Effects of Wind Energy Production on Growth, Demography, and Survivorship of a Desert Tortoise (*Gopherus agassizii*) Population in Southern California with Comparisons to Natural Populations

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Abstract.—We studied a Desert Tortoise (*Gopherus agassizii*) population at a large wind energy generation facility near Palm Springs, California over six field seasons from 1997 to 2010. We compared growth and demographic parameters to populations living in less disturbed areas; as well as populations of the closely-related and newly-described *G. morafkai* elsewhere in the Sonoran Desert of Arizona. We marked 69 individuals of all size classes and estimated a population size of 96 tortoises, or about 15.4/km². Growth rates for males were lower than reported elsewhere, although maximum body size was larger. The smallest female with shelled eggs was 221 mm and males mature at over 200 mm. Mean male size was greater than that of females. The adult sex ratio was not significantly different from unity. Size frequency histograms were similar over time and when compared to most, but not all, *G. morafkai* populations in the Sonoran Desert. For a cohort of adult females, we estimated mortality at 8.4% annually due, in part, to site operations. This value was low in comparison to many other populations during the same time period. Other than possible differences in growth rate of males and the high survivorship of females, there appear to be few differences between this population and those in more natural areas. The high productivity of food plants at the site and its limited public access may contribute to the overall stability of the population. However, the effects of utility-scale renewable energy development on tortoises in other, less productive, areas are unknown. Additional research (especially controlled and replicated before and after studies) is urgently needed to address this deficiency because of forecasted expansion of utility-scale renewable energy development in the future.

Key Words.—demography; Desert Tortoise; growth; renewable energy; survivorship; wind energy

Introduction

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). In a literature review, Andrews (1982) noted that post-natal growth is affected by extrinsic factors such as food and water quality and availability (see also Kozlowski 1992), temperature (especially in the case of ectotherms like reptiles), and the social environment as related to inter- or intra-specific resource competition potentially due to density dependent phenomena (Bjorndal et al. 2000). Others add injuries that slow growth to the list of extrinsic factors (Dunham and Gibbons 1990). Intrinsic factors affecting post-natal growth include sex-specific and genetic factors (Sinervo and Adolph 1989) especially as

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related to incubation temperatures and post-incubation temperatures (Reiber et al. 1999) in organisms with temperature dependent sex determination (Rhen and Lang 1995). While rapid growth may seem to be advantageous in most cases, there are associated costs including increased fluctuating asymmetry, reduced immune capacity, and limited capacity to respond to environmental stress (Arendt 1997).

Extrinsic factors can affect post-natal growth with either positive or negative effects to individuals and populations (Case 1978; Arendt 1997). In particular, environmental perturbations that reduce habitat quality or resource availability may have negative consequences on post-natal growth. For example, habitat disturbance can impede growth causing a delay in sexual maturity (Aresco and Guyer 1999), which then could alter sex ratio (Lovich and Gibbons 1990) and fecundity (Stearns 1976). Likewise, anthropogenically induced thermal stress is known to influence growth rates and age of sexual maturity (Gibbons et al. 1981).

The desert landscape of the southwestern United States, particularly in California, is becoming increasingly altered due to a variety of human activities (Lovich and Bainbridge 1999; Wilshire et al. 2008). Within this region the Desert Tortoise (*Gopherus agassizii*), found north and west of the Colorado River, is protected under the Endangered Species Act (U.S. Fish and Wildlife Service 1994). Population declines have occurred due to the negative effects of off-road vehicles, military training activities, overgrazing, and urban development that altered the desert landscape with adverse effects on population viability (Doak et al. 1994; U.S. Fish and Wildlife Service 1994; Brooks 1995; Bury and Luckenbach 2002; Grandmaison et al. 2010). A rapidly emerging threat to the Desert Tortoise is utility-scale renewable energy development (USRED) where projects occur in tortoise habitat. Existing and planned USRED sites leave large footprints in the desert landscape and result in direct habitat destruction (Pearson 1986) and subsequent erosion problems (Wilshire and Prose 1987) that further degrade habitat and cause wildlife mortality (Lovich et al. 2011). Although recognized as a potential threat to Desert Tortoise populations 25 years ago (Pearson 1986), there is a paucity of literature on the effects of USRED on the tortoise (Lovich and Daniels 2000) and other terrestrial wildlife species (Lovich and Ennen in press). This is surprising because facilities developed for USRED can cause environmental disturbances with the potential to degrade the quality of wildlife habitat and thus affect growth rates and demographic parameters.

We studied a population of Desert Tortoises at a wind energy generation facility in southern California, known locally as the Mesa Wind Farm (MESA), which was permitted for construction and operation in 1983. Because Desert Tortoise populations are often characterized by their growth rate, demography (density, size/age structure, sex ratio), and survivorship (Berry 1986; Germano 1988; Ernst and Lovich 2009), our objective was to estimate these parameters and compare our data to published estimates for other populations, including the closely-related, recently-described *G. morafkai* in the Sonoran Desert of Arizona.

While this paper was in review, we learned that what was long known as *G. agassizii* was split into two species, one west of the Colorado River, *G. agassizii*, and one east of the river, *G. morafkai* (Murphy et al. 2011). The new taxonomy necessitated a change from an intraspecific to interspecific comparison between populations at MESA and those in Arizona. Given that they are relatively recently separated (Lamb et al. 1989) and possibly sister lineages (Robert Murphy, pers. comm.), both occupying the Sonoran Desert ecosystem in mountainous terrain, we believe comparison between the two is still relevant for the purposes of this paper. Our overall hypothesis was that the demographic parameters of interest would differ between our disturbed site and other more natural areas, perhaps due to habitat alteration and the attendant effects of environmental stress given the industrial nature of the MESA energy facility.

MATERIALS AND METHODS

*Study site.—*MESA is located on the extreme western edge of the Sonoran Desert ecosystem in the southeastern foothills of the San Bernardino Mountains near Palm Springs, California (see Lovich and Daniels 2000). 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 consistent 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). MESA has many anthropogenic features including 460 turbines, 51 electrical transformers, and an extensive network of unpaved roads (Lovich and Daniels 2000). Prior to and for a short period after the wind energy facility was in operation, the site was grazed by cattle under permit with the Bureau of Land Management (BLM). Further, several

small to large fires have occurred at the site during the course of our studies, some as a result of facility operations. Overall, much of the landscape is disturbed by overlapping human activities (Lovich and Bainbridge 1999).

Collection.—Prior to initiation of our studies on reproductive ecology (Lovich et al. 1999), one of the authors (GMG) started marking and measuring Desert Tortoises at the site in 1992. Later, we captured tortoises during six field seasons (1997–2000 and 2009–2010), primarily from April-July. On initial capture, we determined sex based on secondary sexual characteristics, and we weighed, measured, and marked individuals. We weighed individuals at each recapture but only recorded body size measurements once or twice during a field season. Body size was 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.

Analysis.—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, 1998). 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 d ($\bar{x} = 167$ d) 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* from three sites (Granite Hills, Eagletail Mountains, and Little Shipp Wash: Fig. 1) elsewhere in the Sonoran Desert of Arizona using Kolmogorov–Smirnov tests. These populations have been monitored every one to five years since 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 by 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.

FIGURE 1. Map showing study sites (red dots) used to compare size frequency distributions. The Sonoran Desert ecoregion boundary (outlined) is from the Level III ecoregions of the continental United States developed by the Environmental Protection Agency (Omernik 1995, 2004). The layer was created in 2010 and denotes areas of general similarity in ecosystems and in the type, quality, and quantity of environmental resources.

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:

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

provided by David J. 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 1,771 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.

RESULTS

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

TABLE 1. Growth parameters and 95% confidence intervals for male and female Desert Tortoises (*Gopherus agassizii*) 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

of determination of 99% for both sexes (Table 1). The growth equation for males is

$$CL = 311.5(1-0.89e^{(-0.054*Age)})$$

and is shown in Fig. 2. 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 in Fig. 2. 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 > 200 mm.

Demography.—Over the six field seasons, 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 about
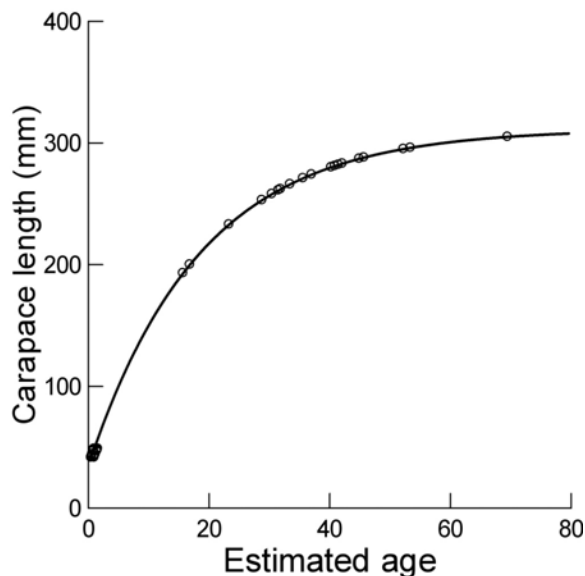

FIGURE 2. Estimated growth curve for male Desert Tortoises (*Gopherus agassizii*) from a wind energy generation facility near Palm Springs, California. Hollow circles designate CL at first capture of all specimens used to estimate the growth curve. The fit is deterministic because age was estimated from our derived growth equation.

11.0 tortoises/km^2. Using all years of data, 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% confidence interval = 80–130) or about 15.4 tortoises/km^2.

All size classes were represented in our sample. Most (72.5%) of the individuals captured were adults (Fig. 3), 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 ($\bar{x}$ = 281.2 mm, SE = 4.8) significantly (F = 34.67, df = 1, P < 0.001) larger than female CL ($\bar{x}$ = 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 (Fig. 3). In contrast to MESA, the Granite Hills population consisted of only 55.0% 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.

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 ($\bar{x}$ = 212 mm, n = 6). A radio-tagged adult female was killed by a vehicle strike in 1997 and a radio-tagged male was entombed in a culvert during winter rains (Lovich et al. 2011). Dead tortoises (not marked during our studies) also 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 raven predation, as evidenced by holes in the top of
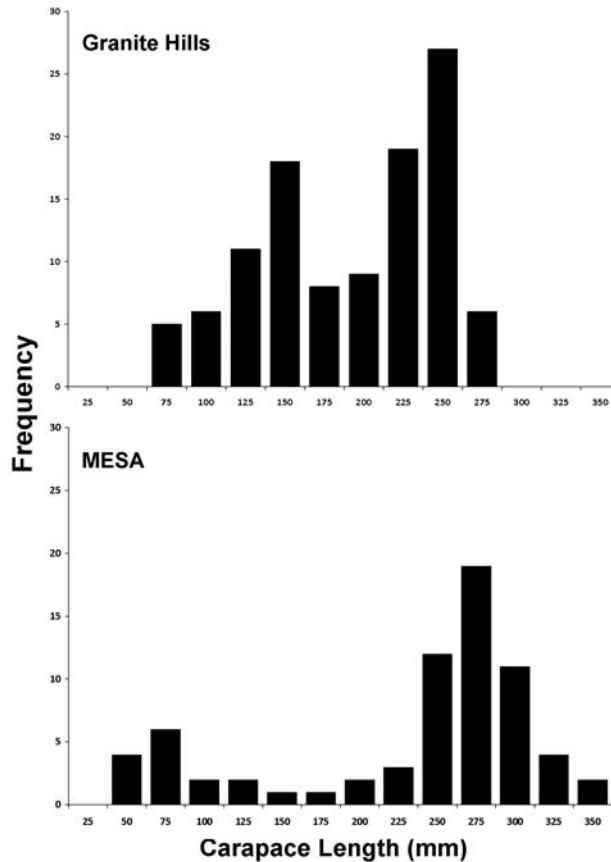
FIGURE 3. Size frequency histograms for Desert Tortoises (*Gopherus agassizii*) near Palm Springs, California (MESA) and Granite Hills, Arizona.

the carapace (e.g., Boarman 2003). The instantaneous mortality rate for the cohort of 11 radio-tagged adult females was 0.084 (95% confidence interval = 0.062–0.123). When converted to an annual survivorship rate, the estimate was approximately 91.6% (95% confidence interval = 90.5–93.5%).

DISCUSSION

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 as well (Peterson 1994; Longshore et al. 2003; Esque et al. 2010). 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.

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. 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 (Fig. 2). 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 individuals experience higher survivorship than smaller individuals 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.

Demography.—From 2001–2005 throughout the Mojave portion of Desert Tortoise range, adult population densities ranged from 0.84–30.11 individuals/km^2 (U.S. Fish and Wildlife Service 2008) 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 the 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% adults (> 215 mm), 4.4% sub-adults (171–214 mm), 4.4% juveniles (101–170 mm), 5.9% very young (61–100 mm), and 11.8% 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% adults and 1–2% 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.

Survivorship.—Our estimated annual survivorship rate of 91.6% (confidence interval = 90.5–93.5%) was based only on adult females and therefore may actually be on the low end because females can experience higher mortality than males (Esque et al. 2010). This value is almost identical to the value of about 90% 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; 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 been 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 study, Esque et al. (2010) reported mortality rates of up to 43.5% 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% of resident, 24.9% of translocated, and 18.7% of control tortoises died from March–December 2008 due to increased predation by coyotes, 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%

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% especially in west Mojave populations.

A major unanswered question is why the tortoise population at MESA exhibits such high survivorship while many 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).

Conclusions.—Determining if wind energy development affects growth, demography, and survivorship 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 direct 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 one major difference our analysis detected was in survivorship. Our estimate is within the range reported in the literature for natural populations (Ernst and Lovich 2009) but much higher than other locations where declines have been reported. Our data for growth are not as conclusive but they do suggest a slower growth rate of males relative to other populations.

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 this growing change agent. 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 14-year span provide an opportunity to assess the impact of wind energy development on a tortoise population over almost one generation for 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. 2011), 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 (Jeff Lovich, unpubl. data), and annual adult survivorship is relatively high as shown in this study. 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 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.

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Errata: A number of minor changes to syntax were made on 14 December 2011.


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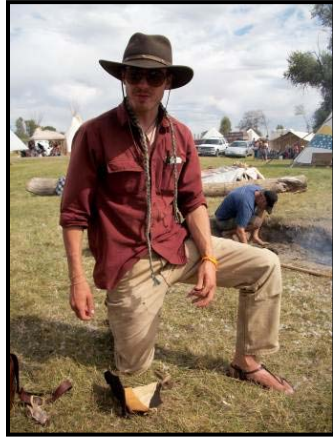
CALEB LOUGHRAN is a Biological Technician affiliated with the USGS Colorado Plateau Research Station in Flagstaff, Arizona, USA. He graduated with a B.S. in Biology from Northern Arizona University in 2009. He is interested in the evolutionary ecology, genetics, and physiology of reptiles, as well as understanding cultural perceptions and phenomena and how they relate to herpetological conservation. He intends to pursue a Master's degree that may allow him to integrate these interests. (Photograph by Dave Wescott)

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The Remaining authors did not provide biographical sketches.