshore et. al, 2003).

Effects of localized climate variation

Gibbons et al. (2000) and Ilhow et al. (2012) both examined how climate variation is suspected to create new conservation challenges for reptiles globally and found that predicted climate change can lead to an array of species extinctions. As a result, several studies have examined how climate warming affects desert tortoise populations (Lovich et al., 2013). In a study carried out at Joshua Tree National Park (JTNP) in California, Barrows (2011) found that in the event of a mean climate shift of +2°C and -50 mm of annual rainfall, current suitable habitat for desert tortoises will diminish by 88% and 68% in the Sonoran desert and Mojave desert expanses respectively. Another study at JTNP revealed that desert tortoise survival decreased with persistent drought, more specifically a three year moving average of estimated winter precipitation (Lovich et al., 2013). Future climate modeling also indicates that the desert southwestern U.S. is expected to have more frequent droughts (below average precipitation) and rising average temperatures, which could be detrimental to desert tortoise populations. In a 22-year analysis of Sonoran desert tortoises, survival of adults decreased with severity of droughts (Zylstra et al., 2012). In conclusion, spatial and temporal variations in drought conditions, further understanding of thermal niche, and activity windows in the southwestern U.S. are important when assessing survival of desert tortoises.

Effects of utility scale wind energy development

Several studies have noted that existing wind energy development of new sites cause mortality of wildlife and excessive habitat damage (Lovich et al., 2011b). Lovich and Ennen (2012; 2013) noted in their assessments of wind energy development impacts on wildlife, that operation and maintenance of large scale facilities causes “habitat fragmentation and barriers to gene flow, increased noise, electromagnetic field generation, microclimate alteration, pollution, water consumption, and fire.” Lovich et al. (2011a) noted that turbine caused fires have long-term effects on spatial ecology and reproduction in desert tortoises. Daily activity of desert tortoises may also be altered by constant ground vibrations from turbines.

In a 14 year study of the effects of wind energy production on growth, demography and survivorship of *G. agassizii* at a wind farm in the southwestern U.S., high annual survivorship was documented in female desert tortoises (Lovich et al., 2011b). However, the study concluded that the stability of the population at the wind farm should not be considered as proof that tortoise populations adjust well to utility scale renewable energy development in all cases.

Thesis objectives

I had three specific research objectives: (*i*) to examine the effects of common research practices applied in tortoise mark-recapture studies, (*ii*) to examine surface activity windows of desert tortoises and to better define the relationship between activity and variable environmental temperatures, and (*iii*) to understand post-construction impacts of industrial wind energy facilities on survivorship of desert tortoises.

CHAPTER TWO

THE EFFECT OF RESEARCH ACTIVITIES AND WINTER PRECIPITATION ON VOIDING BEHAVIOR OF AGASSIZ'S DESERT TORTOISES (*GOPHERUS AGASSIZII*)

Introduction

Understanding stress responses of wildlife to handling and research manipulation has become an important issue in wildlife monitoring and management. Both single-event handling and repeated handling of wildlife have been documented to be a significant stressor as these activities can result in stress-related physiological and behavioral responses (e.g., Cabanac and Aizawa 2000; Cabanac and Bernieri 2000; Clinchy et al. 2001; Holding et al. 2013; Oers and Carere 2007). Likewise, research manipulation, capture, and captivity are known to promote stress responses in both terrestrial and aquatic vertebrates (Kenagy and Place 2000; Mazeaud et al. 1977). Furthermore, both long-term survival and the ability to respond to future stressors are adversely influenced by handling and research manipulation (Berry et al. 2002; Lynn et al. 2010; Sigismondi and Weber 1988). The diversity of species that exhibit stress responses to handling and research manipulation accentuates the importance of understanding the short- and long-term effects of such duress on the well-being of study animals, especially imperiled species.

Agassiz's desert tortoise, a threatened species, is actively monitored by both state and federal agencies throughout its range in the Sonoran and Mojave deserts, USA (USFWS 1990; 2011). Monitoring often involves handling (e.g., weighing, examining, or marking individuals with coded shell notches) and other forms of research manipulation (e.g., affixing radios for telemetry, X-radiography of mature females, etc.). The desert tortoise inhabits an environment where summer temperatures consistently exceed its thermal maxima (43.1°C; Hutchison et al. 1966), and climate is predicted to become increasingly arid (Seager et al. 2007) with negative consequences for tortoises (Lovich et al. 2014). Tortoises compensate for high temperatures by constructing deep burrows and limiting activity to air temperatures of 25 to 30° C (Bulova 1994; Nagy and Medica 1986; Zimmerman 1994). Similar to other desert vertebrates, the desert tortoise has exaptations and adaptations (Morafka and Berry 2002) to survive in the desert and conserve water. Notably, the desert tortoise uses its bladder as a water reservoir by concentrating waste and subsequently reabsorbing the remaining water (Averill-Murray 2002; Minnich 1977; Nagy and Medica 1986, Peterson 1996a; see also review in Ernst and Lovich 2009).

During research handling of tortoises, it is not uncommon for tortoises to excrete the contents of their bladder (urea, uric acid) in a process known as voiding (Jacobson et al. 1993; Longshore et. al 2003; Peterson 1996a, b; Pike et al. 2005). Although voiding may be a predator-deterrent defensive behavior (Bjurlin and Bissonette 2004; Patterson 1971) or natural behavior (Ernst and Lovich 2009), there could be immediate and long-term costs associated with this behavior (Averill-Murray 1998, 2002), as the animal is then potentially subjected to dehydration in a water-limited environment. Ultimately, by releasing stored water in a response to handling by researchers, voiding may potentially place desert tortoises at risk of dehydration and possible death (see Averill-Murray 2002), although this has not been demonstrated empirically.

To minimize negative investigator effects and defensive behavior leading to potential stress in desert tortoises during processing, it is essential to consider how handling and environmental variables affect the probability of voiding and long-term apparent survivorship. Specifically, we examined the effects of common research practices applied in turtle mark-recapture studies, by paying close attention to measured handling (restraint) time, individual number of captures, sex, and abiotic conditions (precipitation) on the probability of voiding in a natural population of Agassiz's desert tortoise in the western Sonoran Desert of California. Secondly, we measured the effects of yearly winter precipitation and individual voiding occurrence or non-occurrence on annual apparent survivorship in the same population of desert tortoises.

Materials and methods

Study site

Our study was conducted at a wind energy generation facility near Palm Springs in Riverside County, California, known locally as Mesa. Monitoring of tortoise populations has been ongoing at this site since the mid 1990s. The study site is located at the western edge of the Sonoran Desert and is roughly bordered on the north and west by the San Gorgonio Wilderness Area (see Lovich and Daniels 2000; Lovich et al. 2011a). Long-term average winter precipitation (October to March) was 15.2 cm at Mesa (RAWS Weather Station: WWAC1; accessed via the MesoWest website (http://mesowest.utah.edu/index.html).

Field techniques

This study began as an investigation of the reproductive ecology of the desert tortoise (Lovich et al. 1999, 2011b, 2012). However, data were collected secondarily on tortoise voiding that allow for a post hoc analysis of the frequency and determinants of that behavior. Voiding behavior in desert tortoises at Mesa was evaluated during capture events over seven study periods (2000, 2001, 2009, 2010, 2011, 2012, 2013) spanning 13 years, during which desert tortoises were repeatedly handled for various lengths of time (1.2 min – 157 min) throughout several research studies (Agha et al. 2013; Ennen et al. 2012; Lovich et al. 2011a, b, 2012), including our long-term survivorship analysis (see below). In these studies, the methodology for tortoise processing was consistent between sexes and juveniles. All tortoises were initially located using intensive time-area constrained searches (Crump and Scott 1994), by radio-telemetery, or by thread trailing. Description of radio-attachment and application of thread-trailers are available in Lovich et al. (2011a) and Agha et al. (2013). After a tortoise was located, the researcher would tap the tortoise from its burrow (Medica et al. 1986), or if it was close to the entrance, they would retrieve the tortoise by hand. During each capture event, the researcher would record start and stop times (time of day) of the data collection process, which included determining the sex, weighing, measuring, and/or marking of tortoises, as required. The researcher would also record environmental variables including air temperature (making sure to abide by standard state and federal permit handling protocols including a 35°C temperature limit). Additionally, adult females were scanned for gravidity using X-radiography (Hinton et al. 1997; Lovich et al. 2012) on a 7 to 10 day schedule from April to July (Lovich et al. 2011b), excluding study year 2012 when data were collected in the fall. In some years, tortoises were thread trailed daily (Agha et al. 2013). During handling or the restraint period for each individual, it was noted if a tortoise voided. Finally, after mark-recapture practices and or x-radiography were completed, the tortoise was returned to the exact location where it was retrieved.

Capture-mark-recapture data were collected from April to July in ten study seasons (1997, 1998, 1999, 2000, 2009, 2010, 2011, 2012, 2013 and 2014) over the span of 18 years, as part of an ongoing study of long-term apparent survivorship in desert tortoises. Surveys were performed by groups of 2-4 individual researchers aligning themselves parallel to one another (equally spaced and < 25 m apart), allowing for visual search overlap, and then proceeding to walk along transects through the study area to visually detect tortoises. Site-specific searches were repeatedly conducted throughout each study year to fully assess the population. Sampling effort varied from full searches to incidental captures during a radio telemetry study. Capture events used in this study include only the first capture of an individual in each study year (indicating pooled result), and therefore are a subsample of the total number of individual tortoise captures at this site.

Researcher handling analysis

We used a generalized linear mixed-effects model (GLMM; Bates et al. 2012; Crawley 2013) to assess the effects of both research manipulation and abiotic conditions on probability of voiding. GLMMs used in our analysis also took into account temporal and spatial pseudo-replication resulting from repeated measurements on the same individuals. We included categorical random effects: individual identification number (ID) and year (YR), and fixed effects: handling time (HT), sex, number times captured (TC), and winter precipitation (PPT). Using ID and YR as random effects, we accounted for individuals who were more likely to void than others and year-to-year variation in voiding, respectively. We included the covariate HT because we expected that the probability of voiding would increase with increased handling time. We added sex to the model since gravid females were X-radiographed on multiple occasions for assessment of reproductive condition and output (leading to extended handling periods), and past studies have documented that gravid females maintain water balance in drought and wet conditions (Averill-Murray 2002; Henen 1997). Therefore, our model would account for females that may or may not be conserving water to benefit reproduction. We also decided to incorporate TC since it has been correlated with lowered survivorship estimates (but not empirically demonstrated mortality) in *G. morafkai* (Averill-Murray 2002). Finally, the food resources of desert tortoises are related to the timing, quantity, and spatial distribution of winter rainfall (Beatley 1974; Bowers 2005; Lovich et al. 2012), hence winter PPT (October to March) was integrated into the model as it is pivotal to water balance in the desert tortoise (Henen et al. 1998; Henen 2002 a, b), and if more water is available, tortoises might be more likely to void during handling and manipulation. Mesa does not receive substantial rainfall during the summer months, and therefore they were not included in our analysis. We then coded the response variable "VOID" (=1) if the tortoise voided during a handling occasion and "VOID" (=0) if the tortoise did not void during handling. Lastly, records were categorized into three separate and distinct groups of individuals based on carapace length (CL) and secondary sexual characteristics (Ernst and Lovich 2009): juveniles (≤ 180 mm CL), adult males (≥ 180 mm CL), and adult females (≥ 180 mm CL). The ID and YR were separated to attain individual intercept and slopes and to accommodate for variation in the number of captures for each individual tortoise.

Using program R (R Development Core Team 2013), we built random effects and fixed effects into our model with the use of a "glmer" function and (lme4) package (Bates et al. 2012; Crawley 2013). Subsequently, we evaluated a series of 45 biologically relevant models corresponding to all possible combinations of fixed and random effects about voiding occurrence; *a priori* we predicted that the likelihood of tortoise voiding would be higher the longer a tortoise was handled due to potential stress levels experienced by the tortoise while data were being collected. We also predicted that below average precipitation prior to the individual being captured would lead to lower probabilities of voiding behavior, since the tortoise would have limited accessibility to hydrating resources and a potentially compromised osmotic condition. Lastly, we projected that as handling of the individual increased, it would be more accustomed to contact by researchers and would therefore have a lower probability of voiding. We then evaluated all 45 models using a multi-model inference. We used Akaike Information Criterion (AIC) corrected for small sample size (AICc) to identify the 'best' model (Burnham and Anderson 1998). To accommodate for multiple models with similar Akaike weights, we calculated covariate parameters by averaging across all models within a given model set that included the covariate.

Survivorship analysis

We used Program MARK (Version 4.3, 2006; White and Burnham 1999) to model apparent survival of adult desert tortoises in this population (carapace length ≥ 18 cm; Ernst and Lovich 2009) with Cormack-Jolly-Seber models. Individuals equipped with radio transmitters had perfect detectability, so an individual, time-varying covariate was used to indicate occasions during which each turtle was equipped with a radio transmitter. This is essentially equivalent to setting capture probabilities equal to one for these individual/occasion combinations as the parameter estimate of radioed individuals converges near one (p[RADIO]). In addition to the effects of radioed individuals, we included the effect of year-specific temporal variation (T) on capture probability (*p*[T+RADIO]). The covariates that potentially influence survival: PPT (winter precipitation), sex, and VOID (coded ‘1’ or ‘0’ indicating pooled result of voiding occurrence or non-occurrence in each year during handling, respectively), and all combinations of these parameters were then fitted as group covariates into a set of time-varying capture probability models (candidate model set). The candidate model set was then ranked using AICc (Burnham and Anderson 1998), and using a delta AICc of <2 we distinguished the top model. Confidence intervals on supported effect sizes were obtained from model averaging the top models within the candidate set. In all survivorship models, the variance was estimated using central difference approximations to the second partial derivative (i.e. 2nd part; Burnham and Anderson 2002).

Results

During our seven study periods, we used data from 1008 total desert tortoise captures involving 62 juveniles (57 juveniles were initially captured in YR 2000 and 2001), 20 adult males and 23 adult females. Of the 62 juveniles and the 43 adults, 8 (13%) and 40 (93%) were recaptured at least once, respectively. However, some adults were captured over 100 times during the study period. Of the 1008 total capture events, voiding was recorded on 83 (8.2%) occasions in 42 different individuals. The handling time of individuals in our study varied greatly (1.2 min – 157 min, Mean: 20.82 min, SD: 23.57 min) due to variation in the distance researchers had to traverse over mountainous terrain and the number of procedures required to process each animal.

The top six models predicting voiding behavior included fixed variables HT, PPT, SEX, TC, and ID and YR as random variables (Table 2.1). The combined Akaike weight of the top six models was 0.98 and Akaike weight demonstrated that no one single model was clearly superior to others within the set (Table 2.1). Consequently, we used model averaging of the top six models to calculate the parameter estimates for each fixed and random effect (Burnham and Anderson, 2002) (Table 2.2.). Our top models indicated that increases in HT led to significantly higher probabilities of voiding for juveniles, females, and males (Figure 2.1; Table 2.2). Similarly, increases in PPT resulted in significantly higher probabilities of voiding for juveniles and females, but not for males (Figure 2.1; Table 2.2). Tortoise capture frequency (TC) was negatively correlated with voiding occurrence, however not significantly (Table 2.2).

Over 10 study years, data was used from 230 capture-mark-recapture events, which included 54 different adult individuals (31 males and 22 females). Juveniles were excluded from the survival analysis as there was insufficient data. Model averaged capture probability varied from 0.50 ± 0.13 (yr 2009) to 0.77 ± 0.13 (yr 2000), and was equal to ‘one’ when all tortoises were radio-telemetered between years. Our top model included the covariate PPT, however, delta AICc did not demonstrate that the top model was the most parsimonious within the candidate set (Table 2.3); therefore model averaging was used for all models within 7 AICc units of the top model(Burnham and Anderson, 2002). Model average parameter estimates of PPT suggested a weak negative effect on survivorship (not significantly different from zero) (Table 2.4). Parameter estimates of SEX and VOID were deemed uninformative (Arnold et al. 2010) (Table 2.4), and exhibited little to no effect on annual apparent survivorship. Overall, model average annual apparent survivorship ranged from 0.91 ± 0.06 (yr 2011) to 0.95 ± 0.02 (yr 2000).

Discussion

This study demonstrated that both research activities and abiotic conditions influence voiding, a possible sign of stress or a natural ‘non-stressful’ response, in desert tortoises. The top six models predicting voiding occurrence, the most influential variable was HT. The significant probability of a voiding response (potential increase in stress level) to HT found in our study is consistent with other studies on *G. agassizii* (Drake et al. 2012) and on other turtles (Cash et al. 1997; Gregory et al. 1996; Ott et al. 2000). Drake et al. (2012) and others (Romero and Reed, 2005; Wingfield and Romero 2001) also suggest that the act of capturing the tortoise and the tortoise’s ability to resist extraction increases HT and acute stress levels. Kahn et al. (2007) described increases of plasma corticosterone occurring within minutes of capture and handling of tortoises, while Drake et al. (2012) specified that plasma corticosterone increased significantly in *G. agassizii* approximately 20 minutes after research activities had been initiated.

Our findings suggest that sensitivity to handling as assessed by voiding frequency varies between adult female, male and juvenile desert tortoises. Juvenile tortoises appear to be most likely to void, followed by adult females and lastly males. Wilson et al. (2001) revealed that regardless of the mechanism by which body water is lost, juveniles lose water at an extremely rapid rate (0.85% of body mass/day) opposed to adults (0.165% of body mass/day), which underscores potential enhanced susceptibility to researcher handling. Thus, research activities may complicate osmoregulation for adult female and juvenile tortoises if animals void more frequently due to handling. However, we found that as PPT increased, the probability of voiding also increased significantly for both adult females and juveniles, but not in males. Averill-Murray (2002) and Henen (1997) indicated that internal water balance is important for reproduction in female desert tortoises. Females may store body water through the winter months and draw on their reserves to aid reproduction in the ensuing spring (Henen 1997; Nagy and Medica 1986; Turner et al. 1984). Correspondingly, Loehr et al. (2011) found that reproduction (gravid vs. non gravid) in female Namalqauland speckled tortoises (*Homopus signatus signatus*) was correlated with the quantity of precipitation in the months preceding nesting. In drought years, handling-induced voiding in reproductive females may affect clutch size and frequency and survival (Lovich et al. 2014).

From our study, we found that long-term effects of voiding behavior on apparent survivorship are negligible in adult tortoises at Mesa. However, due to the extreme temporal and spatial variability of precipitation in the southwestern United States, access to water resources is unpredictable and sporadic (MacDonald 2010; Noy-Meir 1973, Seager and Vecchi 2010); therefore excessive handling and manipulation at other study sites that have been subject to stochastic trends in precipitation may have negative consequences for survivorship and population size of tortoises, especially during times of drought (Lovich et al. 2014). These consequences may disproportionally affect juveniles and gravid females in the short-term.

Populations of the desert tortoise (*Gopherus agassizii*) have declined throughout the range due to a variety of natural perturbations, including droughts (U.S. Fish and Wildlife Service, 1994). Although temporally and spatially stochastic, winter rainfall (Oct-March) in the Mojave and western Sonoran desert regions of the U.S. is characteristically the antecedent for successful annual plant production in the spring (Beatley 1974; Bowers 2005). For most reptilian herbivores in the Mojave and Sonoran deserts annual plant productivity is vital to water homeostasis. In Agassiz's desert tortoise, obtaining and conserving water is the difference between survival and presumably death (Henen 1997; Henen et al. 1998; Longshore et al. 2003; Medica et al. 1980; Peterson 1994; Zylstra et al. 2013). Our study at Mesa suggested that lower totals of winter precipitation leads to lower annual estimates in apparent survivorship (Table 2.3, 2.4). In addition, Lovich et al. (2014) revealed that specifically three year moving average winter rainfall (Oct-March) strongly influenced adult survivorship in a population of desert tortoises in the Sonoran desert.

It is important to note that we do not know the extent to which long-term wind turbine operation at the site contributed to chronically elevated stress and voiding behavior in tortoises, although that remains as a research question that needs additional investigation. Wind energy generation produces chronic noise, vibration and shadow flicker, electromagnetic fields, macro- and micro-scale climate changes, predator attraction, and increased fire risk, all with potentially negative effects to wildlife including desert tortoises (Lovich and Ennen 2013). In addition, construction and long-term maintenance at the site contribute to direct mortality of tortoises and environmental impacts due to destruction and modification of habitat, including the impacts of a dense network of roads associated with the facility. It is possible that these factors contributed to voiding behavior of tortoises but the degree to which that may be is currently unknown.

Currently, recovery permits issued by the U.S. Fish and Wildlife Service to conduct research on desert tortoises state the following, "*The permittee shall make every effort, when handling desert tortoises, to release each tortoise within one-half hour of its capture*." We made a good faith effort to abide by both the letter and the spirit of our permit requirements for handling time, but the terrain and logistics sometimes required longer handling times than anticipated. The range we experienced provided a unique opportunity to empirically test the effect of variance in handling time on voiding probability of tortoises, and our analyses should be useful to resource managers for evaluating the efficacy of permit requirements in recovery of the desert tortoise.

Implications for wildlife management

Our research suggests that in order to minimize the effect of research activities on studied desert tortoise populations, defined procedures or protocols must be followed by the investigators to reduce the contact period with a specimen to the extent feasible (Berry and Christopher 2001; Berry et al. 2002; Drake et al. 2012), and these protocols might need to be modified depending on age class or sex of the animals. When processing a tortoise, investigators can attempt to minimize probability of voiding to a safe level by regulating time spent restraining the individual (based on age class and sex). Our results suggest that to remain under a 10% probability of voiding during a research handling event, juveniles should be held for a maximum of 25 min, females for 40 min and males for 70 min. However, current handling guidelines appear to adequately minimize probability of voiding in adults. Three important factors make research procedures of *G. agassizii* difficult for resource management to address: (1) most research projects require some degree of handling or manipulation (Averill-Murray 2002), (2) duration of droughts are gradually increasing in arid-environments of the Desert Southwest (Cayan et al. 2010; Seager et al. 2007), and (3) although negative effects of voiding on annual apparent survivorship were not seen at Mesa, research handling and drought conditions are associated with decreased survivorship in desert tortoise populations in other areas of the

Mojave and Sonoran desert (Averill-Murray 1998, 2002; Berry et al. 2002; Longshore et al. 2003; Lovich et al. 2014; Peterson 1994; Zylstra et al. 2012). Negative effects of voiding may be mitigated by rehydration through soaking the individual, creating access to artificial water catchments, or providing electrolytes or dextrose solution (McLuckie et al. 1999), yet further research on rehydration effectiveness and its impact on stress levels must be empirically assessed.

Table 2.1.The top six models (explaining 98% of the data) determining voiding behavior in Agassiz's desert tortoise. Voiding behavior (VOID) based on 45 combinations of fixed effects: handling time (HT), preceding winter precipitation (PPT), Sex (SEX), total number of captures (TC), and random effects: identification number (ID) and year (YR). All models are ranked by corrected AICc and listed with number of model parameters (K), negative log likelihood (NLL), difference in AICc relative to the best model (ΔAICc), and Akaike weight ($_{W}$AICc).

GLMM Formula	**K**	**NLL**	**AICc**	**ΔAICc**	**$_{W}$AICc**
VOID ~ HT + PPT + SEX + TC + (1 | ID)	5	198.22	412.86	0.00	0.29
VOID ~ HT + PPT + SEX + TC + (1 | YR)	5	198.43	413.36	0.50	0.22
VOID ~ HT + PPT + SEX + TC + (1 | ID) + (1 | YR)	6	197.3	413.48	0.62	0.21
VOID ~ HT + SEX + TC + (1 | YR)	4	200.41	414.89	2.00	0.11
VOID ~ HT + SEX + TC + (1 | ID) + (1 | YR)	5	199.5	415.48	2.61	0.08
VOID ~ HT + PPT+ SEX + (1 | ID)	4	200.86	415.79	2.93	0.07

Table 2.2. Model average parameter estimates, standard error and confidence intervals from top 6 models. GLMMs incorporate HT, PPT, SEX, and TC as fixed effect variables and ID and YR as random effects. SEX: FEMALES are implicit within the INTERCEPT. [*] Effects with 95% confidence interval (CI) not overlapping zero were significant at *P* <0.05.

Fixed Effects	**Parameter Estimates**	**Standard Error**	**95% CI**
INTERCEPT	-3.71	0.93	-1.89, -5.53*
HT	2.43	0.32	3.06, 1.8*
PPT	0.16	0.05	0.26, 0.06*
SEX: JUVENILES	1.56	0.50	2.55, 0.58*
SEX: MALES	-0.97	0.52	0.04, -1.98
TC	-0.14	0.14	0.12, -0.41

Table 2.3. Summary of apparent survivorship model testing for desert tortoises marked at Mesa Wind Site. Models are sorted by increasing AICc weights (W_i) > 0.01 are listed. Symbols reflect different factors in the model (= apparent survivorship, PPT = winter precipitation (Oct-March), RADIO = capture probability = 1.0 for individuals radioed between capture occasions, T = time, *K* = number of parameters).

Model	**AICc**	**ΔAICc**	**W_i**	**Model Likelihood**	***K***	**Deviance**
(PPT) ***p*(RADIO + T)**	340.05	0.00	0.26	1.00	11	316.78
(.) ***p*(RADIO + T)**	340.12	0.08	0.25	0.96	10	319.07
(SEX + PPT) ***p*(RADIO + T)**	342.13	2.08	0.09	0.35	12	316.62
(SEX) ***p*(RADIO + T)**	342.15	2.10	0.09	0.35	11	318.88
(VOID) ***p*(RADIO + T)**	342.16	2.11	0.09	0.35	11	318.89
(VOID+PPT) ***p*(RADIO + T)**	342.22	2.17	0.08	0.34	12	316.72
(.) ***p*(RADIO)**	342.77	2.72	0.07	0.26	2	338.72
(SEX + VOID) ***p*(RADIO + T)**	344.36	4.3	0.03	0.12	12	318.85
(SEX +VOID + PPT) ***p*(RADIO + T)**	344.39	4.3	0.03	0.11	13	316.62

Table 2.4. Survivorship model average parameter estimates on the logit scale. Standard error and confidence intervals from top competing models including covariates winter precipitation (PRECIP), sex and voiding occurrence (VOID).

Parameter Effects	Parameter Estimate	95% CI	Standard Error
PRECIP	-0.014	-0.23, 0.20	0.11
SEX	-0.038	-0.42, 0.34	0.19
VOID	0.045	-0.49, 0.58	0.27
(Intercept)	2.98	2.12, 3.83	0.43

CHAPTER THREE

USING MOTION-SENSOR CAMERA TECHNOLOGY TO INFER SEASONAL ACTIVITY AND THERMAL NICHE OF THE DESERT TORTOISE (*GOPHERUS AGASSIZII*)

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 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 (USFWS 2011). Desert tortoises inhabit an extreme environment where ambient temperatures frequently exceed the tortoise's critical thermal maximum (43.1°C; Hutchinson 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; Osario 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.

Materials and methods

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).

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, b; Lovich et al. 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. 2014) (Figure 3.1). All cameras were programmed to take 1-5 high definition photographs (camera trap events) when triggered (0.2 sec 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 minutes 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.

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 that 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 ($P < 0.05$). 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, 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).

Mixture Models

To investigate temporal partitioning of activity across DOY, we used normal mixture models (Benaglia et al. 2009; Connette et al. 2014; 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=1,000). 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).

Results

In study year 2013 at Mesa, we obtained 2,754 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° C – 41.67° C).

The top RSF model included the covariates SEX, T, T^2, DOY, DOY^2, SEX*DOY, and SEX*T (Table 3.1). Parameter estimates within the relative probability of activity model for females was: $y = -15.39+0.06*DOY-0.0001*DOY^2 + 0.42*T-0.007*T^2$, and for males: $y =-15.39+0.08*DOY-0.0001*DOY^2 + 0.38*T-0.007*T^2$. We found strong support for models including all covariates (at least $\Delta QIC >15.94$ for all non-competing models) except for models including the interaction between SEX and T which had almost equal support as the second ranked model ($\Delta QIC=1.36$) (Table 3.2). Relative probability of activity was higher for males than for females (Figure 3.2). 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 3.3), which largely matched up in timing and duration (Figure 3.3). The mean (μ) and duration (σ) of each activity period overlapped between sexes for activity periods 2 and 3 (Table 3.4). 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 3.5). Although model selection determined HOD mixture models with 3 distinct activity periods were best for males (Table 3.5), we selected 2 periods due to daily temperature trends (Figure 3.4). 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 3.6).

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; Chelazii 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 (Zimmermann 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 (Figure 3.2). 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 3.4, Figure 3.3), potentially searching for mates or taking advantage of necessary resources prior to hibernation. In contrast, females were more active during the first period, 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 (Figure 3.4) 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) (Figure 3.4).

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; Figure 3.3) 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. 2009) 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 (Zimmermann et al. 1994), as well as biophysical models of ectotherm activity (Kearney et al. 2009). 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. 2014) 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.

Table 3.1. 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**
$T + T^2 + SEX$ + SEX*T + DOY + DOY^2+DOY*SEX	8	2868	0.00	0.66
$T + T^2 + SEX$ + DOY + DOY^2+DOY*SEX	7	2870	1.36	0.34

Table 3.2. 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^2), DOY*SEX interaction, SEX*T 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
DOY*SEX(Male)*	0.0106	0.0018	0.0194
SEX(Male)*T	-0.0324	-0.0797	0.0149

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

Table 3.3. 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.

		Female			Male		
Components	K	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

Table 3.4. 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.

		Female			Male		
Par	Period	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 3.5. 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.

		Female			Male		
Periods	K	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

Table 3.6. 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.

		Female			Male		
Par	Period	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 $P < 0.05$.

CHAPTER FOUR

TURBINES AND TERRESTRIAL VERTEBRATES: VARIATION IN TORTOISE SURVIVORSHIP BETWEEN A WIND ENERGY FACILITY AND AN ADJACENT UNDISTURBED WILDLAND AREA IN THE DESERT SOUTHWEST (USA)

Introduction

Technological advancements in clean energy production coupled with a rapidly increasing global human population have bolstered a resurgence of utility-scale renewable energy development (USRED) (Lund 2007). Installation and operation of utility-scale renewable energy facilities offers the potential to address ongoing depletion of fossil fuels, while enhancing local economies (Bergmann et al. 2007; Krohn and Damborg 1999; Wei et al. 2010). One form of USRED, wind energy, is quickly expanding worldwide (EIA 2013; Leung and Yang 2012), and by 2020 is predicted to yield 5% of the world's total energy (Joselin et al. 2007). In the United States, production of industrial wind power facilities is flourishing with approximately 60 Gigawatt (GW) installed capacity at the third-quarter of 2013 (AWEA 2013). However, these industrial wind energy facilities (WEF) produce environmental impacts (Leung and Yang 2012); in fact, wind energy development has one of the largest footprints (i.e., disturbance area) per GW ratings compared to other forms of renewable energy generation (Kiesecker et al. 2011; McDonald et al. 2009; AWEA 2013). Among future areas of industrial development, wind energy impact to North American (US and Canada) shrublands will be most severe, converting upwards of an estimated 5.6 million ha of shrubland to industrial wind power facilities by the year 2030 (Pocewicz et al. 2011).

Until recently, the direct and indirect impacts of USRED to flora and fauna have been relatively unknown (Kuvlesky 2007; Lovich and Ennen 2011, 2013b). With increasing energy demand, consumption, and USRED development (Hoogwijk, de Vries and Turkenburg 2004), researchers have become concerned about the response of wildlife and conservation of critical habitat (Carrette et al. 2013; Kiesecker et al. 2011; Masden et al. 2010; Northup and Wittemyer 2013; Parsons and Battley 2013). It is well-documented that wind turbines are a significant source of mortality to volant wildlife (i.e., birds and bats; Erickson et al. 2001; Kunz et al. 2007). Furthermore, there is a growing body of evidence that anthropogenic infrastructure associated with USRED such as power lines, roads, and turbine pads, negatively impact a variety of terrestrial vertebrates (Fahrig and Rytwinski 2009; Groot et al.1996; Harte and Jassby 1978; Langen et al. 2009; Lovich and Bainbridge 1999; Santos et al. 2010). In addition, wildland fires can be ignited by wind turbines and malfunctioning machinery, and the long- and short-term effects of these fires on terrestrial vertebrate populations may be significant (Lovich et al. 2011c; Lovich and Ennen 2013b).

Although initial construction of new WEF can cause considerable impacts to wildlife and their habitat, it is also argued that the facilities themselves may assist in conservation of some species since public access, mineral extraction, and intensive cultivation are greatly limited (Kelcey 1975; Lovich and Daniels 2000). A recent study reported that there was little evidence of wildlife population declines during the period of post-construction (maintenance and operation; Pearce-Higgins et al. 2012), supporting a claim that many USREDs may enable wildlife populations to persist (Kelcey 1975). However, a general paucity of research exists documenting the long-term effects of USRED on terrestrial wildlife populations.

Agassiz’s desert tortoise (*Gopherus agassizii*), a long lived, semi-fossorial turtle species, has experienced significant population declines largely due to habitat degradation caused by a variety of human activities throughout their range in the North American desert southwest (Lovich and Bainbridge 1999; USFWS 2011; Wilshire et al. 2008). The growth of USRED in the desert southwest can cause further fragmentation of desert tortoise habitat (Vandergast et al. 2013) and possibly stress populations through increased fire frequency, vibration, noise and regional climate change (Lovich and Ennen 2011, 2013b). Although threats to desert tortoises associated with USRED were identified over 30 years ago (Pearson 1986), only recently have studies emerged focusing on the impacts of USRED on this species (Lovich and Daniels 2000; Lovich et al. 2011a, b, c; Ennen et al. 2012a, b).

To understand the post-construction impacts of industrial WEFs on threatened terrestrial vertebrates (USFWS 1990; USFWS 2011), we used a long-term capture-mark-recapture dataset to examine activity centers and survivorship of a natural population of Agassiz's desert tortoises at a WEF in southern California (USA). We tested two predictions: (*i*) desert tortoises within or immediately adjacent to the footprint of an operating WEF would have a higher probability of being affected by anthropogenic features and operations, and would therefore have lower estimates of apparent survival in comparison to tortoises near a wilderness area (NWA), and (*ii*) individual activity areas would be smaller within the boundaries of the WEF due to modified habitat (i.e., potentially increased resource availability from artificial rain catchments on turbine pads and edge enhancement of vegetation along roads; see Lovich and Daniels 2000).

Materials and Methods

Our study site, known as Mesa, is near Palm Springs in Riverside County, California and located on federal lands (i.e., Bureau of Land Management). Detailed monitoring of tortoise populations has been ongoing at this site since 1997. Mesa is situated on the western edge of the Sonoran desert, with an elevation range of 600-900 m and long-term average winter precipitation of 15.2 cm (range 2.9 – 44.1 cm) (estimated using WestMap PRISM data; http://www.cefa.dri.edu/Westmap/; Lovich et al., in press). Vegetation at Mesa includes a variety of plant species typical of the Mojave and Sonoran deserts along with plants from coastal southern California (see Lovich and Daniels 2000; Lovich et al. 2011b). Several fires have altered the plant community since the wind facility became operational after 1983 (Lovich et al. 2011b, c). The Pacific Crest Trail runs through Mesa and roughly divides the study site into "disturbed (i.e., WEF)" and "undisturbed (i.e., NWA)" landscapes (Figure 4.1). To the east and south of the Pacific Crest Trail, the site is bounded by an operating utility-scale WEF (including 460 turbines, 51 electrical transformers, and an extensive network of roads; Lovich and Daniels 2000). To the north and west of the Pacific Crest Trail, the site is not modified by industrial activities (i.e., NWA) and adjacent to the San Gorgonio Wilderness. The footprint of the NWA study area was 152.8 ha and the footprint of the WEF study area was 185.81 ha (area analysis presented below). In our study, the Pacific Crest Trail is used as a dividing line for the two habitat types at Mesa and does not inhibit desert tortoise movement.

Field Techniques

Desert tortoise surveys at Mesa were conducted from early April to late July over ten field seasons (1997-2000, 2009-2014) spanning 18 years. Due to limited funding, surveys in 2012 were only conducted from October to December. During all study periods, we used intensive time-area constrained searches (Crump and Scott 1994; Walker 2012) to detect desert tortoises, making sure to explore all available disturbed and undisturbed habitats at Mesa. Surveys were performed by groups of 2-4 individual researchers aligning themselves parallel to one another (equally spaced and < 25 m apart), allowing for visual search overlap, and then proceeding to walk along transects through the study area to visually detect tortoises. Over each study period, the study site was repeatedly sampled to ensure full assessment of the population. When a tortoise was located, we recorded their location using a GPS device (accurate to within about 3m). Upon hand capture of the individual, sex was determined using secondary sexual characteristics (Ernst and Lovich 2009). If it was a sexually mature adult, we recorded weight (g) using a Pesola® spring scale, and straight-line carapace length (mm). If it was a first capture event, the individual would be given a unique mark on the marginal scutes and upper shell or carapace (Cagle 1939), using a triangular metal file. In addition to notching the carapace, epoxy tags were applied to the fourth left pleural scute with the corresponding identification code. Properly marking an individual allowed us to determine a recapture event in a subsequent study year. Tortoises were kept for no longer than 30 minutes, on average, and released at the point of capture.

Additionally, our study coincided with research on movements and reproductive ecology; therefore, numerous individuals in the population were located using radio-telemetry throughout portions of the study at Mesa (Lovich et al. 1999; Lovich et al. 2011a, b, c; Lovich et al. 2012; Ennen et al. 2012a, b; Agha et al. 2013). Sampling effort varied from full searches to incidental captures during a radio telemetry study (specified in survival analysis below). The number of tortoises that were monitored via radio telemetry varied from year to year during the study (mean ~ 8 per year). Thus, capture events used in this survival analysis include only the first capture of an individual in each study year (i.e., including telemetered and non-telemetered individuals), and therefore are a subsample of the total number of captures at this site. We handled all animals following approved field methods and under permits from the United States Fish and Wildlife Service, Bureau of Land Management and the California Department of Fish and Wildlife.

Activity Area and Survival Analysis

Boundaries for San Gorgonio Wilderness and Pacific Crest Trail were acquired from resource management agencies including the Bureau of Land Management and U.S. Forest Service (USFS), respectively. Using ArcGIS 10.1.1 (ESRI 2014) and yearly first captures for all individual tortoises in the study we created 100% minimum convex polygons (MCP), and then estimated activity area values for each individual based on a 10-m digital elevation model (DEM). We created a separate MCP including yearly first capture locations for all individual tortoises in the study to determine the footprint of each study area in hectares (NWA = 152.8 ha, WEF = 185.81 ha). Due to the linearly dependent relationship between number of captures and accurate estimations of activity areas, and because several of the tortoises in this study had relatively small number of relocations (Mares et al. 1980), we performed a linear regression of number of locations vs. activity area size (= 0.05). Although most tortoises in the study had a low number of recaptures, linear regressions were not significantly different from zero (p = 0.869), demonstrating that our activity area estimates were not adversely affected by the number of tortoise relocations (Harless et al. 2010). Since some tortoises moved between the NWA and WEF, we generated polygon centroid points for each individual's overall tortoise activity area. For tortoises with only one to three capture occasions, we plotted their location and categorized them as NWA or WEF relative to the Pacific Crest Trail. We performed a non-parametric Kolmogorov-Smirnov Test to assess overall activity area differences between NWA tortoises and WEF tortoises (two-sample K-S test; 0.05; SAS Version 9.3, SAS Institute 2011).

We used Program MARK (Version 4.3, 2006; White and Burnham 1999) to model apparent survival of adult desert tortoises in this population (carapace length ≥ 18 cm; Ernst and Lovich 2009) with Cormack-Jolly-Seber models, using pooled results within years (Freilich et al. 2000). Individuals equipped with radio transmitters had perfect detectability by design, so an individual, time-varying covariate was used to indicate occasions during which each turtle was equipped with a radio transmitter. This is essentially equivalent to setting capture probabilities equal to one for these individual/occasion combinations as the parameter estimate of radioed individuals converges near one (not exactly one since parameters were estimated on the logit scale) and MARK automatically reduces the parameter count to exclude this parameter. Prior to conducting the survival analysis, we first constructed candidate models that varied in capture probability (p) to find the best-fit model for desert tortoise detection. Candidate models included: constant capture probability including radio effects (p[RADIO]), time (T) varying capture probability including radio effects (p[T+RADIO]), time varying and determined by habitat type ((HT): NWA or WEF) (p[T+HT+RADIO]), time varying and determined by HT and gender (SEX) (p[T+HT+SEX+RADIO]), constant and determined by HT (p[HT+R]), and constant and determined by HT and SEX (p[HT+SEX]). Constant capture probability models were used only for comparison since such a parameterization is “an unrealistic assumption for desert tortoises” (Freilich et al. 2005). Using a group within a group input structure in Program MARK (Cooch and White 2006), we coded four groups: (1) adult male WEF tortoises (inferring that the individual's activity area was located east of the Pacific Crest Trail, (2) adult male NWA tortoises (inferring that the individual's activity area was located west of the Pacific Crest Trail), (3) adult female WEF tortoises, and (4) adult female NWA tortoises.

The top model for capture probability was identified using the survival constant model .) and ranking all combinations of capture probability parameters (T, HT, SEX and RADIO) using AIC (Akaike 1973; Burnham and Anderson 2002). The covariates of interest (HT and SEX) were then fitted as group covariates in the survival analysis to the most parsimonious capture probability model, and we used AIC to determine the weight of the top models. The inclusion of the individual, time-varying covariates precluded the estimation of goodness-of-fit and the estimation of the overdispersion parameter, *c*, so we assumed no overdispersion was present. Confidence intervals on supported effect sizes were obtained from the most parsimonious model. In all mark-recapture models, the variance was estimated using central difference approximations to the second partial derivative (2nd part; Burnham and White 2002).

Results

We used data from 234 tortoise capture events of 54 different individuals (13 male and 14 female within the boundaries of the WEF and 19 male and 8 female within the boundaries of the NWA) over the 10 field seasons. Mean activity area (including standard error) of individuals in the WEF portion of the site was 6.25 ± 2.13 ha, and mean activity area of individuals in the NWA portion of the site was 4.13 ± 1.23 ha. Mean overall activity area for adult male and female individuals combined was 5.48 ±

0.05 ha (range 0.06 to 43.98 ha). The two sample K-S test identified that the 100% MCP size of the two populations (WEF and NWA) were not significantly different (KS: 0.097, D: 0.202, p = 0.913).

Capture probability of the top model varied from year to year based on new and repeat tortoise captures (Figure 4.2) and was equal to ‘one’ only when all tortoises captured in one year were radioed continuously until the next year of sampling. The top weighted parameterization of capture probability included the effects of HT, T and Radio. Parameter estimate for ‘HT’ was 0.60 ± 0.38, suggesting greater capture probability in WEF than in NWA. Over the entire study period, capture probability estimates on the WEF ranged from 0.48 ± 0.1 (yr 2012) to 0.84 ± 0.07 (yr 2000), and on the NWA side ranged from 0.33 ± 0.1 (yr 2012) to 0.74 ± 0.11 (yr 2000) (excluding 1.00 capture probabilities; Figure 4.2). Overall, the average, annual capture probability for both adult male and females combined was 0.56 ± 0.05.

The top ranked apparent survival model included HT effects on apparent survival (Table 4.1). With an AIC_C difference of 2.25 units from the (.) model (i.e., null model), and an AIC_C weight of 0.51, the top model ((HT)) was considered to have weak to moderate support (Arnold 2010; Table 4.1). The null model had an AIC_C weight of 0.16 and a likelihood of 0.32. Model estimates of HT and SEX effect size, apparent survival, and capture probability are presented with unconditional standard errors (See Table 4.2). The top model effect size of HT indicated that survival was greater for WEF tortoises, and the top model HT estimate was significantly different from zero (Table 4.2). The effect size of SEX, in the highest ranking model where it occurred, suggested that it was an uninformative parameter (Arnold 2010), and that there was negligible difference in survivorship between sexes (Table 4.2). Our top model indicated that annual apparent survival of WEF tortoises (0.96 ± 0.01) was significantly different from that of NWA tortoises (0.92 ± 0.02). Overall constant apparent survival from the null model was 0.94 ± 0.01 for both adult male and female tortoises in the study.

Discussion

Our results indicate that long-term tortoise survivorship within the WEF (96.7%) was significantly higher than in the nearby NWA (92.1%); thus rejecting our first hypothesis that survivorship would be lower at the WEF. Furthermore, size of activity areas were larger (although not significantly) within the WEF than in the adjacent NWA, which did not support our second prediction that individual activity areas would be smaller within the boundaries of the WEF. Despite the variation in survivorship between site types, our survival estimates are at the high end in comparison to previous estimates based on adult females (91.6%) at the same site (Lovich et al. 2011b), and conspecific undisturbed populations in nearby regions of the Mojave and Sonoran desert (Freilich et al. 2000; Riedle et al. 2010; Zylstra et al. 2013). These high survivorship estimates contrast with other studies that found lower survivorship often attributed to persistent drought, disease and predation (Berry, 1997; Esque et al. 2010; Longshore et al. 2003; Lovich et al. 2014; Peterson 1994).

Larger activity areas within the WEF in comparison to the NWA may suggest that tortoises can traverse the modified landscape with little difficulty. This assumption is based on tortoise sightings as they moved along dirt roads (J. E. Lovich, personal observation), as has been documented in other turtle species in modified environments (Nieuwolt 1996). Overall, activity area estimates at Mesa were less than those presented in previous research studies (see Harless et al. 2010 for a recent review) on Agassiz's desert tortoise (sensu Murphy et al. 2011). Low activity area estimates in our study may be attributed to our limited number of relocations per individual used to create each activity area, and site fidelity toward highly productive pockets of landscape at Mesa. Due to the variable topography and spatial arrangement of plant assemblages at Mesa, desert tortoises may prefer specific habitat along ecotones (Lovich and Daniels 2000). Patterns of space use by desert tortoises at Mesa can also be influenced by roadside plant productivity within the study site (Lovich and Daniels 2000), sex of the individual, social interactions and sampling regime (Harless et al. 2010).

Overall, average capture probability of desert tortoises (not including radio-telemetered individuals) within the WEF and NWA were higher than previously conducted long-term mark-recapture studies (Zylstra et al. 2013: 0.41 for all populations). Annual capture probabilities for desert tortoises fluctuated greatly, similar to the findings of Lovich et al. (2014a) from nearby Joshua Tree National Park. The NWA section of Mesa had lower annual capture probability estimates than did the WEF, which may have resulted from the precipitous terrain in the NWA which made it difficult to find tortoises during our initial surveys. Over extended study periods (i.e., multi-year studies), enhanced capture probability of desert tortoises is associated with precipitation and subsequent germination of annual food plants (Lovich et al. 2014a; Freilich et al. 2000); however, lower estimates in 2012 may be attributed to reduced effort and timing of those surveys (October – December).

Altered resource availability facilitated by the WEF may be the cause for disparity in survivorship between the NWA and WEF landscapes at Mesa. Lovich and Daniels

(2000) and Lovich et al. (2011b) hypothesized that tortoises at Mesa benefited from edge enhancement of vegetation (food resources), turbine pads (artificial rain catchments), reduced subsidized predators and low traffic. Previous studies have documented that desert tortoise populations removed from areas developed by humans and exposed to dirt roads with lower volumes of vehicle traffic exhibit little decline (Berry and Medica 1995; Nafus et al. 2013). Furthermore, Lovich and Daniels (2000) noted that burrow locations for Agassiz's desert tortoise at Mesa were located closer to dirt roads and turbine structures than expected, which may also be due to roadside water collection and subsequent increased plant production. An investigation of desert tortoises inhabiting areas near roads in the Mojave Desert reported adult tortoises gathering at the sides of roads during rainstorms (B. Todd and M. Peaden, personal communication).

Desert tortoise activity, detection and survival within the WEF may be linked to the spatial dynamics (geographic placement and distance between turbines) of turbines and maintained dirt road structures. Since Mesa was constructed in the mid-1980s, it uses closely-spaced, lattice-style turbines. Modern wind farms tend to use more widely-spaced, monopoles with larger turbines. The differences between these layouts and their associate road structure, as far as tortoises are concerned, are currently unknown.

Grandmaison and Frary (2012) found that probability of desert tortoise detection was highest on maintained gravel roads. Furthermore, roads and culverts may cause mortality in adult tortoise populations (Berry et al. 2006; Boarman and Sazaki 1996; Lovich et al. 2011a; Nafus et al. 2013), and they may also facilitate increased movement (Diemer 1992; McRae et al. 1981; Nieuwolt 1996). It appears that conditions at Mesa are suitable for desert tortoise populations (Brooks 2000; Lovich et al. 2011b), although some mortality has been documented in the past (Lovich et al. 2011a, c). Tortoise mortality has been attributed to livestock grazing; direct impacts include burrow collapse (Agha et al., in press; Ernst and Lovich 2009; Nicholson and Humphreys 1981), while indirect effects may be competition and loss of food resources and therefore a reduction in the quantity and quality of suitable habitat.

Predator populations may be lower at the Mesa WEF than in adjacent NWA, which may result in variation in survivorship of desert tortoises between landscapes. During the 2013 field season at Mesa, 48 motion sensor cameras were placed at the mouth of tortoise burrows, and recorded several occurrences of large terrestrial predators at various locations throughout the study site (i.e., both WEF and NWA). On two different occasions a potential predation event was recorded on camera: once where black bears (*Ursus americanus*), a known predator of turtles, investigated a tortoise burrow on the NWA section of the site (Lovich et al. 2014b), and another instance where a bobcat approached a sleeping tortoise also on the NWA section (D. Delaney, personal observation). Additionally, it is not unusual for large birds of prey (family *Accipitridae*) to consume turtles (Clark 1982; Means and Harvey 1999). However, rarely have volant predators (i.e. golden eagles; *Aquila chrysaetos*) of desert tortoises (Ernst and Lovich 2009) been documented at the WEF in recent decade, which may be attributed to high mortality caused by turbines shortly after construction (Lovich, in press). Among bird species, increased mortality caused by wind facility development has been well-documented (Desholm and Kahlert 2006; Drewitt and Langston 2006). Furthermore, in some cases golden eagles have been recorded to avoid wind energy farms altogether (Chamberlain et al. 2006; Walker et al. 2005). Conservation of the desert tortoise may rely on further understanding of predator-prey relationships (Esque et al. 2010) within landscapes modified by USRED.

Turbine-caused fires were documented at the Mesa WEF on two separate occasions in 2012. Desert fires directly impact terrestrial vertebrates and cause loss of vegetation cover (Esque et al. 2003); however, annual survivorship estimates at Mesa did not dramatically decrease post-fire in 2013 (Lovich et al. 2011c). Due to high precipitation and elevated plant productivity at Mesa (Lovich et al. 2011c), desert tortoises may have been buffered from potential indirect effects of fire (Esque et al. 2003).

Populations appear to be stable at Mesa in comparison to other populations of this threatened species (Berry, 1997; Esque et al. 2010; Longshore et al. 2003; Lovich et al. 2014; Peterson 1994). This is likely due in large part to favorable environmental conditions (i.e., above average precipitation) at the site and the associated ability of females to produce extraordinary numbers of eggs annually (Lovich et al., in press). However, since tortoises are long-lived animals, populations can be comprised largely of old adults for many years, despite a lack of recruitment (Mortimer 1995), giving the illusion of population stability. New adult and sub-adult tortoises have seldom been documented at Mesa in the last decade suggesting the possibility of limited recruitment into the adult population. Despite the relative productivity at Mesa, lower recruitment may be due to recent drought conditions that have caused adult mortality in other populations of the desert tortoise (Lovich et al. 2014a; Morafka 1994).

Conclusion

Our study detected high (>0.92) annual apparent survivorship estimates of federally threatened Agassiz's desert tortoises in southwestern California, with WEF tortoises exhibiting slightly greater, significantly different, survivorship than those in in the adjacent NWA. Wind energy facility estimates are opposite of what we predicted based on known and potential negative effects of wind energy on wildlife (Lovich and Ennen 2013b). Our findings call attention to the potential importance of spatial dynamics (turbine and road placement) within wind facilities, post-disturbance operation and maintenance, and how a "protection factor" might contribute to high estimates of desert tortoise survival. More research is needed on the mechanisms responsible for high survivorship within the WEF at Mesa, which may lead to useful information to mitigate negative effects in other wind facilities. Lastly, future work including pre- and post-disturbance demographic data, including data on population recruitment, may better reveal the full impact of USRED on terrestrial vertebrates. Such studies are by necessity long-term since desert tortoises are long-lived animals with generation times as high as 25 years (Lovich et al. 2014a). Despite several studies regarding renewable energy effects on wildlife, true pre- and post-construction evaluations of wildlife utilizing the "before-after-control-impact" (BACI) study design are scarce (Kuvlesky et al. 2007; Lovich and Ennen 2011, 2013). Studies like these could better address conservation issues associated with renewable energy, endangered species and compliance with legislation protecting such species (Ruhl 2012).

Table 4.1. Summary of model testing for desert tortoises marked at Mesa. Models are sorted by increasing AIC_C weights (W_i) > 0.01 are listed. Subscripts reflect different factors in the model (= apparent survivorship, Habitat Type (HT) = NWA individuals vs. WEF individuals, RADIO = capture probability = 1.0 for individuals radioed between capture occasions, T = time, *K* = number of parameters.

Model	**AIC_C**	**ΔAIC_C**	**W_i**	**Model Likelihood**	***K***	**Deviance**
(HT) ***p*(RADIO+HT+T)**	348.17	0.00	0.51	1.00	12	322.71
(HT+SEX) ***p*(RADIO+HT+T)**	350.41	2.25	0.16	0.32	13	322.70
(.) ***p*(RADIO+HT+T)**	350.86	2.69	0.13	0.26	11	327.63
(.) ***p*(RADIO+T)**	352.69	4.53	0.05	0.10	10	331.67
(.) ***p*(RADIO+HT+SEX+T)**	352.89	4.72	0.05	0.09	12	327.43
(SEX) ***p*(RADIO+HT+T)**	352.90	4.73	0.05	0.09	12	327.44
(.) ***p*(RADIO+HT)**	354.37	6.20	0.02	0.04	3	348.26
(.) ***p*(RADIO+SEX+T)**	354.90	6.73	0.02	0.03	11	331.67

Table 4.2. Top model parameter estimates on the logit scale. Standard error and confidence intervals from top model including covariate habitat type (HT) and top model including covariate (SEX).

Parameter Effects	**Parameter Estimate**	**95% CI**	**Standard Error**
HT*	0.94	0.08 – 1.81	0.44
SEX	-0.03	-0.88 – 0.82	0.44
(Intercept)	2.46	1.92 – 2.99	0.27

*95% CI non-overlapping with zero indicate significant parameter estimate ($p < 0.05$).

Appendix A

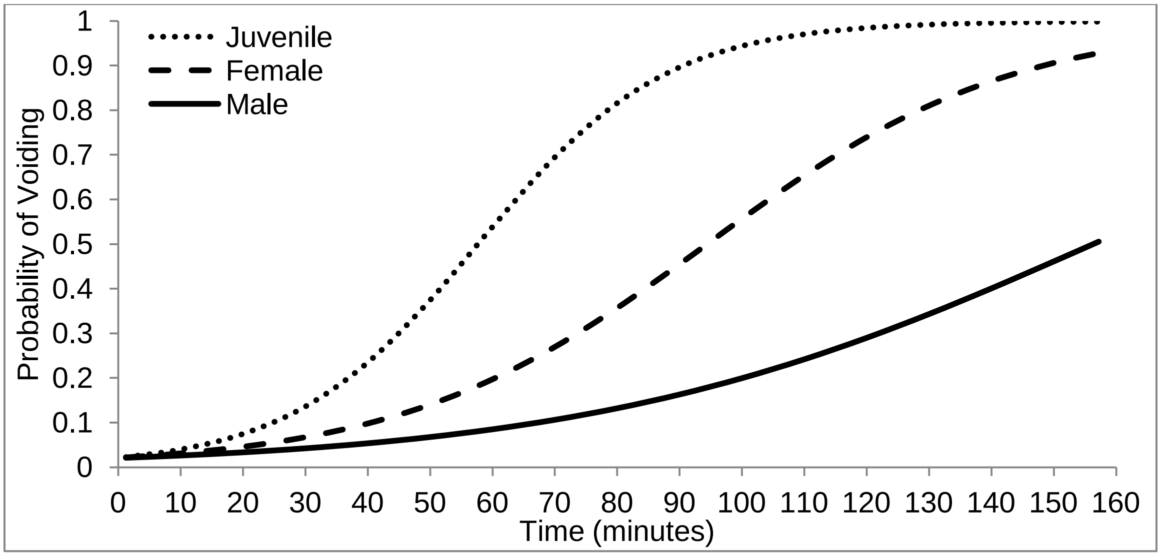

Figure 2.1. Mean probabilities of voiding in juvenile, female, and male Agassiz's desert tortoises in 10 minute intervals using GLMM that incorporates HT, PPT, SEX, and TC as fixed effect variables and ID as random effect (model averaging of top 6 models).

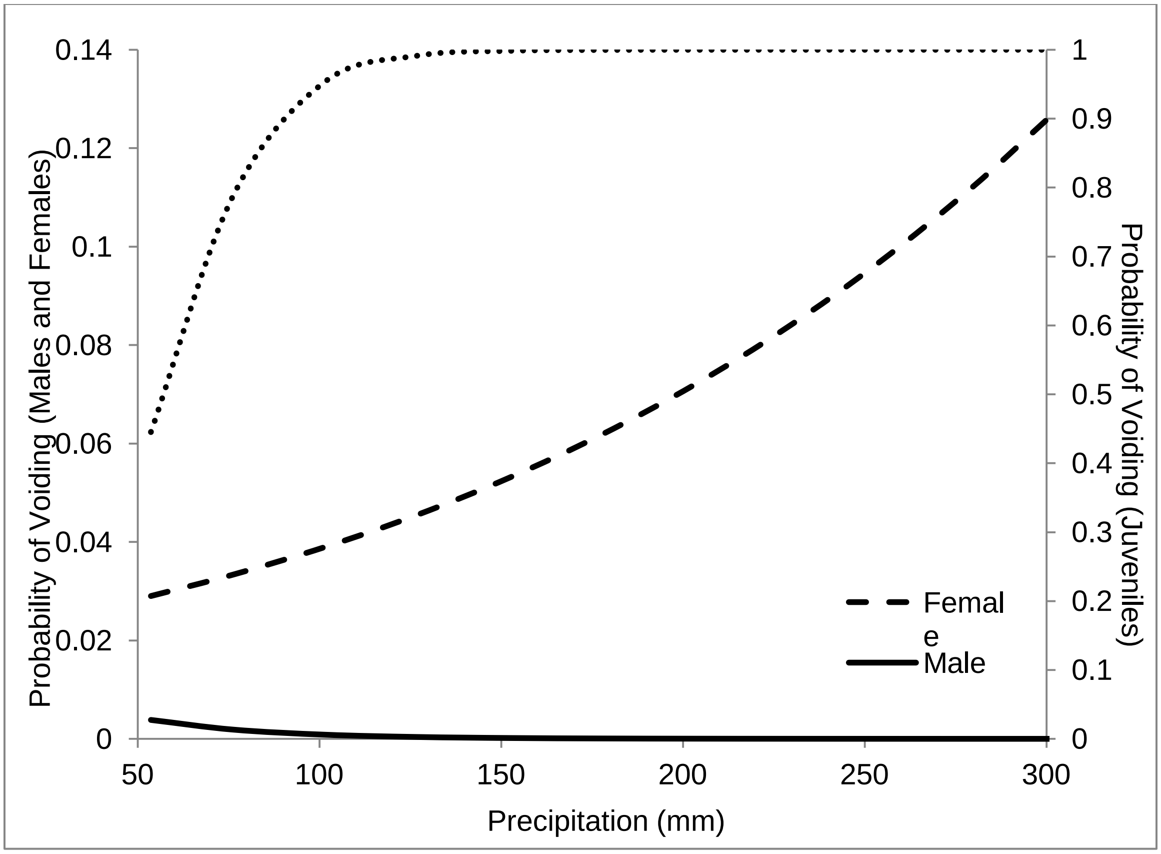

Figure 2.2. Probability of voiding in juvenile, female, and male Agassiz's desert tortoises in 50 mm intervals of average winter precipitation (Oct.-Mar.) GLMM that incorporates HT, PPT, SEX, and TC as fixed effect variables and ID as random effect (model averaging of top 6 models).

Figure 2.3. A radio-telemetered adult male desert tortoise walking just above its burrow at Mesa.

Appendix B

Figure 3.1. Motion sensor camera placed at the mouth of desert tortoise burrows at Mesa.

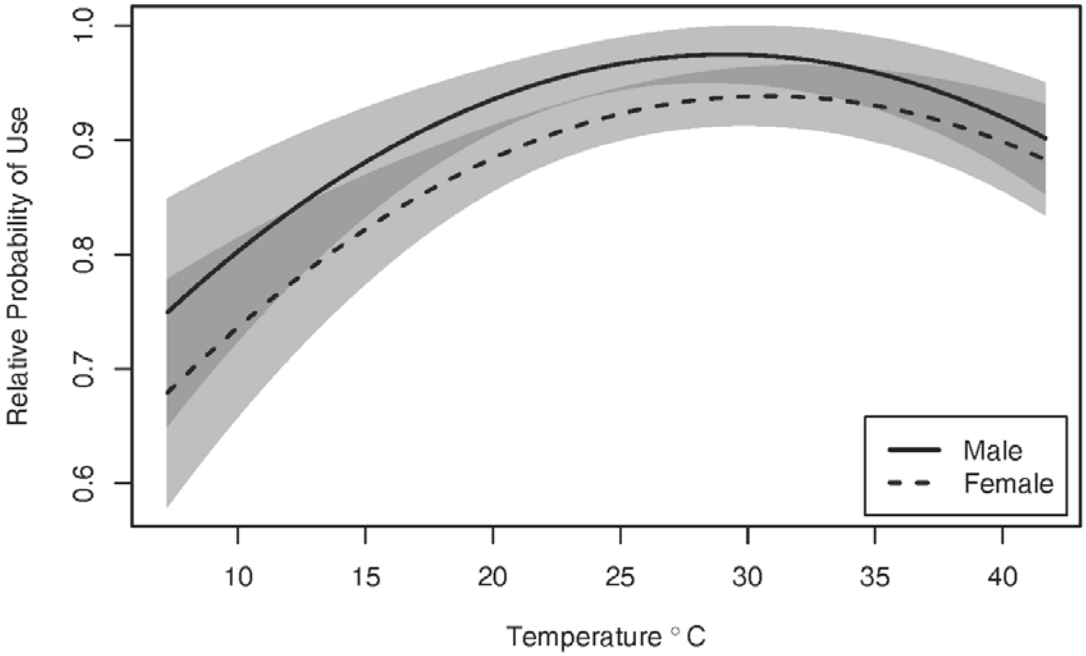

Figure 3.2. Relative probability of activity in male and female Agassiz's desert tortoises using model average of top two generalized estimating equation models. Light grey shading represents unconditional standard error. Dark grey shading represents unconditional standard error overlap between males and females.

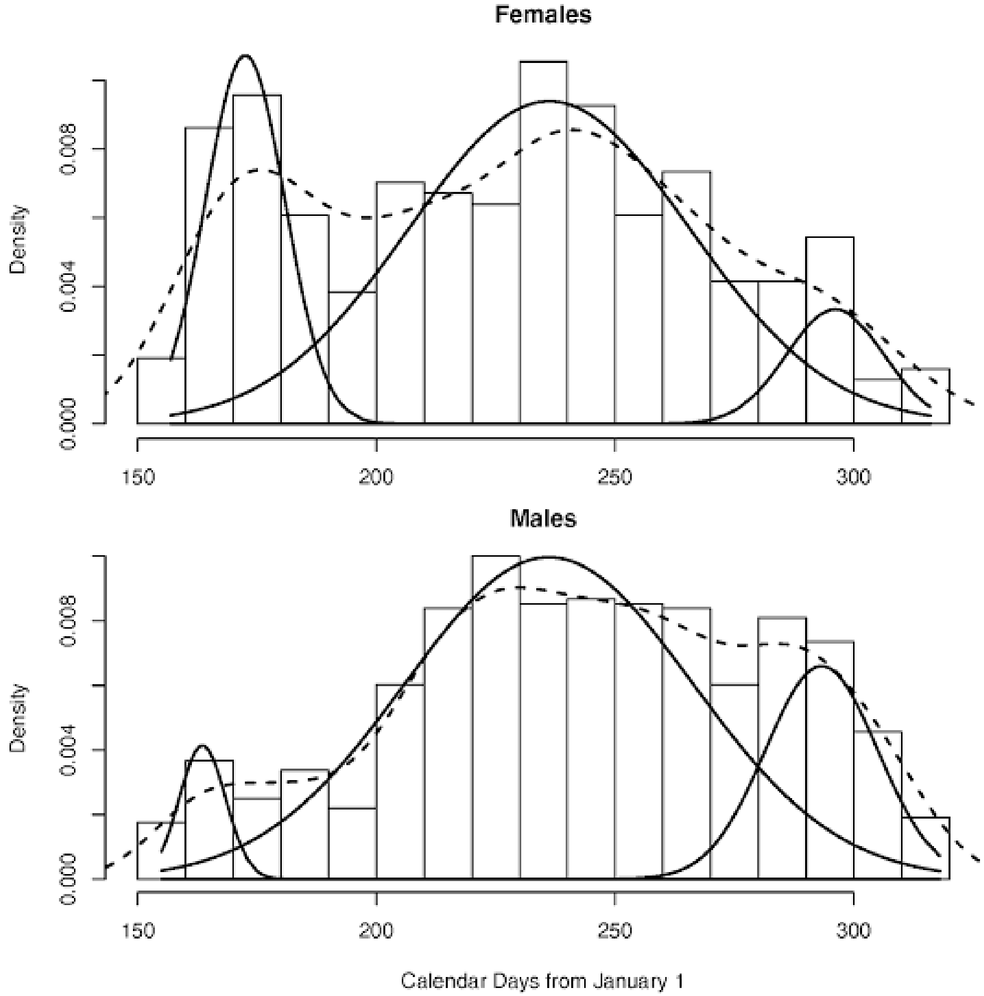

Figure 3.3. Normal mixture models assessing patterns of activity in desert tortoises across calendar days from January 1 (day 150 to 318). Histogram bars represent probability density of the number of active tortoise records per day. Gaussian components (peaks in histogram) are fitted with an Iterative 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.

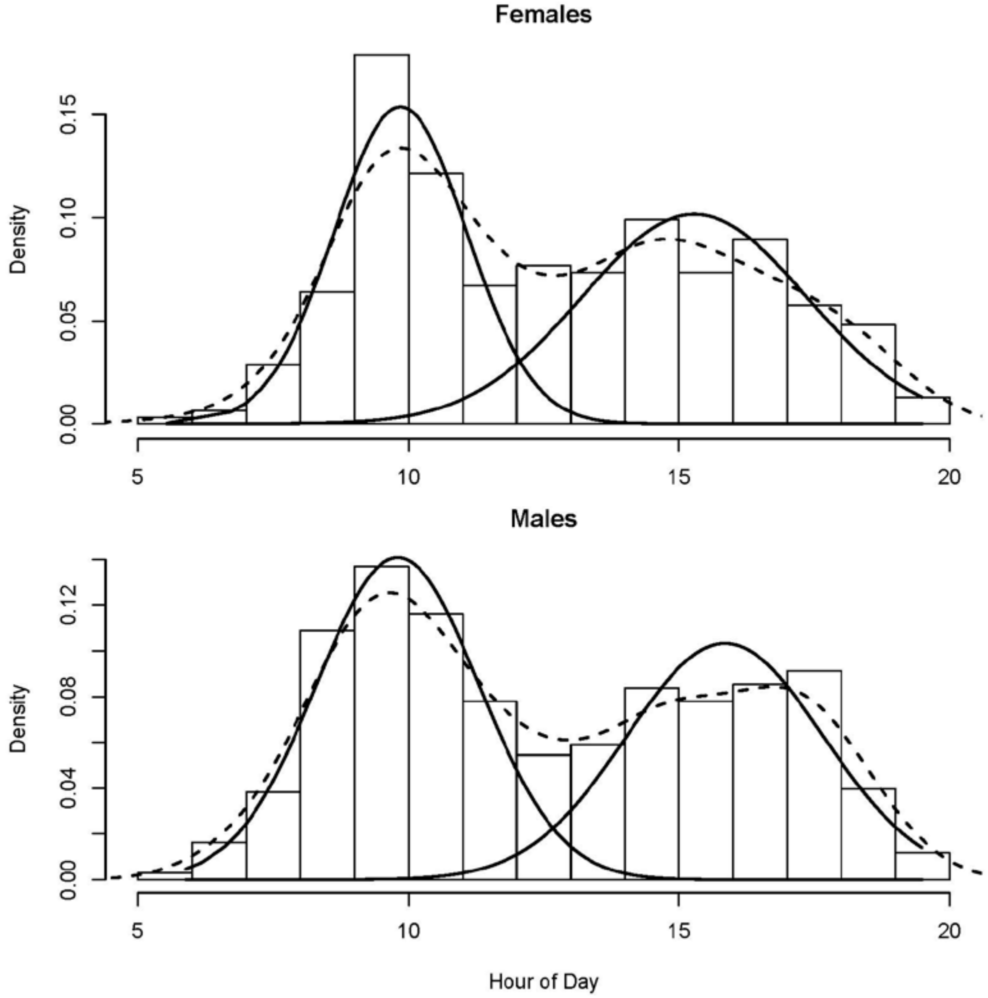

Figure 3.4. Normal mixture models assessing patterns of activity in desert tortoises across hour of day (hour 0 to 24). Histogram bars represent probability density of the number of active tortoise records per hour. Gaussian components (peaks in histogram) are fitted with an iterative expectation maximization 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.

Appendix C

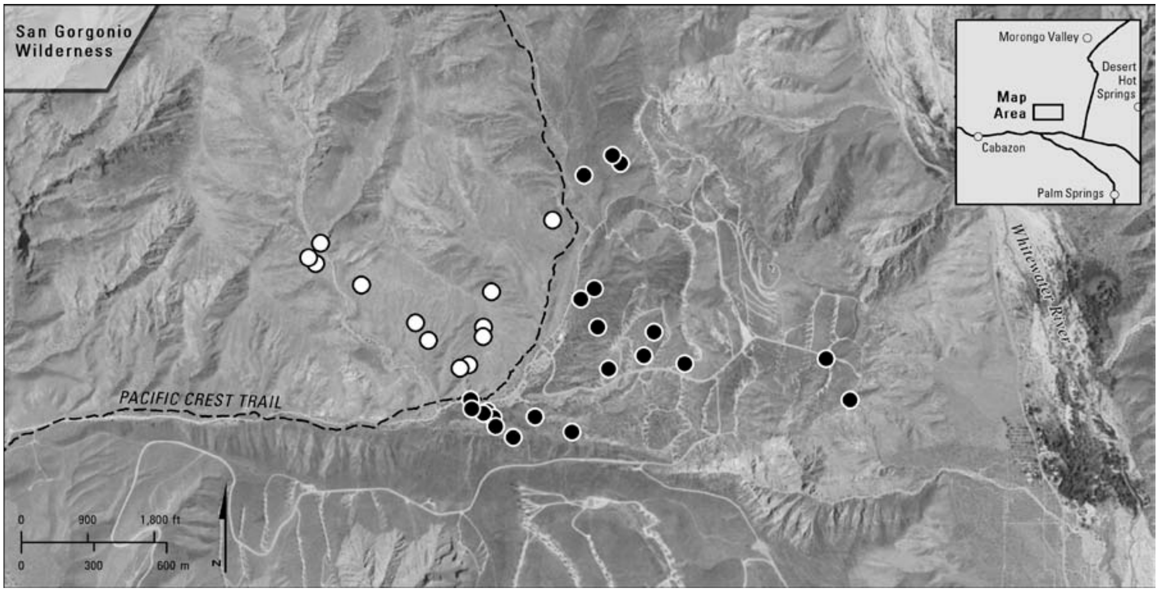

Figure 4.1. Minimum convex polygon (MCP) centroids for individuals captured during the study period at Mesa. Dark circles represent WEF tortoises and light circles represent NWA tortoises, separated by the Pacific Crest Trail.

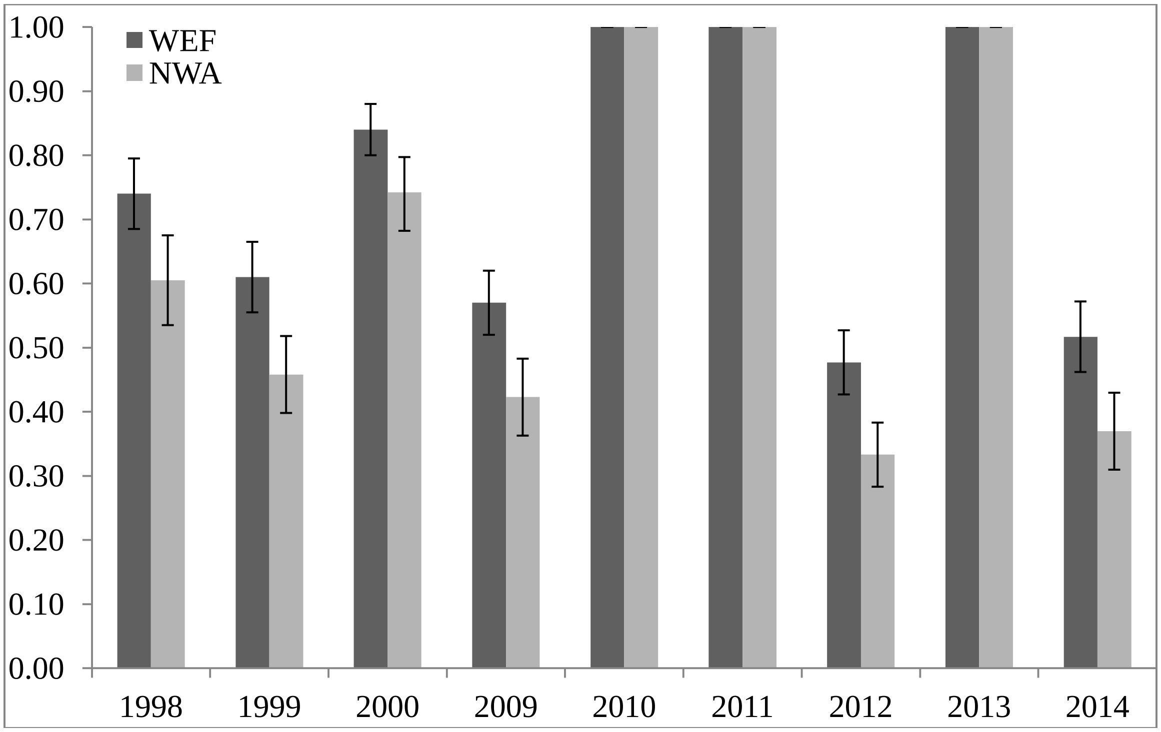

Figure 4.2. Capture probability of desert tortoises for all study years (using the top parameterization of *p*(Radio+HT+T)) at Mesa. One-hundred percent capture probabilities correspond to years when all tortoises in the previous year were radioed tracked continuously until the following year. Error bars denote unconditional standard error.

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