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Turbines and Terrestrial Vertebrates: Variation in Tortoise Survivorship Between a Wind Energy Facility and an Adjacent Undisturbed Wildland Area in the Desert Southwest (USA)

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Abstract With the recent increase in utility-scale wind energy development, researchers have become increasingly concerned how this activity will affect wildlife and their habitat. To understand the potential impacts of wind energy facilities (WEF) post-construction (i.e., operation and maintenance) on wildlife, we compared differences in activity centers and survivorship of Agassiz's desert tortoises (*Gopherus agassizii*) inside or near a WEF to neighboring tortoises living near a wilderness area (NWA) and farther from the WEF. We found that the size of tortoise activity centers varied, but not significantly so, between the WEF (6.25 ± 2.13 ha) and adjacent NWA (4.13 ± 1.23 ha). However, apparent survival did differ significantly between the habitat types: over the 18-year study period apparent annual survival estimates were 0.96 ± 0.01 for WEF tortoises and 0.92 ± 0.02 for tortoises in the NWA. High annual survival suggests that operation and maintenance of the WEF has not caused considerable declines in the adult population over the past two decades. Low traffic volume, enhanced resource availability, and decreased predator populations may influence annual survivorship at this WEF. Further research on these proximate mechanisms and population recruitment would be useful for mitigating and

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managing post-development impacts of utility-scale wind energy on long-lived terrestrial vertebrates.

Keywords Activity center · Desert tortoise · *Gopherus agassizii* · Landscape disturbance · Renewable energy

Introduction

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

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

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

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

To understand the post-construction impacts of industrial WEFs on threatened terrestrial vertebrates (USFWS 1990; USFWS 2011), we used a long-term capture–mark–recapture dataset to examine activity centers and survivorship of a natural population of Agassiz's desert tortoises at a WEF in southern California (USA). We tested two predictions: (1) desert tortoises within or immediately adjacent to the footprint of an operating WEF would have a higher probability of being affected by anthropogenic features and operations, and would therefore have lower estimates of apparent survival in comparison to tortoises near a wilderness area (NWA), and (2) individual activity areas would be smaller within the boundaries of the WEF due to modified habitat (i.e., potentially increased resource

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availability from artificial rain catchments on turbine pads and edge enhancement of vegetation along roads; see Lovich and Daniels 2000).

Materials and Methods

Our study site, known as Mesa, is near Palm Springs in Riverside County, California and located on federal lands (i.e., Bureau of Land Management). Detailed monitoring of tortoise populations has been ongoing at this site since 1997. Mesa is situated on the western edge of the Sonoran desert, with an elevation range of 600–900 m and long-term average winter precipitation of 15.2 cm (range 2.9–44.1 cm) (estimated using WestMap PRISM data; http://www.cefa.dri.edu/Westmap/; Lovich et al.). Vegetation at Mesa includes a variety of plant species typical of the Mojave and Sonoran deserts along with plants from coastal southern California (see Lovich and Daniels 2000; Lovich et al. 2011b). Several fires have altered the plant community since the wind facility became operational after 1983 (Lovich et al. 2011b, c). The Pacific Crest Trail runs through Mesa and roughly divides the study site into "disturbed (i.e., WEF)" and "undisturbed (i.e., NWA)" landscapes (Fig. 1). To the east and south of the Pacific Crest Trail, the site is bounded by an operating utility-scale WEF (including 460 turbines, 51 electrical transformers, and an extensive network of roads; Lovich and Daniels 2000). To the north and west of the Pacific Crest Trail, the site is not modified by industrial activities (i.e., NWA) and adjacent to the San Gorgonio Wilderness. The footprint of the NWA study area was 152.8 ha and the footprint of the WEF study area was 185.81 ha (area analysis presented below). In our study, the Pacific Crest Trail is used as a dividing line for the two habitat types at Mesa and does not inhibit desert tortoise movement.

Field Techniques

Desert tortoise surveys at Mesa were conducted from early April to late July over ten field seasons (1997–2000, 2009–2014) spanning 18 years. Due to limited funding, surveys in 2012 were only conducted from October to December. During all study periods, we used intensive time–area constrained searches (Crump and Scott 1994; Walker 2012) to detect desert tortoises, making sure to explore all available disturbed and undisturbed habitats at Mesa. Surveys were performed by groups of 2–4 individual researchers aligning themselves parallel to one another (equally spaced and <25 m apart), allowing for visual search overlap, and then proceeding to walk along transects through the study area to visually detect tortoises. Over each study period, the study site was repeatedly sampled to ensure full assessment of the population. When a tortoise was located, we recorded their location using a GPS device (accurate to within about 3 m). Upon hand capture of the individual, sex was determined using secondary sexual characteristics (Ernst and Lovich 2009). If it was a sexually mature adult, we recorded weight (g) using a Pesola® spring scale, and straight-line carapace length (mm). If it was a first capture event, the individual was given a unique mark on the marginal scutes and upper shell or carapace (Cagle 1939), using a triangular metal file. In addition to

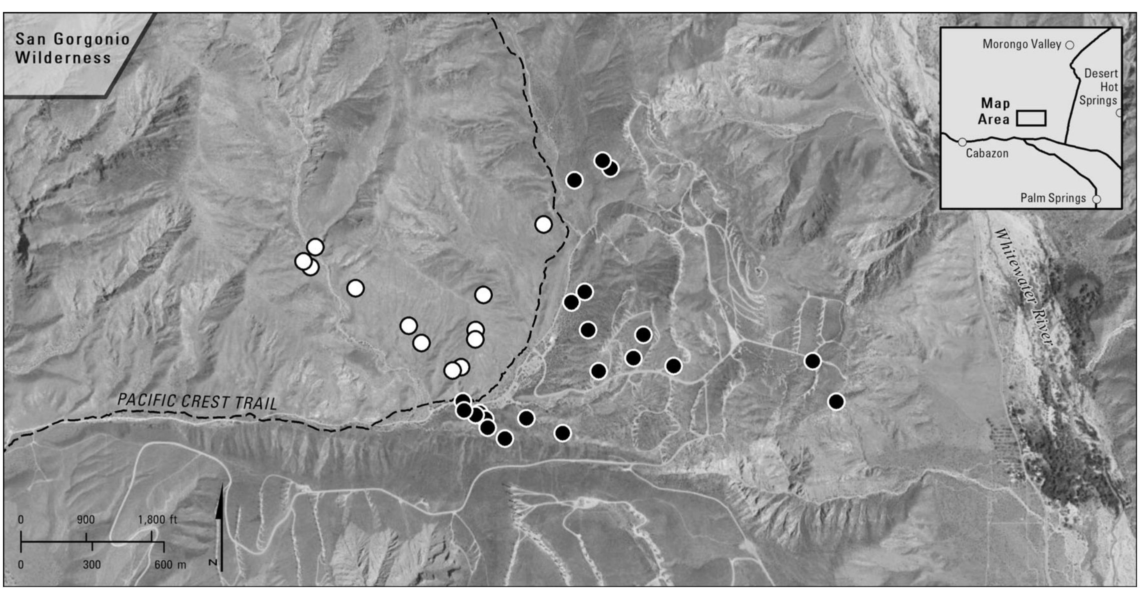

Fig. 1 Minimum convex polygon (MCP) centroids during the study period at Mesa. *Dark circles* represent WEF tortoises and *light circles* represent NWA tortoises separated by the Pacific Crest Trail

notching the carapace, epoxy tags were applied to the fourth left pleural scute with the corresponding identification code. Properly marking an individual allowed us to determine a recapture event in a subsequent study year. Tortoises were kept for 30 min, on average, and released at the point of capture.

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

Activity Area and Survival Analysis

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

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

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

Results

We used data from 234 tortoise capture events of 54 different individuals (13 male and 14 female within the boundaries of the WEF and 19 male and 8 female within the boundaries of the NWA) over the ten field seasons. Mean activity area (including standard error) of individuals in the WEF portion of the site was 6.25 ± 2.13 ha and mean activity area of individuals in the NWA portion of the site was 4.13 ± 1.23 ha. Mean overall activity area for adult male and female individuals combined was 5.48 ± 0.05 ha (range 0.06–43.98 ha). The two sample K-S test identified that the 100 % MCP size of the two populations (WEF and NWA) were not significantly different (KS: 0.097, *D*: 0.202, $P = 0.913$).

Capture probability of the top model varied from year to year based on new and repeat tortoise captures (Fig. 2) and was equal to 'one' only when all tortoises captured in one year were radioed continuously until the next year of sampling. The top weighted parameterization of capture probability included the effects of HT, *T*, and radio. Parameter estimate for 'HT' was 0.60 ± 0.38, suggesting greater capture probability in WEF than in NWA. Over the entire study period, capture probability estimates on the WEF ranged from 0.48 ± 0.1 (year 2012) to 0.84 ± 0.07 (year 2000), and on the NWA side ranged from 0.33 ± 0.1 (year 2012) to 0.74 ± 0.11 (year 2000) (excluding 1.00 capture probabilities; Fig. 2). Overall, the average, annual capture probability for both adult male and females combined was 0.56 ± 0.05.

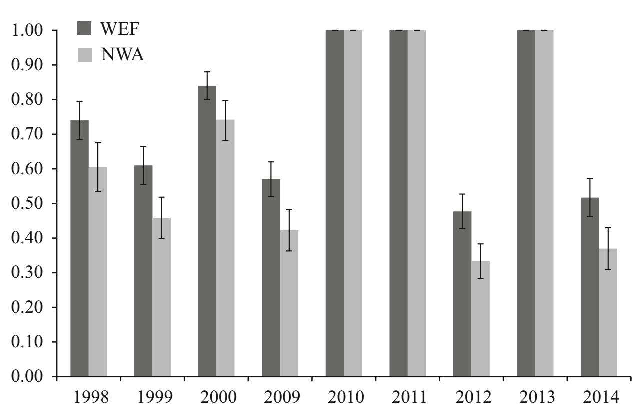

Fig. 2 Capture probability of desert tortoises for all study years (using the top parameterization of [*P*(radio + HT + *T*)] at Mesa. One hundred percent capture probabilities correspond to years when all tortoises in the previous year were radioed tracked continuously until the following year. *Error bars* denote unconditional standard error

The top ranked apparent survival model included HT effects on apparent survival (Table 1). With an AIC_C difference of 2.25 units from the (·) model (i.e., null model), and an AIC_C weight of 0.51, the top model [φ (HT)] was considered to have weak to moderate support (Arnold 2010; Table 1). The null model had an AIC_C weight of 0.16 and a likelihood of 0.32. Model estimates of HT and sex effect size, apparent survival, and capture probability are presented with unconditional standard errors (See Table 2). The top model effect size of HT indicated that survival was greater for WEF tortoises, and the top model HT estimate was significantly different from zero (Table 2). The effect size of sex, in the highest ranking model where it occurred, suggested that it was an uninformative parameter (Arnold 2010), and that there was negligible difference in survivorship between sexes (Table 2). Our top model indicated that annual apparent survival of WEF tortoises (0.96 ± 0.01) was significantly different from that of NWA tortoises (0.92 ± 0.02). Overall constant apparent survival from the null model was 0.94 ± 0.01 for both adult male and female tortoises in the study.

Discussion

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

Larger activity areas within the WEF in comparison to the NWA may suggest that tortoises can traverse the modified landscape with little difficulty. This assumption is based on tortoise sightings as they moved along dirt roads (Lovich, personal observation), as has been documented in other turtle species in modified environments (Nieuwolt

Table 1 Summary of model testing for desert tortoises marked at Mesa

Model	AIC_C	ΔAIC_C	W_i	Model likelihood	K	Deviance
φ(HT) [P(radio + HT + T)]	348.17	0.00	0.51	1.00	12	322.71
φ(HT + sex) [P(radio + HT + T)]	350.41	2.25	0.16	0.32	13	322.70
$\varphi(\cdot)$ [P(radio + HT + T)]	350.86	2.69	0.13	0.26	11	327.63
$\varphi(\cdot)$ [P(radio + T)]	352.69	4.53	0.05	0.10	10	331.67
$\varphi(\cdot)$ [P(radio + HT + sex + T)]	352.89	4.72	0.05	0.09	12	327.43
φ(sex) [P(radio + HT + T)]	352.90	4.73	0.05	0.09	12	327.44
$\varphi(\cdot)$ [P(radio + HT)]	354.37	6.20	0.02	0.04	3	348.26
$\varphi(\cdot)$ [P(radio + sex + T)]	354.90	6.73	0.02	0.03	11	331.67

Models are sorted by increasing AIC_C weights (W_i) >0.01 are listed. Subscripts reflect different factors in the model (φ = apparent survivorship, habitat type (HT) = NWA individuals versus WEF individuals, radio = capture probability = 1.0 for individuals radioed between capture occasions

T time, K number of parameters

Table 2 Top model parameter estimates on the logit scale

Parameter effects	Parameter estimate	95 % CI	Standard error
HT[a]	0.94	0.08 to 1.81	0.44
Sex	−0.03	−0.88 to 0.82	0.44
φ(intercept)	2.46	1.92 to 2.99	0.27

Standard error and confidence intervals from top model including covariate habitat type (HT) and top model including covariate (sex)

[a] 95 % CI non-overlapping with zero indicate significant parameter estimate ($P < 0.05$)

1996). Overall, activity area estimates at Mesa were less than those presented in previous research studies (see Harless et al. 2010 for a recent review) on Agassiz's desert tortoise (sensu Murphy et al. 2011). Low activity area estimates in our study may be attributed to our limited number of relocations per individual used to create each activity area, and site fidelity toward highly productive pockets of landscape at Mesa. Due to the variable topography and spatial arrangement of plant assemblages at Mesa, desert tortoises may prefer specific habitat along ecotones (Lovich and Daniels 2000). Patterns of space use by desert tortoises at Mesa can also be influenced by roadside plant productivity within the study site (Lovich and Daniels 2000), sex of the individual, social interactions, and sampling regime (Harless et al. 2010).

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

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

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

Grandmaison and Frary (2012) found that probability of desert tortoise detection was highest on maintained gravel roads. Furthermore, roads and culverts may cause mortality in adult tortoise populations (Berry et al. 2006; Boarman and Sazaki 1996; Lovich et al. 2011a; Nafus et al. 2013), and they may also facilitate increased movement (Diemer 1992; McRae et al. 1981; Nieuwolt 1996). It appears that conditions at Mesa are suitable for desert tortoise populations (Brooks 1995; Lovich et al. 2011b), although some mortality has been documented in the past (Lovich et al. 2011a, c). Tortoise mortality has been attributed to livestock grazing; direct impacts include burrow collapse (Agha et al. 2015; Ernst and Lovich 2009; Nicholson and Humphreys 1981), while indirect effects may be competition and loss of food resources and therefore a reduction in the quantity and quality of suitable habitat.

Predator populations may be lower at the Mesa WEF than in adjacent NWA, which may result in variation in survivorship of desert tortoises between landscapes. During the 2013 field season at Mesa, 48 motion sensor cameras were placed at the mouth of tortoise burrows, and recorded several occurrences of large terrestrial predators at various locations throughout the study site (i.e., both WEF and NWA). On two different occasions a potential predation event was recorded on camera: once where black bears (*Ursus americanus*), a known predator of turtles, investigated a tortoise burrow on the NWA section of the site (Lovich et al. 2014b), and another instance where a bobcat approached a sleeping tortoise also on the NWA section (Delaney, personal observation). Additionally, it is not unusual for large birds of prey (family *Accipitridae*) to consume turtles (Clark 1982; Means and Harvey 1999). However, rarely have volant predators (i.e. golden eagles; *Aquila chrysaetos*) of desert tortoises (Ernst and Lovich 2009) been documented at the WEF in recent decade, which may be attributed to high mortality caused by turbines shortly after construction (Lovich 2015). Among bird species, increased mortality caused by wind facility development has been well documented (Drewitt and Langston 2006). Furthermore, in some cases golden eagles have been recorded to avoid wind energy farms altogether (Chamberlain et al. 2006; Walker et al. 2005). Conservation of the desert tortoise may rely on further understanding of predator–prey relationships (Esque et al. 2010) within landscapes modified by USRED.

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

Populations appear to be stable at Mesa in comparison to other populations of this threatened species (Berry, 1997; Esque et al. 2010; Longshore et al. 2003; Lovich et al. 2014a, b; Peterson 1994). This is likely due in large part to favorable environmental conditions (i.e., above average precipitation) at the site and the associated ability of females to produce extraordinary numbers of eggs annually (Lovich et al. 2015). However, since tortoises are long-lived animals, populations can be comprised largely of old adults for many years, despite a lack of recruitment (Mortimer 1995), giving the illusion of population stability. New adult and sub-adult tortoises have seldom been documented at Mesa in the last decade suggesting the possibility of limited recruitment into the adult population. Despite the relative productivity at Mesa, lower recruitment may be due to recent drought conditions that have caused adult mortality in other populations of the desert tortoise (Lovich et al. 2014a; Morafka 1994).

Conclusion

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

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