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FINAL PROJECT REPORT

ASSESSING THE LONG-TERM SURVIVAL AND REPRODUCTIVE OUTPUT OF DESERT TORTOISES AT A WIND ENERGY FACILITY NEAR PALM SPRINGS, CALIFORNIA

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PREFACE

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Assessing the long-term survival and reproductive output of desert tortoises at a wind energy facility near Palm Springs, California is the final report for the Assessing the Long-term Survival and Reproductive Output of Desert Tortoises at a Wind Energy Facility Near Palm Springs, California wind energy and tortoise project (Contract number 500-09-020) conducted by Jeffrey E. Lovich of the U.S. Geological Survey. The information from this project contributes to Energy Research and Development Division's Energy-related Environmental Research Program.

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ABSTRACT

Wind energy development is experiencing renewed growth. A great deal has been published on the effects of wind energy development and operation on flying wildlife species. Very little information is available in the peer-reviewed scientific literature regarding wind energy facility impacts on non-flying wildlife. Detailed studies on the demography and reproductive ecology of Agassiz's desert tortoise (*Gopherus agassizii*), a state and federally protected species, began at a wind energy facility in the San Gorgonio Pass near Palm Springs, California in 1997 and continued through 2009. California Energy Commission funding allowed additional data collection in 2010-2011, facilitating a long-term perspective on how this long-lived, threatened species responded to the presence and operation of a wind energy facility. The research had four objectives: 1) generating tortoise population size estimates; 2) determining the survivorship rate of tortoises based on long-term data; 3) determining if tortoises are still reproducing at the same rate observed from 1997-2000; and 4) identifying scientifically-defensible methods to mitigate the possible negative impacts of wind energy development on tortoises. The population was characterized by comparatively high survivorship and reproductive output, the latter most likely because the site was located where rainfall was more reliable than interior desert locations. Researchers observed few other differences relative to the ecology of tortoises living in more natural areas. Industrial operations at the site during the study resulted in at least two known tortoise mortalities through vehicle strikes or entrapment in culverts. Mitigating the negative effects of wind energy development on tortoises may require proper site selection and design, slow vehicle speeds on site, proper culvert design, maintenance staff awareness, fire prevention and suppression, and continued research and monitoring. Carefully designed before and after studies are needed to determine cause and effect relationships between renewable energy development and operation and impacts to wildlife.

Keywords: California Energy Commission, Agassiz's desert tortoise, *Gopherus agassizii*, wind energy, growth, survivorship, population, demography, reproductive ecology

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EXECUTIVE SUMMARY

Introduction

Wind energy development is experiencing renewed growth. A great deal has been published on the effects of wind energy development and operation on flying wildlife species (birds and bats). Little is known about the effects of renewable energy development and operation, including wind energy, on non-volant (non-flying) terrestrial wildlife species despite a large increase in applications to develop wind and solar energy on public land.

Project Purpose

This report provided an analysis of the long-term effects of wind energy operation and maintenance on the ecology of a population of federally protected (threatened) Agassiz's desert tortoises (*Gopherus agassizii*) at a study site known as Mesa, near Palm Springs, California from 1997-2011. The site was developed for wind energy in 1983 on land administered by the Bureau of Land Management (BLM). The research had four objectives: 1) estimating the population size of the tortoises at the wind energy facility; 2) estimating the survivorship of tortoises at the site over time; 3) examining the reproductive output of the population to examine possible changes over time; and 4) developing science-based recommendations to mitigate the possible negative impacts of wind energy development on desert tortoises.

Project Results

Tortoises were captured, measured, marked for permanent identification, and a subsample was outfitted with radio transmitters for periodic relocation. Different sample sizes were studied during seven field seasons spanning 15 years, but some individuals were recaptured every year of the study. Sex was determined for each tortoise using external anatomical features and they were measured and weighed at various times during the study. Growth is a fundamental characteristic of all organisms, ultimately affecting fitness through its influence on key life history characteristics and demographic parameters including age at maturity, potential reproductive capacity, population structure, and sex ratios. Fabens' interval-based growth equation was used to estimate growth rates of males and females. The cumulative size frequency distributions for the Mesa site were compared to other tortoise populations. Annual survivorship was calculated using the regression method of catch curve analysis. Population size was estimated using the computer program Capture. Females were X-rayed at weekly to 10-day intervals during the reproductive season from April-July to determine clutch frequency, clutch size, and egg size.

Researchers captured 69 individual tortoises at Mesa from 1997-2010, not including hatchlings recovered from nests in 2000, or 11.0 tortoises per square kilometer (km^2). Heterogeneity of capture probability required using data from 1997-2009 to effectively estimate a population size for the site as 96 tortoises or 15.4 tortoises per km^2. All size classes were represented in the sample. The adult sex ratio was biased, with 30 males to 21 females. Tortoises at the study site attained large sizes relative to other populations. The largest male was 350 millimetres (mm) and the largest female was 270 mm. Size frequency histograms were similar to those of

Morafka's desert tortoise populations in Arizona, also in the Sonoran Desert. Males and females grew to a mature body size of about 200 mm or more from a hatchling size of about 44.5 mm.

Researchers found the remains of only 11 dead tortoises with measurable remains from 1997-2010. A small number of tortoises were known to have been killed by site operations. A radioed female with a clutch of eggs was killed by a vehicle strike in 1998 and a radioed male was entombed in a culvert during winter rains only to die shortly after excavation. Annual survivorship of radioed females at the site was estimated at 91.6 percent, relatively high compared to other populations during the same time period, but still at the lower end of what is considered normal. However, deaths above the normal rate in adult females can have significant negative effects on desert tortoise populations.

Eggs were detected in X-radiographs from 11 April to 28 July although there was substantial variation among years. Clutches were deposited in nests 1-12 days after eggs were last detected in X-radiographs. Clutch size varied among years and females and ranged from 3.8-5.6 eggs per clutch. Females produced 1-3 clutches per year. Third clutches were rare, accounting for only 4.6 percent of overall egg production. Annual egg production ranged from 0-15 eggs per female. Larger females produced more eggs per clutch but not more clutches per year. Larger females also produced larger eggs. Reproductive output was very high compared to other populations, a likely result of the reliable rainfall received at the study site that caused consistent germination of food plants for tortoises.

Researchers observed few differences in the ecology of tortoises at Mesa relative to populations in more natural areas. Exceptions included differences in growth rates of males, high reproductive output, and high survivorship observed in adult females at Mesa. Tortoises appear to be buffered by the highly productive nature of the site resulting from reliable rainfall.

Effectively mitigating the negative impacts of wind energy development on tortoises could be achieved with the following measures: 1) good site selection that minimizes impacts on high quality tortoise habitat; 2) slow maintenance and construction vehicle speeds; 3) culvert design that minimizes animal use as refugia; 4) increasing staff awareness of the needs of wildlife; 5) fire prevention and suppression; and 6) continued research and monitoring. Decreasing the mortality of adults, especially females, is essential to the persistence of long-lived, late-maturing species like the desert tortoise.

This research increased the scientific knowledge about the effects of wind energy operation on desert tortoises, but carefully controlled before and after studies are needed to establish cause and affect relationships.

Project Benefits

Information in this study can be used to facilitate the siting and permitting of wind energy through documenting the demographic response of tortoises to an existing wind farm and through identifying effective mitigation strategies.

CHAPTER 1: Introduction

1.1 Background

In the Sonoran Desert of California, Agassiz's desert tortoises (*Gopherus agassizii*) reach their westernmost distribution near a large wind energy facility (460 turbines) in the foothills of the southeastern San Bernardino Mountains in Riverside County (Figure 1). This location, known as Mesa, was the subject of intensive studies of desert tortoise reproductive biology, habitat utilization, nesting ecology, and hatchling behavior from 1996-2001 (Lovich et al., 1999; Lovich and Daniels, 2000; Meyer and Lovich, 2004). During that time, over 136 individual tortoises (20 males, 28 females, and 88 hatchlings and juveniles) were captured, marked, and monitored in an area of about one square mile. The observed density of tortoises was relatively high compared to other sites during the same time (Lovich et al., 2011a).

Figure 1: Male Agassiz's desert tortoise (*Gopherus agassizii*) photographed at the Mesa wind farm near Palm Springs, California in 2011.

Photo Credit: Jeff Lovich

Human land use and activities have had dramatic impacts on the California deserts (Lovich and Bainbridge, 1999) and have been invoked as causes of desert tortoise population declines (U.S. Fish and Wildlife Service, 1994). A preponderance of published information (Ernst and Lovich, 2009) suggests that most tortoise populations north and west of the Colorado River have experienced some level of decline since listing as threatened under the Endangered Species Act in 1990. Yet the tortoise population at Mesa appeared to be healthy and reproductively vigorous in the late 1990s (Lovich et al., 1999), over 14 years after wind energy development commenced on site in 1983. A key unanswered question at the time was: why did the Mesa population thrive in a human-altered habitat during the same time that tortoises in more "pristine" habitats, like Joshua Tree National Park, declined (Lovich, unpublished data)?

Surprisingly, earlier research at Mesa suggested that tortoises may have selected for some of the human-induced features in the landscape associated with wind energy production (Lovich and Daniels, 2000), using them for shelter and foraging activities. However, success in the short-term does not guarantee success in the long-term. Desert tortoises, like many turtle species, are long-lived and may take 15 or more years to reach maturity (Ernst and Lovich, 2009). As such, earlier studies at Mesa took place at a time when wind energy facilities were in place for less than the span of a tortoise generation. Given the success of tortoises at Mesa in the short-term, it is critically important to determine their long-term status (greater than a generation). Almost 30 years after wind energy development began at the site, there was an unprecedented opportunity to measure the long-term survival, population status, and viability of tortoises at Mesa, and that formed the basis for the research summarized in this report.

The importance of determining the long-term survival, population status, and viability of tortoises at an existing wind energy facility is evidenced by increasing demand for renewable energy development in desert tortoise habitat. Renewable energy development is once again flourishing and the Bureau of Land Management (BLM) is receiving many applications to develop additional wind energy facilities, some in desert tortoise habitat. If it can be demonstrated that development and activities associated with wind energy generation at Mesa are compatible with desert tortoise conservation and recovery, then the successes there could be replicated through development of reasonable and prudent alternatives and management strategies for other sites.

The research had four objectives: 1) generate tortoise population size estimates for the site; 2) determine the rate of survivorship of tortoises based on long-term data; 3) find out if tortoises are still reproducing at the same rate observed from 1997-2000; and 4) identify scientifically-defensible methods to mitigate the negative impacts of wind energy development on tortoises.

1.2 What do We Know About the Effects of Renewable Energy Development on Wildlife?

A great deal has been published in the scientific literature regarding the effects of wind energy development and operation on volant (flying) wildlife including birds (Drewitt and Langston, 2006) and bats (Arnett et al., 2007; Kunz et al., 2007), although knowledge of how to mitigate negative impacts is still imperfect (Kuvlesky et al., 2007). Lovich and Ennen (in press) reviewed

the peer-reviewed scientific literature for information on the known and potential effects of utility-scale wind energy development and operation (USWEDO) on terrestrial and aquatic non-volant wildlife and found that very little has been published on the topic. Their review found only 15 publications regarding the effects of land-based and off-shore wind energy development and operation on non-volant wildlife, including five on Agassiz's desert tortoise (the latter all based on the research by the author).

Following a similar review for solar energy (Lovich and Ennen, 2011) Lovich and Ennen (in press) identified known and potential effects due to construction and eventual decommissioning of wind energy facilities. Many of the effects are similar and include direct mortality, environmental impacts of destruction and modification of habitat including impacts of roads, and offsite impacts related to construction material acquisition, processing, and transportation. Known and potential effects due to operation and maintenance of facilities include habitat fragmentation and barriers to gene flow, as well as effects due to noise, vibration, electromagnetic field generation, microclimate change, predator attraction, and increased fire risk. The scarcity of before-after-control-impact studies hinders the ability to rigorously quantify the effects of USWEDO on non-volant wildlife. Lovich and Ennen (in press) conclude that more empirical data are currently needed to fully assess the impact of USWEDO on non-volant wildlife.

Little was known about the effects of utility-scale renewable energy development on Agassiz's desert tortoises, even after more than a quarter century after the recognition of that deficiency (Pearson, 1986). Research supported by the California Energy Commission PIER program made substantial contributions to the published scientific literature on the effects of renewable energy generation (especially from wind) on that species' ecology (Ennen et al., 2011, 2012a, b; Loughran et al., 2011; Lovich et al., 2011 a, b, c; Lovich and Ennen, 2011). The results are summarized in this report.

CHAPTER 2:
Materials and Methods[1]

2.1 Study Site Description

The study site, known as Mesa, is located on the extreme western edge of the Sonoran Desert ecosystem (locally referred to as the Colorado Desert due to its adjacency to the river of the same name) in the southeastern foothills of the San Bernardino Mountains near Palm Springs, California (see Lovich and Daniels, 2000). The site was developed for utility-scale wind energy generation starting in 1983 on land administered by the Bureau of Land Management. This resulted in construction of an extensive network of dirt roads to provide access to each of 460 turbines, along with 51 electrical transformers and associated infrastructure (e.g., substation and maintenance buildings). A matrix consisting of native vegetation remained within and around the footprint of construction, although the entire site was grazed by cattle until sometime around the year 2000 when grazing was eliminated.

Concordant with knowledge of ecosystem boundaries (Burk, 1977), recent genetic analysis confirms that Mesa tortoises are more similar to tortoises in the western Sonoran Desert of California than those in the western Mojave Desert (Hagerty and Tracy, 2010). Because of its location on the fringe of the Sonoran Desert, Mesa sits at the intersection of several other ecosystems including coastal sage scrub, chaparral, montane, and Mojave Desert plant communities. The climate at Mesa is coastally influenced resulting in variable but annually reliable rainfall (Lovich et al., 1999; Lovich and Daniels, 2000) in quantities sufficient to trigger germination (Beatley, 1974; Bowers, 2005) of food plants for the tortoise. In contrast, tortoise habitat in more interior desert is periodically affected by significant drought, sometimes with adverse impacts on tortoise survival (Peterson, 1994; Longshore et al., 2003; Esque et al., 2010).

Prior to the Verbenia Fire of 1995 (Lovich et al., 2011b), Mesa was characterized by a mixture of plant communities representing several ecosystems. Sitting at the interface between coastally influenced plant associations and the desert, Mesa had exceptional perennial plant diversity. North-facing slopes and the western edge of the study area were visually dominated by chaparral and coastal sage scrub plant species (Schoenherr, 1992) including chamise (*Adenostoma fasciculatum*) and California sage brush (*Artemisia californica*). Other cismontane species (*sensu* Schoenherr, 1992) included California juniper (*Juniperus californica*), condalia (*Condalia parryi*), and isolated oaks (*Quercus* spp.). South-facing slopes and the eastern edge of the study area were characterized by typical Mojave Desert (Vasek and Barbour, 1977) and Colorado Desert (a subdivision of the Sonoran Desert, Burk, 1977) plants, including creosote bush (*Larrea tridentata*), burrobush (*Ambrosia dumosa*), honey mesquite (*Prosopis* spp.), cholla (*Cylindropuntia* spp.), bladder pod (*Isomeris arborea*), linear-leaved goldenbush (*Haplopappus linearifolius*), encelia (*Encelia farinosa*), and cheesebush (*Hymenoclea salsola*). A signature species of the Colorado Desert that occurred on site prior to the Verbenia Fire of 1995 (Lovich et al.,

[1] Excerpted with modifications from Ennen et al. (2012), Lovich and Daniels (2000), Lovich et al. (2011a, b)

2011b) was teddy-bear cholla (*Cylindropuntia bigelovii*). Another species, spiny hopsage (*Grayia spinosa*), a common plant of the Mojave Desert, but rare in the Colorado Desert except for the Whitewater Hills (Jaeger, 1940), was relatively abundant.

Mesa is mountainous with elevations at desert tortoise capture locations ranging from about 660 m in the valleys to over 880 m on the peaks and ridges. The topography at the northern boundary of the study site limited the distribution of tortoises, which usually occur below 1500 m (Germano et al., 1994), as elevation rises sharply to over 3500 m. The steep terrain and unique plant associations at Mesa are atypical of desert tortoise habitat elsewhere in the Colorado Desert (Ernst and Lovich, 2009; Luckenbach, 1982; Patterson, 1982).

The human-ignited Verbenia Fire, unrelated to wind-energy operations, started on 4 August 1995, about 2.65 km from the core of our study site. This time of year is near the end of the spring-summer active season for desert tortoises at the study site, with aboveground activity usually confined to early morning and late afternoon due to high air temperatures in August. The fire spread rapidly to encompass 71 percent (4.44 km2) of the total area occupied by desert tortoises at the study site (Lovich et al., 2011b). Fire intensity was rated as low to moderate by the responding fire crew: hot enough to kill a large percentage of the creosote bush, all of the teddybear cholla, and many of the other desert perennial plants at the site. Areas with low fire intensity resulted in spotty mortality of individual creosote bushes, while moderate fire intensity areas sustained complete mortality. Other smaller fires affected different parts of the study area from 1979 to 2011 (many started by industrial operations on site) ranging in size from 0.02 ha to 58.71 ha. Prior to the 1970s, wildland fire was almost unknown in the immediate vicinity of our study site according to Brown and Minnich (1986). The Verbenia Fire may have been the first major wildland fire to affect the study site in modern history (R. Minnich; University of California, Riverside; personal communication). The long-term impact of this major fire on tortoises that were not killed outright or scarred by fire appears to be minimal (Lovich et al., 2011b). The effects of recurring fires burning the same tortoise habitat, one as recently as June, 2012, are unknown.

2.2 Methodology

Research and analysis supported by the California Energy Commission was conducted from March, 2010–June, 2012 and compared and contrasted with legacy data collected earlier to obtain a long-term perspective on the ecology of Agassiz's desert tortoises living in and around an operating wind energy facility. Our analysis is based on data collected during seven field seasons (1997–2000 and 2009–2011), primarily during the months from April-July. In addition, tortoise body size data collected in 1992 were incorporated into the analyses as discussed elsewhere in the report and in Lovich et al. (2011a).

The study site was systematically searched for desert tortoises by walking transects through promising habitat during the early spring when above-ground activity was highest. On initial capture, we determined tortoise sex based on secondary sexual characteristics (Ernst and Lovich, 2009), and weighed, measured, and marked individuals. Individuals were marked by notching various combinations of their marginal scutes (Cagle, 1939) and by gluing clear epoxy

numbered tags on the posterior of their carapaces. Adult females (7 to 17 females each year) were outfitted with radio transmitters (radios weighed 50g; model R1540; Advanced Telemetry Systems, Isanti, Minnesota, USA) following the procedures outlined by Boarman et al. (1998a). They were tracked at 7-10 day intervals during the time of year when eggs are visible via X-radiography (April – July). Relocations of radio-tagged individuals generally occurred at monthly intervals outside the egg production season. A GPS unit was used to collect location data at every tortoise capture.

We weighed individuals at each recapture but only recorded body size measurements once or twice during a field season. Body size was measured as straight-line carapace length (CL) in mm down the middle of the carapace. We X-rayed females (Gibbons and Greene, 1979; Hinton et al., 1997) during the egg-laying season (April–July) as part of ongoing reproductive studies started in 1997 (Lovich et al., 1999). The ability to detect tortoises above ground is biased by variation in yearly rainfall and its effect on availability of food plants, which can affect estimates of population size (Freilich et al., 2000). Although our study site was affected by both El Niño and near-drought years (Lovich et al., 1999) during the study, winter rainfall was sufficient to trigger germination of annual food plants, and thus tortoise activity, in all years of field work.

2.2.1 Methods Used for Growth, Demography, Survivorship, and Population Size Estimation Analyses

Age in many turtle species can be reliably determined by counting growth rings on scutes (Germano and Bury, 1998), and accurate estimates in *G. agassizii* are possible up to 20–25 years (Germano, 1988). We used the method of Fabens (1965) to generate growth equations for tortoises when age was unknown. This method has been validated against known age data and found to produce reliable parameter estimates (Frazer et al., 1990). Fabens rearranged the von Bertalanffy growth equation to produce an interval-based version of the form:

$$L_r = a - (a - L_c)e^{-kd}$$

where L_c is the length (CL) at first capture, L_r is CL at the time of last capture, a is an estimate of asymptotic CL, e is the base of natural logarithms, k is an estimate of the intrinsic rate of growth, and d is the time interval (years) between first and last captures. The variable b in the von Bertalanffy growth equation was calculated using the method outlined by Frazer et al. (1990) where

$$b = e^k(1 - h/a)$$

and h is CL at some known age. We used data for seven juvenile tortoises that were radio-tracked for 115–284 days in 2000 (x = 167 days) after they left their nests and assumed that their final mean CL represented size at year one. Although this may be a slight underestimate of size,

we believe it is preferable to use data from our population rather than published estimates from elsewhere with different hatchling sizes and growth rates (Germano, 1994). Following Day and Taylor (1997), we did not use data from von Bertalanffy growth equations to estimate age and size at maturity. Instead we report the minimum size of females carrying shelled eggs. Male maturity was estimated by the appearance of secondary sexual characters. Males and females were analyzed separately due to sexual size dimorphism (Gibbons and Lovich, 1990), but the same juvenile tortoises were used in both growth estimates under the premise that juvenile turtles of both sexes grow at the same rate (Gibbons and Lovich, 1990). Nonlinear models were parameterized using SYSTAT 13 software (SYSTAT Software, Inc., San Jose, California, USA).

Cumulative size frequency histograms for our site were compared to similar data for *G. morafkai*, another closely-related species in the Sonoran Desert. We compared Mesa data to data from three sites (Granite Hills, Eagletail Mountains, and Little Shipp Wash) in Arizona using Kolmogorov–Smirnov tests (see Lovich et al., 2011a for a map showing the locations of these sites). These populations have been monitored every one to five years since established in 1987 (Eagletail Mountains) and 1990 (Granite Hills and Little Shipp Wash) as part of the Arizona Game and Fish Department's long-term demographic study plots. Habitat is primarily Sonoran Upland, with elements of Interior Chaparral on the north facing slopes of the Little Shipp plot, and elevations from 450 – 970 m. Details of these populations are given by Averill-Murray et al. (2002) and various final reports to the Arizona Game and Fish Department.

Because we had six years of data to examine cumulative size frequency distributions at Mesa, we wanted to investigate the role of sampling duration on the perception of population size structure. This analysis would allow us to test if long–term studies would show different population size structure trends than a study of shorter duration. Therefore, we compared the cumulative size frequency histograms from one year of data (i.e., 1997) to data sets containing 2–6 years of population size data again using Kolmogorov–Smirnov tests. Sex ratios were tested for departure from 1:1 with a Chi-square test. Sexual size dimorphism was calculated using the technique of Lovich and Gibbons (1992). CL data met the assumption of normality for each sex (Shapiro–Wilk W Test: $W = 0.94–0.98$, $P = 0.34–0.91$). However, the variances between males and females were unequal (Bartlett's Test: $F = 7.33$, df = 1, $P = 0.007$). Therefore, we conducted a Welch's Test to determine if CL was different between males and females.

We also compared data for mean CL of all tortoises collected in 1992 to data from 1997–2010 to see if body size distribution changed over time. We used CL at first capture for each individual tortoise. Data collected in 1992 used curved-CL measured down the midline of the tortoise. We converted those measurements to straight-line CL using the equation:

$$\textit{straight-line CL}=0.741(\textit{curved-CL})+5.84$$

provided by David Germano (unpubl. data). This relationship provided an accurate way to convert measurements as shown by a coefficient of determination of 0.99 based on a sample size

of 47. We used a Kolmogorov–Smirnov test to compare cumulative size frequency histograms between the time periods.

Survivorship was calculated using the regression method of catch curve analysis (Chapman and Robson, 1960; Dunn et al., 2002) for a cohort of 11 adult female tortoises fitted with radio transmitters and monitored from 1997–2010 under the assumptions of a closed population, constant mortality, constant vulnerability, and unbiased sampling. The instantaneous mortality parameter was estimated as the negative of the slope of a semi-log regression fitting the number of surviving tortoises over time.

We estimated population sizes using Program Capture with each year (1997–2000, 2009–10) as a capture interval (White et al., 1982). Population density estimates were based on an estimate of total occupied tortoise habitat over all years. To generate this estimate we used 1771 capture locations and circumscribed the cloud of points with a line buffered at the edges to 12 m based on the GPS accuracy values. Surface area of the enclosed space was estimated at 6.25 km^2. Visual inspection of the circumscribed area revealed that this method provided an excellent predictor of actual and potential tortoise habitat at our site based on our experience (e.g., the area largely excluded extremely steep canyon walls).

Alpha was set at 0.05 for all statistical tests and data were inspected for normality and heterogeneity of variances.

2.2.2 Methods Used for Analysis of Reproductive Ecology Data

During the spring egg-producing season (early April to late July), we monitored the reproductive output of *G. agassizii* using X-radiography (Figure 2). Females were located at approximately weekly intervals from 1997-2000 and 10 day intervals in 2010-2011 using radio-telemetry. From 1997-2000, most X-radiographs were taken using a portable x-ray machine (model HF60, Min-Xray, Northbrook, Illinois, USA) at a dosage of 60 kilovolts for 0.10 seconds at a distance of 69.6 cm. This setting and the use of 3M's Imation Trimax Regular Rare Earth Cassettes subjected individuals to low levels of radiation exposure (Hinton et al., 1997). From 2010-2011 we used a fully digital system custom made by Canon with a Min-Xray TR-80 generator. Both of these systems allowed us to non-invasively determine clutch presence, clutch size, clutch frequency, and egg width.

Figure 2: Female Agassiz's desert tortoise (*Gopherus agassizii*) X-radiographed at the Mesa wind farm near Palm Springs, California on 26 May, 2011. Seven shelled eggs are clearly visible as are bits and pieces of food in the digestive tract, the radio transmitter and its antenna.

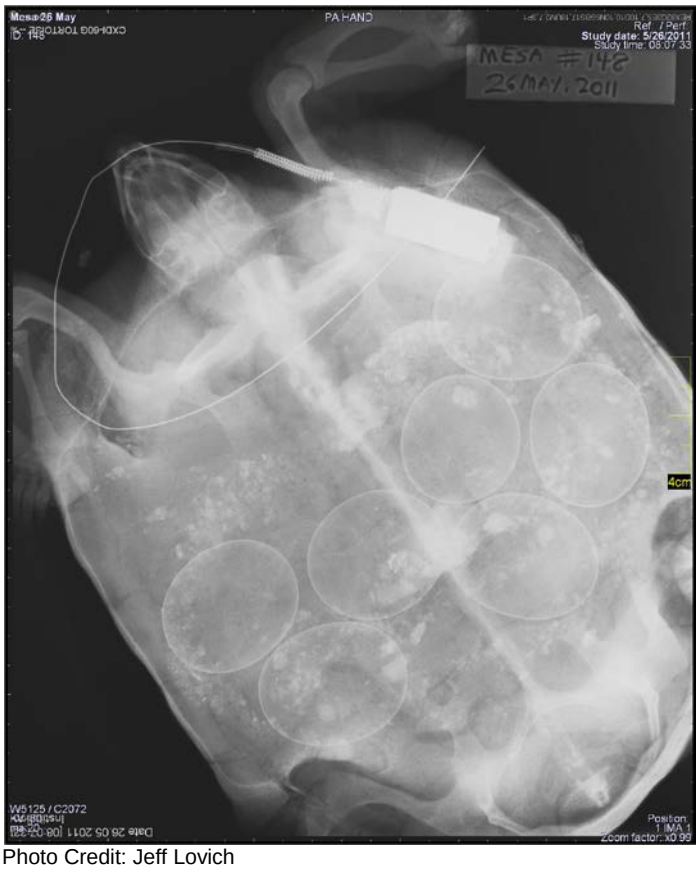


Photo Credit: Jeff Lovich

Similar to Wallis et al. (1999), all statistical analyses included only egg-laying females. However, the descriptive statistics (i.e., means and standard deviations) reported included non-egg laying females. We tested all our data for normality and conducted the proper transformations and parametric tests. Where appropriate, we conducted post-hoc tests (i.e., Tukey's Honestly Significant Difference).

For all the between–year comparisons of annual reproductive output (i.e., annual egg production [AEP] and clutch frequency) and number of days to egg detection, we conducted incomplete block design analysis of covariance (ANCOVA) using CL as the covariate and individual tortoise nested within year as a random effect. Clutches frequency would not transform to meet the assumption of normality. Therefore, we relied on the robustness to deviation of normality of the ANCOVA. For the between-year comparisons of clutch size and egg width, we conducted a two-factor, incomplete block design ANCOVA with year nested within individual tortoise as a random effect, year and clutch number as fixed effects, CL as the covariate, and the four interaction terms between the fixed and covariate effects. Because of the limited number of 3rd clutches (n = 8), we only included 1st and 2nd clutches in the statistical tests using clutch number as a fixed effect. Due to the small sample size, 3rd clutches were removed from the clutch–size analysis using a two-factor ANOVA. Also, to determine if annual clutch

frequency or clutch size had a relationship with AEP, we used incomplete block designed ANCOVAs with clutch frequency or clutch size as covariates and individual tortoise nested within year as a random effect. All statistical analyses were performed using Jmp 8 (Statistical Analysis Software [SAS], SAS Institute, Cary, NC, USA) at an alpha of 0.05.

CHAPTER 3: Results[2]

Understanding the structure, dynamics, and persistence of a population requires integration of knowledge on birth and death rates, individual growth and maturity rates, and population size and structure. Growth is a fundamental characteristic of all organisms, ultimately affecting fitness through its influence on key life history characteristics and demographic parameters including age at maturity, fecundity, population structure, sex ratios (Lovich and Gibbons, 1990), and population vital rates (Kirkpatrick, 1984; Barry and Tegner, 1990). The following summarizes the results of research on the Mesa tortoise population.

3.1 Growth, Demography, Survivorship, and Population Size Estimation Analyses

3.1.1 Growth

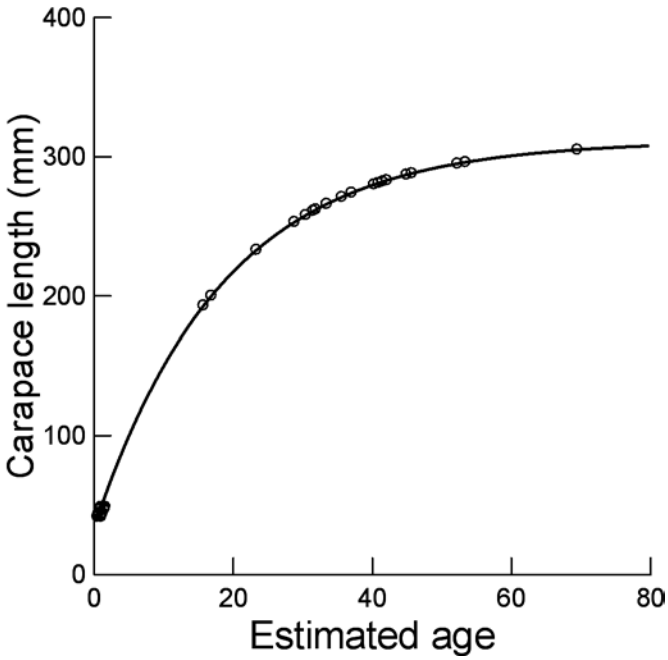
Mean CL of hatchlings in 2000 was 44.5 mm (range 36.1–49.7; SD = 2.6; n = 74). Fabens' method provided what appeared to be accurate estimates of growth parameters *a* and *k* as indicated by coefficients of determination of 99 percent for both sexes (Table 1). The growth equation for males is $CL = 311.5(1-0.89e^{(-0.054*Age)})$ and is shown in Figure 3. However, the fully-fitted von Bertalanffy growth model for females did not produce a biologically meaningful curve based on previously published data (Germano, 1992, 1994) for the desert tortoise: CL was greatly underestimated for a given age so is not shown. The smallest mature female, as shown by the presence of eggs, was 221 mm CL. Based on the onset of pronounced secondary sexual characteristics, male tortoises appear to mature when CL > 200 mm.

Table 1: Growth parameters and 95% confidence intervals for male and female desert tortoises based on the von Bertalanffy equation using body size in mm. Estimates were generated using the interval based technique of Fabens (1965) as detailed in Frazer et al. (1990). Parameter estimates for females provided a poor fit to the growth model (refer to text for details).

Sex	*a*	*k*	*b*	R^2 (Fabens)
Females	263.5 (24.47-28.23)	0.019 (0.002-0.03)	0.83	0.99
Males	311.5 (29.57-32.73)	0.054 (0.03-0.08)	0.89	0.99

[2] Excerpted largely from Lovich et al. (2011a)

Figure 3: Estimated growth curves for male desert tortoises from a wind energy generation facility near Palm Springs, California. Hollow circles designate CL at first capture of all specimens used to estimate the growth curve. The fit is deterministic since age was estimated from our derived growth equation.



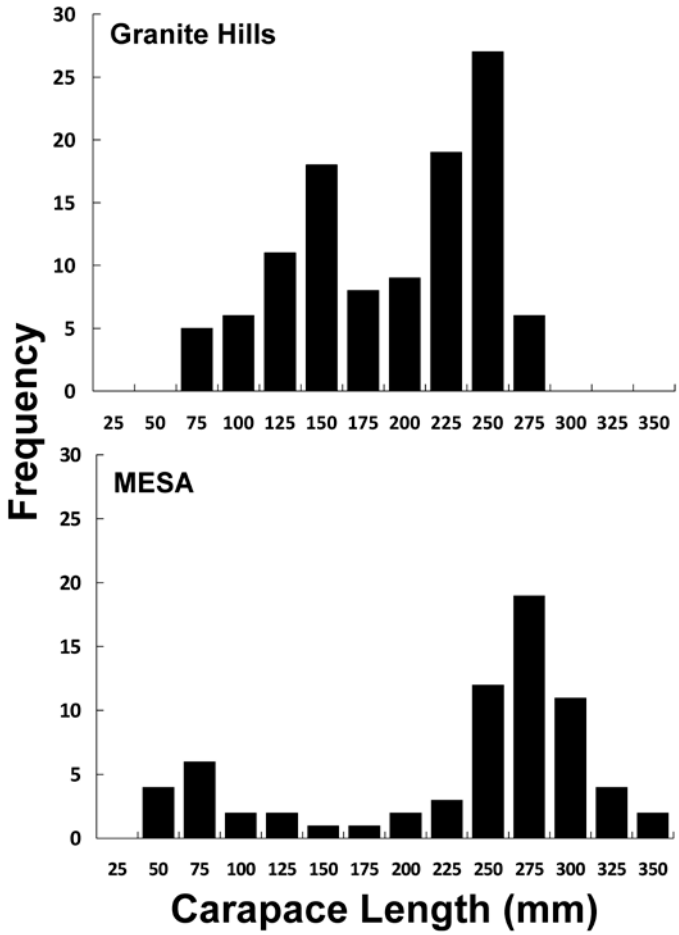
3.1.2 Demography and Population Size Estimation

Over the six field seasons from 1997-2010, and excluding hatchlings recovered from nests in 2000 (Lovich et al., unpubl. data), we captured 69 individuals at Mesa (cumulative numbers of marked individuals by year were: 1997 – 31, 1998 – 42, 1999 – 49, 2000 – 59, 2009 – 63, 2010 – 69) for a population density of 11.0 tortoises/km^2. Using data from 1997-2010, Program Capture was unable to generate a population estimator based on selection of a model with significant effects due to time, behavioral response, and heterogeneity of capture probability. Eliminating data for 2010 and using captures and recaptures from 1997–2009 (five field seasons, 64 tortoises) yielded a model recommendation of Chao's M(th) with a population estimate of 96 tortoises (SE = 12.3; 95 percent confidence interval = 80–130) or 15.4 tortoises/km^2.

All size classes were represented in our sample. Most (72.5 percent) of the individuals captured were adults (Figure 4), and the adult to non–adult ratio was 2.63:1. Our sample included 30 males and 21 females (1.43:1) but the proportion was not statistically different from 1:1 (X^2 =1.59, df = 1, P = 0.21). The population displayed sexual dimorphism with male CL ($\bar{\mathbf{x}}$ = 281.2 mm, SE = 4.8) significantly (F = 34.67, df = 1, P<0.0001) larger than female CL ($\bar{\mathbf{x}}$ = 247.6 mm, SE = 3.1). The sexual dimorphism index was -1.14. Our largest male was 350 mm (but we did not have growth interval data for him) while the largest female was 270 mm. Size frequency distributions at Mesa did not differ significantly when comparing data from 1992 to 1997–2010 (D = 0.25, P = 0.17). When comparing Mesa's population structure with three other Sonoran Desert populations of *G. morafkai* in Arizona, only the Granite Hills population was significantly

different (D = 0.501, *P*< 0.001) from Mesa, where tortoises were larger (Figure 4). In contrast to Mesa, the Granite Hills population consisted of only 55.0 percent adults. There were no differences (D = 0.113–0.155, *P* = 0.53–0.94) in the cumulative size frequency histograms between one year of data and data sets using multiple years (i.e., 2–6 years of data) at Mesa.

Figure 4: Size frequency histograms for desert tortoises near Palm Springs, California (Mesa) and Granite Hills, Arizona.



3.1.3 Survivorship

From 1997–2010 we found only 11 dead tortoises with measurable remains (some did not have complete carapaces) ranging in size from 83–339 mm CL (x = 212 mm, n = 6). Nine of these were the carcasses of animals not marked while alive during our studies. A radioed adult female was killed by a vehicle strike in 1997 and a radioed male was entombed in a culvert during winter rains (Lovich et al., 2011c). The unmarked dead tortoises included two additional males, two other females, three immature specimens, and two for which sex was undetermined. Some of the mortality events for hatchling and juveniles appeared to be caused by common raven (*Corvus corax*) predation (as evidenced by holes in the top of the carapace; Boarman, 2003). The instantaneous mortality rate for the cohort of 11 radio-tagged adult females was 0.084 (95

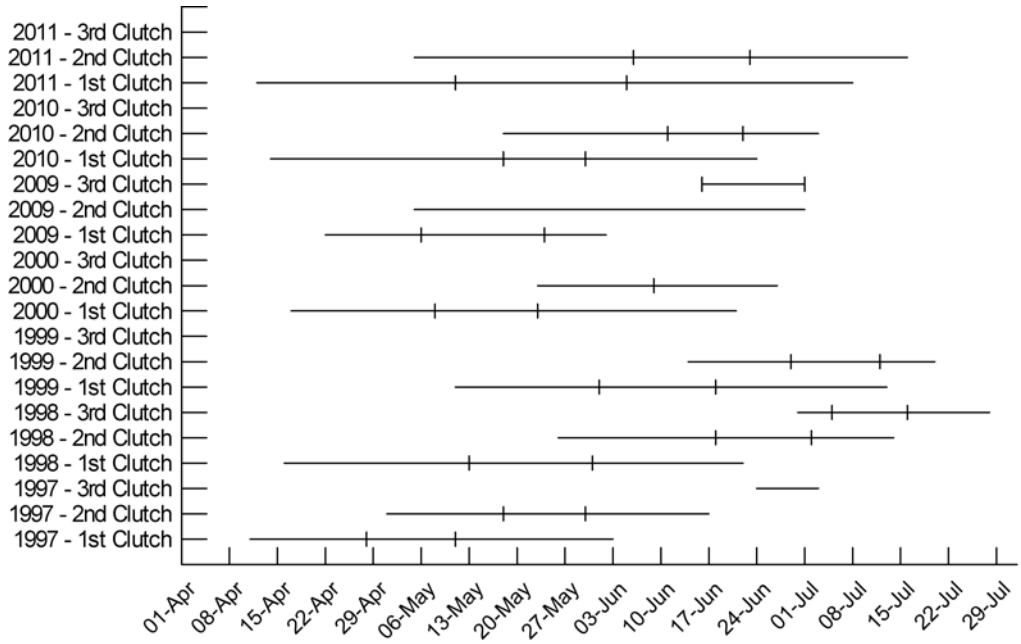
percent confidence interval = 0.062–0.123). When converted to an annual survivorship rate the estimate was approximately 91.6 percent (95 percent confidence interval = 90.5–93.5 percent).

3.2 Reproductive Ecology

3.2.1 Nesting Season

Throughout the study the earliest eggs were detected was 11 April, and the latest was 28 July. Eggs were visible in X-radiographs for intervals of the following numbers of days in each year (Figure 5): 84 (1997), 105 (1998), 71 (1999), 81 (2000), 58 (2009), 92 (2010), and 89 (2011). A Chi-square test revealed that these intervals were significantly different from the expected proportionally equal values ($X^2 = 16.59$, df = 6, $P = 0.01$). Actual dates of oviposition for both 1st and 2nd clutches at Mesa in 2011 (based on finding nests and inferring oviposition dates based on significant weight loss) ranged from 1-12 days after eggs were last detected in X-radiographs, with a mean of 6.4 days and a SD of 2.8 (n = 10 females and 14 clutches).

Figure 5: Clutch phenology of desert tortoises (*G. agassizii*) determined by X-radiography near Palm Springs, California. Horizontal lines represent range of dates when shelled eggs were visible in X-radiographs for years and clutch numbers indicated. Vertical tick marks show mean clutch appearance and disappearance dates for all clutches of that order (1st, 2nd, or 3rd) in a particular year. Lines with no tick marks represent single clutches. The line for 2nd clutches in 2009 does not have a tick mark since the means for appearance and disappearance were essentially the same. From Lovich et al. (in press).



3.2.2 Annual Reproductive Output

Annual egg production ranged from 0 – 15 eggs per female, and the mean annual reproductive output varied among years ranging from 1.50 – 2.20 clutches/female and 4.44 – 10.82 eggs/female (Table 2). AEP significantly differed among years (ANCOVA: $F_{(6, 47)} = 4.25$, $P = 0.002$) with 1998 ($\bar{x} = 10.82$, SD = 4.38) significantly differing from 1999 ($\bar{x} = 6.85$, SD = 1.91), 2000

($\bar{x}$ = 8.33, SD = 3.24), and 2011 ($\bar{x}$ = 6.18, SD = 3.11) using a Tukey's HSD (Figure 6). The interaction term was not significant (Table 3). Clutch frequency significantly differed among years (ANCOVA: $F_{(5, 42)} = 2.52$, $P = 0.04$), but only 1998 ($\bar{x}$ = 2.20, SD = 0.87) and 1999 were significantly different ($\bar{x}$ = 1.46, SD = 0.66) using a Tukey's HSD (Figure 7). The interaction term was not significant (Table 3).

Table 2: Summary statistics (mean and standard deviation) of reproductive characteristics and nesting season duration (i.e., egg detection) for 7 years of reproductive data from a population of *Gopherus agassizii* inhabiting a utility-scale renewable energy facility in Southern California. Some individuals were not including in some analyses and descriptive statistics due to the lack of complete reproductive history with a year.

				Clutch Size		
Year	N	Clutch Frequency	Egg Production	1st	2nd	3rd
1997	10	1.75±0.89	7.88±4.49	4.3±1.3	5.0±1.9	3
1998	14	2.20±0.87	10.82±4.38	4.8±2.0	5.6±1.6	3.3±1.3
1999	13	1.46±0.66	7.00±2.05	4.3±1.2	4.4±1.4	
2000	17	1.93±0.46	8.33±3.24	4.2±1.6	4.5±1.8	4
2009	16	1.60±1.14	6.60±4.77	4.0±2.6	5.3±2.1	1
2010	10	1.33±1.12	4.44±4.07	4.3±1.0	3.6±0.9	5
2011	11	1.55±0.69	6.18±3.11	3.8±1.6	4.3±1.4	

Table 3: Statistical results of egg detection, annual egg production (AEP), clutch frequency, clutch size, and egg width of a population of *Gopherus agassizii* inhabiting a wind energy facility in Southern California.

		Parameter			
Factors/ Interactions	Egg Detection	AEP	Clutch Frequency	Clutch Size	Egg Width
Year	$F_{6,51} = 4.69$; $P = 0.0007$	$F_{6,47} = 4.25$; $P = 0.002$	$F_{6,50} = 2.88$; $P = 0.02$	$F_{6,51.6} = 1.46$; $P = 0.21$	$F_{6,50.5} = 1.20$; $P = 0.34$
Clutch No.	NA	NA	NA	$F_{1,52.8} = 1.36$; $P = 0.25$	$F_{1,38.0} = 3.70$; $P = 0.06$
CL	$F_{1,51} = 2.30$; $P = 0.14$	$F_{1,47} = 7.92$; $P = 0.007$	$F_{1,50} = 2.29$; $P = 0.14$	$F_{1,65.2} = 1.94$; $P = 0.17$	$F_{1,51.8} = 21.6$; $P < 0.0001$
Year*Clutch No.	NA	NA	NA	$F_{6,51.7} = 0.26$; $P = 0.95$	$F_{6,36.2} = 1.2$; $P = 0.35$
Year* CL	$F_{6,51} = 0.42$; $P = 0.86$	$F_{6,47} = 2.06$; $P = 0.08$	$F_{6,50} = 2.23$; $P = 0.06$	$F_{6,57.1} = 1.23$; $P = 0.30$	$F_{6,52.0} = 0.47$; $P = 0.83$
CL*Clutch No.	NA	NA	NA	$F_{1,65.1} = 0.14$; $P = 0.71$	$F_{1,50.0} = 0.63$; $P = 0.43$
Year*Clutch No.* CL	NA	NA	NA	$F_{6,57.3} = 0.25$; $P = 0.96$	$F_{6,37.9} = 0.20$; $P = 0.98$

Figure 6: Mean egg production per female significantly differed among years in a population of *Gopherus agassizii* inhabiting a wind energy facility in Riverside County, California. Years not connected by same letter are significantly different.

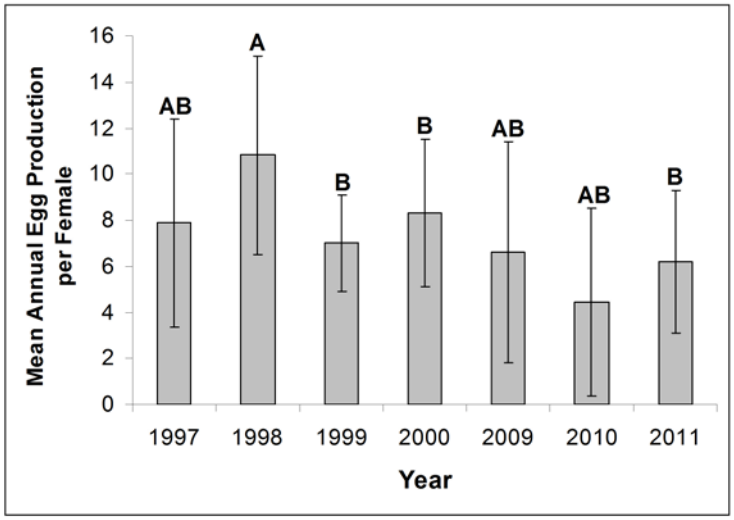
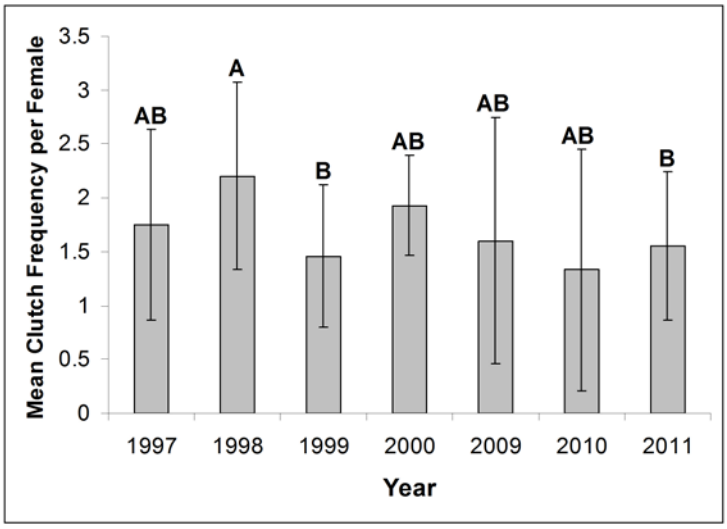


Figure 7: Mean clutch frequency per female significantly differed among years in a population of *Gopherus agassizii* inhabiting a wind energy facility in Riverside County, California. Years not connected by same letter are significantly different.



3.2.3 Clutch Size

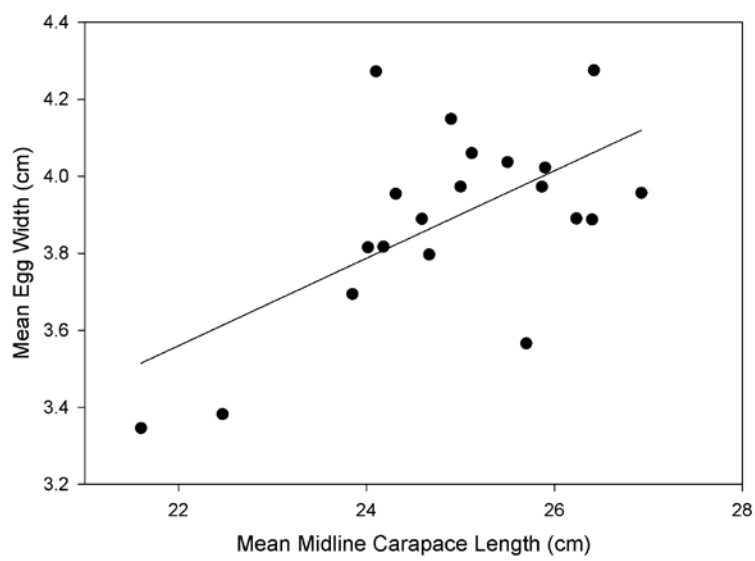
Mean clutch size varied among the years and ranged from 3.8 – 5.6 eggs/clutch (Table 2). Tortoises produced 3rd clutches in five out of seven years (71.4 percent). However in 1998, 4 individuals produced a 3rd clutch. Third clutches only contributed to 4.6 percent of the overall egg production. First clutches accounted for 51.1 percent and 2nd clutches accounted for 44.3

percent of total egg production. Overall, clutch size did not differ significantly between years (ANCOVA: $F_{(6, 51.6)} = 1.46$, $P = 0.21$) or between 1st ($\bar{x} = 4.25$, SD = 0.33) and 2nd ($\bar{x} = 4.67$, SD = 0.68) clutches (ANCOVA: $F_{(1, 52.8)} = 1.36$, $P = 0.25$). The interaction terms were not significant (Table 3).

3.2.4 Maternal Body Size Effects

Maternal body size (CL) did not influence any reproductive variable measured in this study with the exception of mean annual egg production (ANCOVA: $F_{(1,47)} = 7.92$, $P = 0.007$). Maternal body size did not influence clutch frequency (ANCOVA: $F_{(1,50)} = 2.29$, $P = 0.14$) or date of 1st clutch (ANCOVA: $F_{(1, 51)} = 2.30$, $P = 0.14$). There was not a significant relationship between clutch size and maternal body size ($F_{(1, 65.2)} = 1.94$, $P = 0.17$). There was a positive maternal influence on egg width (ANCOVA: $F_{(1,51.8)} = 21.6$, $P < 0.0001$) as shown in Figure 8.

Figure 8: Relationship between female Agassiz's desert tortoise carapace length and mean egg width.



3.2.5 Egg Size

For all years, mean egg width was 38.9 mm (SD = 2.4) and individual eggs ranged from 31.0 – 45.0 mm. Egg widths were not significantly different between years (ANCOVA: $F_{(6,50.5)} = 1.2$, $P = 0.34$) or between 1st ($\bar{x} = 39.5$ mm, SD = 2.5) and 2nd ($\bar{x} = 39.2$ mm, SD = 2.0) clutches (ANCOVA: $F_{(1,38.0)} = 3.7$, $P = 0.06$). Similarly, egg width did not significantly differ between 1st and 2nd clutches among the years (ANCOVA: $F_{(6,36.2)} = 1.2$, $P = 0.35$; Table 4). The interaction terms were not significant (Table 3).

Table 4: Mean egg width (mm) and standard deviation for 7 years of reproductive data from a population of *Gopherus agassizii* inhabiting utility-scale renewable energy facility in Southern California.

	Clutch			
Year	1st	2nd	3rd	Overall
1997	38.2±2.8	38.7±1.2	36.6	38.3±2.2
1998	39.2±2.2	38.9±2.0	37.5±2.3	38.8±2.1
1999	39.6±2.7	39.9±1.3	NA	39.7±2.2
2000	39.0±2.7	38.1±2.3	32.1	38.6±2.4
2009	38.3±3.6	39.1±4.1	40.9	38.9±3.3
2010	38.2±2.4	38.3±2.5	36.92	38.1±2.2
2011	39.1±3.6	39.6±2.4	NA	39.3±3.1

CHAPTER 4: Discussion[3]

As noted by Gibbons (1990) and others (Averill-Murray et al., 2002) it is difficult, or impossible, to identify clear ecological patterns from one- or two-year studies of an organism that may live for over half a century (Germano, 1992; Germano et al., 2002). Longer-term studies like ours spanning 14 years provide an opportunity to begin to assess demographic parameters in desert tortoises. However, short-term studies of desert tortoises that are coincident with major demographic perturbations can provide important insights (Peterson, 1994; Longshore et al., 2003; Esque et al., 2010) as well. It is also important to conduct desert tortoise surveys during years when rainfall is adequate to cause germination of annual food plants that cause tortoises to emerge from their burrows to forage and be detected. Failure to do so will result in underestimates of population size (Freilich et al., 2000; Inman et al., 2009). Germination occurred every year during our study, and tortoises were detectable even though Program Capture noted a significant effect of time (year) on capture probability. Differences in capture probability are not unusual when sampling desert tortoises due to the effects of periodic drought (Freilich et al., 2000). Comparisons of population size structure over time were not significantly different, which suggests that our sampling efforts were effective throughout the study and tortoises were detectable.

4.1 Growth, Demography, Survivorship, and Population Size Estimation

4.1.1 Growth

According to Curtin et al. (2009) growth rates differ between *G. agassizii* in the western Mojave Desert and *G. morafkai* in the Sonoran Desert. Tortoises grow faster in the former and slower in the latter. In addition, females reach sexual maturity earlier (17-19 years) vs. 22-26 years, respectively. The differences were attributed to climatic differences between the regions and the effects of natural selection on life-history traits. Germano (1994) generated growth parameters for populations in four desert regions within the range of the tortoises (western Mojave, eastern Mojave, Sonoran and Sinaloan [the latter two now assignable to *G. morafkai* and perhaps another undescribed species; Murphy et al., 2011]) using the Richards growth model but did not differentiate between males and females. Our asymptotic parameter estimate for males is far greater than for any population he reviewed, including the closest geographically (Western Mojave). Our data on growth in females are limited to a small range of body sizes in comparison to males, which likely affected our parameter estimates and caused the poor fit for female data.

There are four potential reasons for the disparity we observed in male growth rates relative to Germano's analyses. First, it is possible that males at our site reach body sizes larger than any other reported for the species, perhaps due to higher productivity at Mesa relative to other sites.

[3] Excerpted largely from Lovich et al. (2011a)

The largest tortoises at our site are substantially larger than in many other populations (Ernst and Lovich, 2009). Second, it is possible that there are differences in how our growth models were parameterized although the von Bertalanffy equation is part of the Richards family of growth curves (Richards, 1959). Third, Germano (1994) combined data for the sexes in his models while we ran separate analyses further complicating direct comparison of parameters. Our estimates of the growth parameter *k* were substantially less than those of Germano (1994) suggesting that growth rates were slower than other populations despite the adult size advantage and high site productivity we observed. The high degree of sexual size dimorphism we observed may be related to slower growth as shown in other tortoise species (Mushinsky et al., 1994). Fourth, differences in growth rates could be attributed to disparate mean hatchling sizes but such was not the case.

Estimates of minimum size at maturity vary geographically as reviewed by Ernst and Lovich (2009) and range from about 176–220 mm at ages of about 14.4–20.0 years in California. Our smallest egg-producing female was near the top of this range at 221 mm but we could not reliably estimate her age with our growth equation (Figure 3). Her CL is essentially the same as the minimum size of maturity (220 mm) for female *G. morafkai* in the Sonoran Desert (Germano et al. 2002). Minimum sizes and ages of maturity are more difficult to determine for male turtles. Germano (1994) suggested that mean age of maturity in desert tortoises (both *G. agassizii* and *G. morafkai*) occurred between 14.4–15.7 years in the United States corresponding to 184 and 193 mm based on our growth equation for males. This closely approximates the size of 200 mm at which secondary sexual characteristics appeared in two male tortoises at our site during the course of the study. It should be noted that it is difficult to determine functional maturity of male turtles without evidence of motile sperm (Gibbons and Lovich, 1990) and successful mating (Kaufmann, 1992).

Like other turtle species (Iverson, 1991), *G. agassizii* possesses size-specific survivorship rates, where larger sizes experience higher survivorships than smaller individuals (Turner et al., 1987) and impediment of growth could alter population demography. Other than increasing survivorship rates, larger sizes of females generally correlate with increases in clutch size (Turner et al., 1986; Mueller et al., 1998; Wallis et al., 1999; McLuckie and Fridell, 2002), clutch frequency (Turner et al., 1986; Wallis et al., 1999; McLuckie and Fridell, 2002), and egg size (Wallis et al., 1999; Averill–Murray, 2002 [for *G. morafkai*]; McLuckie and Fridell, 2002) in *G. agassizii*. Because our growth rate parameter *k* is substantially lower than that of Germano (1994), disturbances within the ecosystem may have affected growth rate of males with the potential for adverse effects on the vital rates of the population.

4.1.2 Demography and Population Size Estimation

Throughout the "Mojave" portion of desert tortoise range, estimated adult population densities range from 1.2–28.1 individuals/km^2 (U.S. Fish and Wildlife Service, 2011) although densities of only 0.4 adults/km^2 have been reported elsewhere in the Mojave (Keith and Berry, 2008). In the Sonoran Desert, population densities of *G. morafkai* range from 5.7–57.7 adults/km^2 (Averill-Murray et al., 2002). A western Sonoran Desert plot at Joshua Tree National Park close to our study site had an estimated 25.9 *G. agassizii*/km^2 (Freilich et al., 2000). Our estimate fits within

the range of variation reported for desert tortoise species. Similar to our population, adult sex ratios are typically balanced throughout the Sonoran and Mojave Deserts with only a few exceptions (see Berry, 1976; Averill-Murray et al., 2002). However adult sex ratios of turtle populations (Lovich and Gibbons, 1990), including *G. agassizii* (Nussear et al., 2008) vary according to several factors so further speculation is precluded without additional data and analyses.

The Mesa population was dominated by adults and larger individuals and did not differ between size data collected in 1992 and the period 1997–2010. Adapting the stage classification of Berry (1976), our population had 73.5 percent adults (>215 mm), 4.4 percent sub-adults (171-214 mm), 4.4 percent juveniles (101-170 mm), 5.9 percent very young (61-100 mm), and 11.8 percent hatchlings (40-60 mm). In comparison to the four populations (two from California, one from Nevada and one from Utah) reported by Berry (1976), our population had considerably more adults and hatchlings than her sites where she reported 42-58 percent adults and 1-2 percent hatchlings. Caution is advised when using size alone as an indicator of population trends in turtles (Bury et al., 2010). Detailed data on age are needed due to differences in rates of growth between populations.

4.1.3 Survivorship

Our estimated annual survivorship rate of 91.6 percent (confidence interval = 90.5–93.5 percent) was based only on adult females and therefore may actually be on the low end since females can experience higher mortality than males (Esque et al., 2010). This value is almost identical to the value of about 90 percent reported by Freilich et al. (2000) for a nearby western Sonoran Desert population of *G. agassizii* at Joshua Tree National Park that included both sexes. Regardless of a lack of survivorship data for males, our annual survivorship estimates are within the range reported for natural populations of desert tortoises (reviewed by Ernst and Lovich, 2009). Given high annual survivorship and recapture rates over 14 years at Mesa, there is no evidence that the adult population has declined appreciably since 1997.

However, it is important to note that although survivorship is high, the mortality of the single adult female desert tortoise we observed could have disproportionate impacts to the population. Long-lived species such as the desert tortoise are especially sensitive to demographic perturbations caused by unnatural mortality (Congdon et al., 1993; see also Rowe et al., 2007), especially deaths to females (Doak et al., 1994), even though changes in population size or structure and growth may not be detectable for a long period of time (Mortimer, 1995; but see Germano and Joyner, 1989). Populations of long-lived vertebrates often give the perception of remaining static for an extended period of time, even with increased mortality (Mortimer, 1995).

The high survivorship we observed is surprising for two reasons. First, our population is located in a greatly-altered, industrial landscape. Desert tortoises have been traditionally viewed as susceptible to human perturbations (U.S. Fish and Wildlife Service, 1994). Second, populations elsewhere in the listed portion of the range of the desert tortoise populations experienced significant mortality rates in the recent past, especially in 2008, and have declined considerably (Esque et al., 2010). In their review, Esque et al. (2010) reported mortality rates of

up to 43.5 percent at nine study sites in California and Nevada in both Mojave and Sonoran Desert locations. At one site in the Mojave Desert (Fort Irwin National Training Center), 20.7 percent of resident, 24.9 percent of translocated and 18.7 percent of control tortoises died from March–December, 2008 due to increased predation by coyotes (*Canis latrans*), something we did not observe at Mesa despite the presence of that predator. From 1997 to 2003, Berry et al. (2006) observed annual death rates for subadult and adult desert tortoises of 1.9–95.2 percent based on 21 study plots at the Fort Irwin National Training Center in the central Mojave Desert of California. Deaths from human sources were highly correlated with surface disturbances, proximity to offices and paved roads.

Early evidence for desert tortoise population declines was controversial, largely due to a perceived lack of peer review and controversy regarding sampling techniques (Bury and Corn, 1995). Significant population declines (measured by mark-recapture and detection of carcasses of dead tortoises) were reported for several desert tortoise populations in relatively undisturbed areas from about 1980–1990 (Berry and Medica, 1995), where declines ranged from 30–90 percent especially in west Mojave populations.

A major unanswered question is why the tortoise population at Mesa exhibits such high survivorship while most other populations in California are experiencing declines. It is well established that desert tortoise physiological condition (Henen et al,. 1998; Peterson, 1996) is closely linked to climate via rainfall and that drought can cause substantial mortality in some populations (Peterson, 1994; Longshore et al., 2003; Esque et al., 2010). Drought may even play a role in disease resistance of desert tortoises (Lederle et al., 1997). Mesa is located at the western edge of the Sonoran Desert ecosystem next to the influence of wetter, more coastal ecosystems. As a result, rainfall, even in drought years, is sufficient to produce germination of food plants (Lovich et al., 1999; Lovich and Daniels, 2000), unlike other locations farther into the interior of the desert. This may translate into higher survivorship of tortoises at Mesa through increased physiological condition or disease resistance.

A second factor that may contribute to high survivorship is the protected status of the study site (Lovich and Daniels, 2000). Berry and Medica (1995) attributed the declines of their populations to human activities (illegal collecting, vandalism, trampling by livestock, vehicle strikes), disease, and predation by common ravens. They concluded that tortoise populations in "*…relatively undisturbed and remote areas with little vehicular access and low human visitation generally were stable, or exhibited lower rates of decline…*" relative to those in areas characterized by the opposite conditions. Berry et al. (2006) observed that the presence of infectious disease in tortoise populations was inversely correlated with distance from human structures.

Mesa is a highly disturbed site but has limited access to humans. To protect the expensive infrastructure required to produce wind energy, public access is restricted by fences and gates. There is limited access only to hikers on the Pacific Crest Trail and maintenance workers. Therefore, some human activities are dramatically decreased at Mesa. It is also possible that the wind turbines depress raven populations, a source of mortality for juvenile desert tortoises (Kristan and Boarman, 2003) at the site but additional research is required to confirm that hypothesis. Because human activities and subsidized predators are correlated with declines of

desert tortoises (Berry and Medica, 1995; Esque et al., 2010), the level of protection afforded Mesa tortoises may be responsible for their high survivorship. However, not all human activity is detrimental to sensitive species and some forms may actually reduce predator activity and thus predation (Leighton et al., 2010).

4.2 Reproductive Ecology

The reproductive characteristics of our population of *Gopherus agassizzi* were variable among years but consistently comparable to or greater than values reported in other studies, which led to some incongruence between our results and other studies. Wallis et al. (1999) reported that variation in annual egg production was a function of clutch size and not clutch frequency. However, our analyses showed that annual egg production was more influenced by variation in clutch frequency than clutch size. For example, clutch frequency significantly differed among years, but clutch size remains fairly constant and did not significantly differ among years or by clutch number. The incongruence between Wallis et al. (1999) and our result was due to the frequency of 3rd clutches at Mesa. In general, 3rd clutches are uncommon under natural conditions (Ernst and Lovich, 2009). However, Mesa produces an unusually high rate of 3rd clutches. For example, Mesa has produced a 3rd clutch in five out of seven years (71.4 percent) when females were monitored; and in the El Nino year, about one-third of monitored females at Mesa produced a 3rd clutches (Lovich et al., 1999). The only other published study to report a 3rd clutch was Turner et al. (1986), where they reported a single 3rd clutch in 1983 and 1985.

The reproductive characteristics of the population of *Gopherus agassizii* at Mesa are, in most years, comparable to reproductive characteristic of other published literature (Table 5). However during an El Niño year (i.e., 1998) with 217 mm of winter precipitation, reproductive output at Mesa was exceptionally high in comparison with these other studies (Table 2). Although others have suggested an asymptotic relationship between winter annual biomass and precipitation after precipitation exceeds 100 mm (Turner and Randall, 1989), during this El Niño year Mesa's annual clutch frequency (x =2.20, SD = 0.87) and annual egg production (x = 10.82, SD = 4.38) were the highest ever reported in a *G. agassizii* population (Table 2). Even in a non-El Niño (i.e., 2000) with only 54.2 mm of winter precipitation, Mesa recorded an annual clutch frequency (x = 1.93, SD = 0.46) and annual egg production (x = 8.33, SD = 3.24) that was greater than any other previous study (Table 2). In comparison, a population of *G. agassizzii* at Goffs, California reported a similar, but slightly lower, annual clutch frequency of 1.89 clutches/female and annual egg production of 7.79 eggs/female with double (120 mm) the of winter precipitation (Turner et al., 1986). Therefore, the productive potential (i.e., fecundity) of this *G. agassizii* population at Mesa is usually higher than most other populations.

Table 5: A comparison between reproductive characteristics reported in this paper and for *Gopherus agassizii* throughout its range. Values marked with an asterisk were calculated from Tables 2-4.

	This study	Wallis et al. (1999)	McLuckie and Fridell (2002)	Turner et al. (1984)	Turner et al. (1986)	Averill-Murray (2002)	Rostal et al. (1994)	Mueller et al. (1998)
Location	CA	CA	UT	CA	CA	AZ	NV	NV
% of Females Reproducing	67.7 - 100%	75 - 100 %	66.70%	80 - 86.7%	95.7 - 100%*	36.4-80%	NA	NA
Clutch frequency	1.33 - 2.20	1.67 - 1.76	1.33±0.14	1.10 - 1.60	1.57 - 1.89	0.36 - 0.80	NA	1.5
Clutch size (eggs)								
1st	3.8 - 4.8	3.9-4.4	5.2±0.47	NA	4.1 - 4.8	3.8 - 5.7	5.1	5.1 ±0.3
2nd	3.8 - 5.6	4.0-4.7	5.5±1.55	NA	4.25 - 5.57	NA	3.7	4.8±0.4
3rd	1.0 - 5	NA	NA	NA	2 - 6	NA	NA	NA
Eggs per Female	4.44 - 10.82	7.0 - 7.3	7.0±1.16	NA	6.6 - 9.0*	NA	NA	6.7 - 7.7
Egg width (mm)	32.1 - 39.9	33.8 - 38.2	37.2±0.26	NA	NA	34.9 - 36.2	NA	NA

Similar to other chelonians (Ernst and Lovich, 2009), most reproductive studies on *Gopherus agassizii* have shown evidence for maternal influences (i.e., body size) on reproductive traits. For example, clutch size (Turner et al., 1986; Mueller et al., 1998; Wallis et al., 1999; McLuckie and Fridell, 2002), clutch frequency (Turner et al., 1986; Wallis et al., 1999; McLuckie and Fridell, 2002), and annual egg production (Mueller et al., 1998; Wallis et al., 1999; McLuckie and Fridell, 2002) were all influenced by female body size in *G. agassizii*. Although maternal influences, such as body size, on reproductive traits appear to be the norm for *G. agassizii*, we found only support for body size influencing annual egg production at Mesa. The lack of maternal influence on the other reproductive traits at Mesa could be explained by Mesa's high winter precipitation and annual plant biomass, which consistently produces an abundant supply of winter annuals in spring that smaller females can utilize. In studies where maternal body size influences reproductive output, winter annuals have been postulated to be the limiting resources that creates this relationship (Wallis et al., 1999), where smaller females cannot store as much nutrients as larger females for reproduction (Henen, 1997). Alternatively, this

phenomenon could be explained by our sample of females at Mesa, which were predominately larger individuals ($\bar{x}$ = 25.1, SD = 1.5, range = 27 – 21.6) than Wallis et al. (1999). Therefore, our sample may not have encompassed the size range need to detect these trends in other reproductive traits.

Similar to other studies (Wallis et al., 1999; Averill–Murray, 2002; McLuckie and Fridell, 2002), maternal body size influenced egg dimensions. For example, several studies (Wallis et al., 1999; Averill–Murray, 2002; McLuckie and Fridell, 2002), including this study, found a positive relationship with egg width (Figure 8), where larger females produce wider eggs. Also, incongruent results between other studies in the literature are reported for the relationship between clutch size and egg width for *G. agassizii*. While Averill-Murray (2002) found no relationship, McLuckie and Fridell (2002) reported a positive relationship. Consistent with Averill-Murray (2002), we found no relationship between clutch size and egg width.

Egg dimensions (i.e., width and length) at Mesa were greater than dimensions reported in other studies. For example, mean egg widths for *G. agassizii* range from 33.8 – 38.2 mm (Wallis et al., 1999; Averill-Murray. 2002; McLuckie and Fridell, 2002) throughout their distribution; while at Mesa, mean egg widths were slightly greater at 38.5 mm (SD = 2.5). In 1999 at Mesa, mean egg widths were the greatest (x = 39.7 mm, SD = 2.2) ever reported for a population of *G. agassizii*. The larger egg widths at Mesa compared to other studies could be explained by the reliable and often high winter precipitation and annual plant biomass in the spring, which provides surplus energy for females to consistently produce larger eggs. Additionally, there appears not to be a tradeoff between egg size and annual egg production at Mesa. In general, most turtles are expected to produce more eggs of the same size when resources are abundant (Lovich et al., 2012, Naimi et al., 2012). Because Mesa is a highly productivity site in terms of plant biomass, the population of *G. agassizii* appears to annually produce more and larger eggs relative to other sites. However, the larger eggs did not equate to larger offspring (Ennen et al., 2012; Lovich et al., unpubl. data), as hatchling size was similar to other studies.

The results of this study suggest that the long–term reproductive characteristics from this population of *Gopherus agassizii* have not been adversely affected by the USRE wind farm when compared to other studies. Interestingly, this population is one of the most productive and fecund when compared to other *G. agassizii* populations throughout the range. These findings are in stark contrast with conventional dogma that populations of *G. agassizii* are sensitive to any anthropogenic perturbation (U.S. Fish and Wildlife Service, 1994). However, this harmonious coexistence between USRE and *G. agassizii* may not be applicable to other areas throughout the desert southwest inhabited by this species. Besides anthropogenic perturbations of a USRE, Mesa is an unusual site, in general, for *G. agassizii*. The site occupies the western extent of the species' range in the Mojave Desert and usually receives over 11 cm of winter (October – March) precipitation annually (Longpré and Hereford, 1998), which in turn consistently produces an abundance of winter annuals that supports the productivity at the site. Therefore in areas with less consistent precipitation, there potentially could be impacts from USRE developments on *G. agassizii* reproduction. If anything, this study highlights the fact that we know little about the effects of USRE development and operation on terrestrial wildlife like desert tortoises. Although the long-term reproductive output of tortoises at Mesa appears not to

be adversely impacted when compared to other studies, we have no knowledge what the productivity of this site was before the installation of the USRE. Therefore, this study only shows that reproduction still occurs long after installation of a USRE facility.

CHAPTER 5: Conclusions[4]

Determining if wind energy development affects growth, demography, survivorship and reproductive ecology in desert tortoises requires a two-step process. First is identification of significant differences in those parameters when compared to tortoise populations living in comparable undisturbed habitats. The second step, more difficult to demonstrate, is showing a cause-effect relationship.

Fortunately, the desert tortoise is one of the best-studied turtles in the United States (Bury and Germano, 1994; Ernst and Lovich, 2009) and comparative data are available for other populations to place ours in context with those living outside the industrial landscape that characterizes the Mesa wind energy facility. Our analysis indicates little difference in the density, age of maturity, population size structure, and sex ratio of tortoises at Mesa relative to the range of variation reported for populations in more natural environments. The two major differences our analysis detected were in survivorship and reproductive output. Our estimate for survivorship is within the lower portion of the range reported in the literature for natural populations (Ernst and Lovich, 2009) but much higher than other locations where declines have been reported (Esque et al., 2010). The high clutch frequency and annual egg production at Mesa are most likely attributable to the annually-reliable rainfall at the site relative to tortoise populations farther into the desert. Our data for growth are not as conclusive but they do suggest a slower growth rate of males relative to other populations. This is paradoxical given the high primary productivity at Mesa.

The lack of carefully controlled before-and-after studies of the effects of energy development on wildlife (Kuvlesky et al., 2007) is a significant impediment to our understanding of how best to manage renewable energy development. Even this study is correlative in that we have no data on the demography of the Mesa tortoise population prior to construction of the wind energy facility in 1983. Still, data collected over a long time span like this study provide an opportunity to assess the impact of wind energy development on a tortoise population over almost one generation of this long-lived species.

While activities and construction associated with wind energy generation on site are known to have contributed directly to habitat destruction and mortality of tortoises since 1997, as documented here and elsewhere (Lovich et al., 2011a, c), the population overall appears to be stable. In addition, tortoises appear to have adjusted their behavior to accommodate anthropogenic features in their landscape (Lovich and Daniels, 2000), they are reproducing (Lovich et al., 1999), hatchlings are emerging from nests and surviving (Lovich, unpubl. data), and annual adult survivorship is relatively high as shown in this study. However, the apparent stability of this particular population during the period of study should not be considered as proof that all tortoise populations are able to live in harmony with USRED. Site selection is a

[4] Excerpted with modifications from Lovich et al. (2011a)

critical factor in minimizing the negative effects of USRED on wildlife. At Mesa, the project proponents unknowingly selected a highly productive site from the standpoint of desert tortoise food plants (Lovich et al., 1999). This productivity may provide a hedge that offsets the negative effects of habitat destruction associated with construction and operation of the facility. The effects of similar energy developments in drier less productive tortoise habitats are currently unknown and urgently need additional study.

5.1 Mitigating Impacts of Wind Farm Development in Desert Tortoise Habitat Based on Science

5.1.1 Site Selection and Design

In the case of Agassiz's desert tortoises living at Mesa, the site was selected with little consideration of the ecological or demographic status of the local population (Lovich and Daniels, 2000). However, by serendipity, the developers selected what appears to be one of the most productive habitats for tortoise food plants in the range of the species. As a result, reproductive output is very high compared to nearby less-productive sites (Lovich et al., 1999) and the tortoise population appears to be able to survive at the facility, almost 30 years after construction (Lovich et al., 2011a). In this example, site selection was not a strategic decision. Leaving site selection to chance is risky at best. It is important to note that I do not advocate placing renewable energy facilities in productive high quality wildlife habitats based on this example.

5.1.2 Roads, Vehicles and Culverts[5]

California has a goal of increasing renewable energy-generated electricity from 11 percent currently, to 33 percent by 2020 (California Energy Commission 2007). Large networks of roads and drainage culverts will be associated with these renewable energy developments that degrade wildlife habitat (Kuvlesky et al., 2007). Roads are known to be barriers to wildlife movements and sources of significant mortality (Ashley and Robinson, 1996; Forman and Alexander, 1998; Andrews et al., 2008; Hagood and Bartles, 2008), especially for reptiles (Dodd, 1989; Rosen and Lowe, 1994). Turtles, including the desert tortoise (*Gopherus agassizii*; Von Seckendorff Hoff and Marlow, 2002), are especially vulnerable to road mortality because of their inability to cross roadways quickly (Fowle, 1996). Additionally, females of many species cross roadways while searching for nest sites (Haxton, 2000; Gibbs and Steen, 2005; Steen et al., 2006) and have an affinity for nesting on road shoulders (Aresco, 2005). As a result, road mortality is a significant factor contributing to the decline of turtles (Gibbs and Shriver, 2002), in part due to disproportionate mortality of females (Steen and Gibbs, 2004).

Numerous methods have been proposed to mitigate the negative effects of roads including wildlife overpasses, underpasses and fences (Forman and Alexander, 1998). Culverts, designed primarily as conduits for streams and stormwater runoff, are ubiquitous features of most roadways that can function secondarily as wildlife passages for some species by increasing the "permeability" of the road and reducing mortality (Andrews et al., 2008; Yanes et al., 1995).

[5] Excerpted with modifications from Lovich et al. (2011c)

However, the overall effectiveness of culverts has received little attention (Spellerberg, 1998; Fowle, 1996) despite their potential importance from a conservation perspective. The paucity of before and after mortality studies following the installation of wildlife-crossing structures further complicates an evaluation of their effectiveness (Glista et al., 2009).

During our studies, we observed a negative effect of culverts on the desert tortoise. Based on this observation we reviewed the scant peer-reviewed literature on the use of culverts by turtles (including tortoises), and make recommendations to minimize a largely unrecognized negative effect.

In 2009 a large male tortoise (33.9 cm carapace length) was outfitted with a radio transmitter and tracked at bi-weekly intervals from 22 April-14 July, 2009 and generally monthly thereafter. Starting on 19 May, 2009 the tortoise began using a corrugated steel culvert (about 60 cm in diameter), designed for storm water runoff, as a burrow surrogate. Since the bottom of the culvert was half-filled with sand and sediment it had an entrance that mimicked the half-moon shape of a natural tortoise burrow. The outlet of the culvert was completely buried under eroded sediment and vegetation. The tortoise used this same culvert, and another that was nearby, intermittently until 26 September, 2009. From 25 October, 2009 through 6 February, 2010, the tortoise used the first culvert as a brumation (hibernation for "cold-blooded" organisms) site.

In mid-February, storms brought significant rain to southern California. As a result, large amounts of sediment were carried into the culvert, entombing the brumating tortoise in a wet slurry of sand and silt. Late on March 26, 2010, during our regularly-scheduled monthly visit to the site to collect data, we found the culvert completely filled from top to bottom with moist loamy soil. Although attenuated due to being surrounded by metal, the radio signal clearly indicated the tortoise was buried deep in the culvert. The following morning a total of five people, including three employees from the wind energy facility, began the process of digging with a pick and shovels to remove the overburden from the point where the tortoise was thought to be located based on radio signal strength. The top of the culvert at this point was approximately 0.6 m below the dirt road bed. An oxygen-acetylene torch was then used to cut the top of the culvert away in an area adjacent to the putative location of the tortoise. Removal of a portion of the culvert revealed that sediment filled the entire inside diameter with no visible air space (Figure 9). After removing two more sections from the top of the culvert to allow a person to get inside, more dirt was carefully removed until the rear carapace of the tortoise was visible (Figure 10), fully three m from the point where it entered the culvert.

Figure 9: Excavation of the culvert to rescue a trapped desert tortoise. Notice the partially excavated entrance used by the tortoise in the foreground.

Photo Credit: Jeff Lovich

The animal was completely encased in tightly packed sediment as if set in concrete (Figure 10). Since the tortoise was likely overwintering and inactive during the time the sediment was deposited (Ernst and Lovich, 2009) motor functions were inhibited preventing it from digging out while the slurry accumulated. Careful excavation eventually allowed the tortoise to be freed seven hours after work started. The head was fully retracted inside the shell and the cavity in front of the nose was tightly packed with dirt that had to be scraped away to free the tortoise completely. The eyes of the tortoise appeared cloudy upon removal but otherwise the individual appeared alert and exhibited locomotion and behavior typical of a healthy tortoise. During the following month of April, the tortoise was located several times and appeared normal in all regards including responding to visual stimuli. However, the tortoise was found dead in a nearby burrow 18 days after excavation from the culvert. A necropsy revealed that the tortoise presented with its right eye desiccated and filled with maggots, and some crusting around the nares from possible exudate or dried mud. The shell and limbs were in good condition, but the tortoise had been dead for an undetermined period of time. The plastron was removed by sawing along the bridge of the shell and dissecting the muscles back to expose the organs, which were inspected grossly. The heart had hemorrhaging in the right ventricle and some necrotic areas in the left ventricle. The lungs were firm and consolidated with caudal areas having multi focal coalescing white regions. The colon was full of plant material that was wet and had been recently consumed. No other abnormalities were noted grossly. The likely cause of death was secondary pneumonia caused by being fully immersed in mud. The animal was eating prior to death, again, consistent with normal behavior as noted previously. Although this is the first case of culvert-related mortality documented at our study site during six field seasons spanning 15 years we have seen other tortoises use culverts on several occasions.

Figure 10: Posterior carapace of a desert tortoise trapped in a steel culvert where it was overwintering near Palm Springs, California. A large volume of tightly compacted dirt was removed to expose and extricate the tortoise.

Photo Credit: Jeff Lovich

This situation underscores a previously unrecognized threat that culverts present to desert tortoises and other wildlife that use culverts for shelter or other purposes like nesting. Desert tortoises at our study site have been documented to use culverts and other human structures associated with wind energy development routinely (Lovich and Daniels, 2000). Desert tortoises in other parts of the California desert are known to use culverts as passages under roads (Boarman, 1995; Boarman and Sazaki, 1996), sometimes spending the night inside (Boarman et al., 1998b). When used in conjunction with culverts, barrier fences effectively reduce mortality and facilitate movements under the busy roadways for desert tortoises (Boarman et al., 1997), Hermann's tortoise (*Testudo hermanni*; Guyot, 1995) and other species of reptiles and amphibians (Dodd et al., 2004). However, in some instances desert tortoises may not be able to excavate themselves if entombed and will experience physiological stress that results in a slow death. Although most studies on entombment of tortoises (*Gopherus polyphemus*—Mendonça et al., 2007; Landers and Buckner, 1981; Diemer and Moler, 1982) have shown little negative effects, some have reported mortalities (Wester, 2004; Burke, 1989). The reported mortalities could be a result of hypoxia and hypercarbia, especially in clay-laden soils (Ultsch and

Anderson, 1986, 1988). However, the entombment described in this paper is not characteristic of the circumstances described in the previously mentioned studies for *G. polyphemus* (i.e., burrow collapse), where tortoises had air pockets and space immediately around them.

On most currently operating utility-scale renewable energy facilities like our study site, road traffic is limited compared to public highways and roads, where wildlife passages are beneficial and often essential to prevent excess mortality (Rees et al., 2009). However, the beneficial effects of culverts as safe passages for wildlife are tempered by the possibility that they can entrap and potentially kill animals like desert tortoises under some circumstances. This is important because even a slight increase in adult desert tortoise mortality, especially females, is detrimental to populations (Doak et al., 1994). Therefore, species that often use wildlife passages and culverts for an extended period of time (i.e., brumation sites, nesting sites, and refugia) and not in an ephemeral fashion (i.e., as a corridor for dispersal) could be negatively impacted. Female tortoises at our study site frequently nest inside their burrows (23 out of 24 nests in the year 2000: Ennen et al., 2012) so entire clutches could be entombed during spring or summer floods if females nest in culverts. During the excavation of the tortoise we found multiple hatched snake eggs so the nests of other species are affected as well.

We believe that the negative effects of culverts can be largely mitigated by adopting several best management practices. First, utility-scale renewable energy developments and road construction projects could install larger diameter culverts to lessen the possibility of blockage with sedimentation and debris. Erosion is a major problem at wind energy facilities in California due to the presence of compacted roads that create large amounts of runoff during rain storms (Wilshire and Prose, 1987). Various species of reptiles and amphibians are known to respond differently to assorted barrier fence and culvert lengths, heights, diameters, placements and designs (Woltz et al., 2008; Patrick et al., 2010) so preconstruction planning should target the needs of local fauna. The use of larger concrete box culverts or corrugated steel culverts with a diameter of one m or greater should be considered since desert tortoises are known to willingly enter such structures in preference to smaller tunnels (Ruby et al., 1994). Although implementing these recommendations on existing facilities could be a costly process and not feasible in some cases, the alternative would be frequent inspections of smaller culverts to prevent blockage and entrapment. As noted by Glista et al. (2009), preconstruction planning is likely to be more economical than retrofitting existing road networks. Furthermore, excluder devices (e.g., wire mesh, rebar, etc.) on the entrances of smaller culverts could be considered to prevent desert tortoises and other sensitive species from entering culverts and potentially becoming entrapped. However properly designed fencing (Ruby et al., 1994) may be required to prevent blocked culverts from forcing desert tortoises onto the road (Yanes et al., 1995).

Although our account of entrapment may be an isolated example, future road design should consider the effectiveness of culverts for facilitating safe passage of wildlife and existing structures should be evaluated for their efficacy as both wildlife conduits and refugia.

5.1.3 Staff Awareness

During my research I noted that maintenance staff at the site consistently attempted to accommodate the needs of both tortoises and tortoise researchers. One worker told me that

"*Tortoises always have the right of way*." with respect to site operations. Another installed a warning sign along the road next to a tortoise burrow. The level of interest and awareness exhibited by the staff may partially explain the high tortoise survivorship observed at Mesa. Training programs that enhance awareness of sensitive species and their needs may contribute to mitigation of negative impacts of energy development to wildlife like the tortoise. Restricted public access to the site (except via the Pacific Crest Trail) may also enhance wildlife protection (Lovich and Daniels, 2000).

5.1.4[6] Fire Prevention and Suppression

Fire has been identified as a significant threat to the recovery of Agassiz's desert tortoise (US Fish and Wildlife Service, 2011). We confirmed the negative effects of fire through observations of direct mortality and fire scarring of surviving tortoises at our study site following a massive wildland fire that occurred in 1995, and smaller subsequent fires.

Fire was historically uncommon in the Mojave Desert of North America (Brooks, 1999, 2002) but is increasing in both frequency and size as a result of the combination of increases in flammable invasive plants, mainly grasses (Brown and Minnich, 1986), and anthropogenic ignitions (Brooks, 1999, Brooks and Esque, 2002, Brooks and Matchett, 2006). Therefore, native species of this region, including the desert tortoise, are very sensitive to fire disturbances (Brooks and Esque, 2002, Esque et al,. 2003, US Fish and Wildlife Service, 2011).

The effects of fire on desert tortoise populations (including Morafka's desert tortoise, *G. morafkai*) were reviewed by Esque et al. (2002) and Schwalbe et al. (2002) and included three possible outcomes. The first is direct mortality caused by exposure to flames or smoke resulting in death of the individual during or sometime after the fire. Fire mortality may dramatically affect the size structure and survivorship of tortoise populations as shown by Stubbs et al. (1985) and Hailey (2000) for the tortoise *Testudo hermanni* in Greece, and Lambert et al. (1998) for the tortoise *Stigmochelys (Geochelone) pardalis* in Africa. The latter study suggests that the effects may persist for decades. Desert tortoises are particularly vulnerable to fire when they are active outside their burrows. Tortoise burrows provide low temperature refugia during fires (Gibson et al., 1990) that may prevent mortality. The second effect of fire on desert tortoises is the alteration of habitat through loss of vegetative cover that may change the above ground thermal environment to the detriment of tortoises. As ectotherms, desert tortoises must resort to the shade of nearby plants or burrows when environmental temperatures exceed their tolerance (Zimmerman et al., 1994). If shade or burrows are not available they will die when body temperature reaches 43.1 °C (Hutchison et al., 1966). Third, fires may indirectly affect habitat quality by altering the future availability or nutritional value of desert tortoise food plants for years following the conflagration. This is especially true when native perennial plants and annual forbs are replaced by nutritionally inferior grasses (Nagy et al., 1998), such as the exotic species Mediterranean split grass (*Schismus* spp.), buffelgrass (*Pennisetum ciliare* L.), and red brome (*Bromus madritensis* subsp. *rubens* L.), that proliferate following fire (Brooks, 1999, Brooks et al., 2004, D'Antonio and Vitousek, 1992, Schwalbe et al., 2002).

[6] Excerpted with modifications from Lovich et al. (2011b).

Although Esque et al. (2002) quantified the effects of direct mortality on desert tortoise populations in the Sonoran Desert following wildfires, the only published study assessing longer-term post-fire effects on the species was conducted at Mesa (Lovich et al., 2011b). They found few changes in activity area use or annual reproductive output during the lengthy monitoring period. Despite changes in plant composition, conditions at this site appear to be suitable for survival of tortoises following a major fire. High productivity at the site may buffer tortoises from the adverse impacts of fire if they are not killed outright. Tortoise populations at less productive desert sites may not have adequate resources to sustain normal activity areas, reproductive output, and body condition following fire.

The actual long-term effects of the 1995 fire on the tortoise population we studied will never be fully understood due to the fact that data are not available for the study site under pre-fire conditions. As such, it is possible that the effects Lovich et al. (2011b) hypothesized may have occurred in the short interval between the fire and the beginning of our study less than two years later. Carefully designed before-and-after studies are needed on the effects of fire on the desert tortoise, but these will be difficult or impossible to conduct outside of serendipity due to the threatened status of tortoises. Until then, *post hoc* long-term studies like ours and others (Sanz-Aguilar et al., 2011) provide the best opportunity to understand how tortoises respond to the effects of fire over time. While awaiting additional studies it is prudent to vigorously prevent and suppress wildland fires in tortoise habitat due to the known potential for direct mortality as noted previously by U.S. Fish and Wildlife Service (2011).

5.1.5 Continued Research and Monitoring

As emphasized by Lovich and Ennen (2011, in press), there is a shortage of published scientific literature documenting the effects of solar and wind energy development and operation on terrestrial and aquatic wildlife. Research such as that supported by the California Energy Commission, PIER program is helping to fill that void. In their review of the effects of solar energy development and operation on wildlife in the Desert Southwest, Lovich and Ennen (2011) identified several research deficiencies/questions that are relevant for wind energy (Lovich and Ennen, in press): 1) What are the cumulative effects of large numbers of dispersed vs. concentrated wind energy facilities on non-volant wildlife and their habitat?; 2) What density or design of development maximizes energy benefits while minimizing effects on wildlife?; and 3) Where are the best places to site wind energy farms (Gamboa and Munda, 2007) relative to the needs of wildlife?

In particular, the authors noted a shortage of before-after-control-impact studies (see also Kuvlesky et al., 2007) needed to obtain scientifically-rigorous cause and effect data. Collection of baseline data, prior to site development, followed with a good research and monitoring plan for collecting post-development data are needed to fully assess impacts on wildlife. As aging wind energy facilities are re-operated with more efficient turbines, additional opportunities for collecting before-after-control-impact data will occur if baseline data (prior to reoperation), as presented in this report, are available.

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