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# Ectoparasite Load Is Reduced in Side-Blotched Lizards (*Uta stansburiana*) at Wind Farms: Implications for Oxidative Stress

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## ABSTRACT

Wind-generated power is one of the fastest growing alternative energy strategies worldwide and will likely account for 20% of US energy production by 2030. The installation and maintenance of wind farms are associated with increased human activity and can generate noise pollution, disturb and fragment habitat, and even alter community composition and structure. These environmental and ecological changes can increase physiological stress for vertebrates and affect important life-history attributes, such as immune function. However, little is known about how wind farms influence physiology and disease or parasite resistance in nonvolant wildlife. Here, we test the notion that renewable wind farms increase physiological stress and correlated aspects of disease resistance (parasite load) in a common desert vertebrate, the side-blotched lizard (*Uta stansburiana*). We captured lizards from three wind farms and three undisturbed reference sites in the San Geronio Pass wind resource area in the Mojave Desert, California. We quantified individual external parasite loads and measured plasma antioxidant capacity and concentrations of reactive oxygen metabolites as a combined metric of oxidative stress. Contrary to our expectations, individuals at wind farm sites had significantly fewer external parasites than at undeveloped sites. Additionally, we found a slight positive correlation between parasite load and oxidative stress for individuals at wind

farm sites but not at reference sites. Our results demonstrate a complex, potentially context-dependent relationship between stress physiology and disease resistance for lizards in anthropogenically disturbed environments. Understanding how wind farms affect the physiology and ecoimmunology of terrestrial fauna is necessary to mitigate the ecological costs of alternative energy development.

**Keywords:** renewable energy, conservation physiology, reactive oxygen metabolites (dROMs), antioxidant capacity (OXY), trombiculid mite (*Neotrombicula*), anthropogenic disturbance.

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## Introduction

The global market for wind-generated power is growing faster than any other renewable energy source (Golait et al. 2009; REN21 2014). The United States alone tripled wind power generation in the last decade, reaching >300,000 GWh and making up 7% of national energy production in 2019 (US Energy Information Administration 2020). By 2050, wind is projected to account for 35% of all energy produced in the United States, resulting in 109,300 km<sup>2</sup> of land use across all 50 states (US Department of Energy 2015). Despite this rapid and widespread development, surprisingly little is known about how wind farms affect surrounding ecosystems, especially fragile desert communities where much of this development will be concentrated (Lovich and Ennen 2013; Agha et al. 2020). Most of the research investigating ecological effects of wind energy has focused on the direct impacts of wind turbines on bird and bat mortality (e.g., Kuvlesky et al. 2007; Cryan and Barclay 2009; Wang et al. 2015; Smith and Dwyer 2016). However, wind turbine development also alters a suite of habitat characteristics on the ground (de Lucas et al. 2005; Keehn and Feldman 2018a) and imposes novel environmental disturbances that could increase physiological demands on nonvolant taxa (de Lucas et al. 2005; Łopucki and Mróz 2016; Łopucki et al. 2018). For populations of terrestrial species with small home ranges and limited dispersal abilities, alterations to the proximate landscape can be detrimental. Thus, there has been a call to quantify and understand the potential impacts that wind farms might impose on nonvolant wildlife (Kuvlesky et al. 2007; Lovich and Ennen 2013; Agha et al. 2020).

Research characterizing the effects of wind farm development on terrestrial wildlife has been slowly accumulating over the past two decades (Menzel and Pohlmeier 1999; de Lucas et al. 2005; Walter et al. 2006; Lovich et al. 2011; Helldin et al. 2012; Winder et al. 2014; Agha et al. 2015; Łopucki and Mróz 2016; Łopucki et al. 2017, 2018; Keehn and Feldman 2018a; Keehn et al. 2019). Wind farms are associated with low-frequency

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noise from generators and blade movements, habitat alteration (e.g., disturbance and fragmentation), and increased human activity (Orloff and Flannery 1992; Lovich and Daniels 2000; Rabin et al. 2006; Arana et al. 2015; Perrow 2017). Wind farms have also been shown to alter community composition and structure, decrease native species richness and diversity, increase exotic species richness, and potentially homogenize ecological communities (Pearce-Higgins et al. 2009; Keehn and Feldman 2018a). These types of biotic and abiotic changes at wind farms have the potential to increase physiological stress for wildlife (Crino et al. 2011; Janin et al. 2011; Blickley et al. 2012; Tennessen et al. 2014; Agnew et al. 2016; French et al. 2017; Injaian et al. 2018; Kleist et al. 2018; Łopucki et al. 2018; Thaker et al. 2018), yet few studies have measured bioindicators of physiological stress in the terrestrial species that inhabit wind farms (Mikolajczak et al. 2013; Agnew et al. 2016; Łopucki et al. 2018; Thaker et al. 2018; Klich et al. 2020). This is important because physiological stress has fitness and survival consequences, including immunosuppression and impaired reproduction (Calow and Forbes 1998; Hofer and East 1998; Möstl and Palme 2002). Thus, environmental disturbances that increase stress may also increase susceptibility to disease or parasitism and affect survival or recruitment (Fitze et al. 2004; Lafferty and Kuris 2005; Martin 2009). Alternatively, wind farms may actually decrease physiological stress for some animals if public access to developed areas is restricted (Lovich et al. 2011; Agha et al. 2015), if wind farms harbor fewer predators (Winder et al. 2014; Keehn and Feldman 2018b; Thaker et al. 2018), or if scrap building materials and storage areas provide additional refuges (Lovich and Daniels 2000). Given the tremendous carbon, water, and economic advantages of wind energy (US Department of Energy 2015), understanding physiological responses of local taxa to wind farms is essential for developing strategies to mitigate the potential ecological costs of wind farms.

Oxidative balance is a well-studied physiological biomarker of both the capacity of organisms to cope with environmental disruption and the deleterious effects of disruption (Cooke et al. 2013; Beaulieu and Costantini 2014). Oxidative balance can be quantified as the blood concentration of reactive oxygen metabolites (dROMs) relative to the neutralizing capacity of blood antioxidants (Costantini 2014). Overproduction of dROMs exceeding the body's natural antioxidant capacity (OXY; e.g., as a result of increased energetic demands) causes oxidative stress and eventual damage to tissues and immune cells (Costantini et al. 2011). Oxidative balance is a particularly useful metric for understanding the effects of chronic physiological stress, as it often increases with chronic glucocorticoid elevation and immune response activation (Costantini et al. 2011) and can sometimes predict survival and reproduction (Bize et al. 2008; Monaghan et al. 2009; Freeman-Gallant et al. 2011; Saino et al. 2011; Losdat et al. 2013; Costantini et al. 2016). Additionally, oxidative balance is a general physiological response that can reflect a variety of disturbances (Isaksson 2010, 2015), including air pollution (Lodovici and Bigagli 2011), noise pollution (Münzel et al. 2017, 2018), urbanization (Lucas and French 2012), predation (Guerra et al. 2013), and infection rates (Isaksson et al. 2013), making it a valuable tool for assessing the compounding effects of multiple stressors

that are often associated with human-induced habitat change (Beaulieu and Costantini 2014). Thus, oxidative balance is useful for investigating the complex relationships between anthropogenic disturbance, physiological stress, and disease. For example, disturbance may increase physiological demands and consequently reduce immunocompetency or directly increase prevalence and transmission of pathogens (Patz et al. 2000; Daszak et al. 2001; McCallum and Dobson 2002), activating immune responses, which can, in turn, increase physiological stress.

We examined the influence of wind farms on oxidative stress and an associated aspect of disease resistance (parasite load) in a common desert reptile. To date, relatively few studies have investigated the effects of wind farms on reptiles (Santos et al. 2010; Lovich et al. 2011; Ennen et al. 2012; Agha et al. 2015; Keehn and Feldman 2018a, 2018b; Thaker et al. 2018; Keehn et al. 2019). Nevertheless, reptiles are essential components of many ecological communities, serving diverse roles in nutrient cycling and trophic interactions and sometimes serving as pollinators, seed dispersers, and ecosystem engineers (Spiller and Schoener 1998; Bouchard and Bjorndal 2000; Godínez-Álvarez 2004; Dorcas et al. 2012; Kinlaw and Grasmueck 2012; Cortes-Gomez et al. 2015; de Miranda 2017; Reiserer et al. 2018). We focused our efforts on the common side-blotched lizard (*Uta stansburiana*), an abundant and widespread inhabitant of western North American deserts (Tinkle 1967; Wilson 1991; Stebbins 2003), where wind farms have recently been established. Side-blotched lizards are ideal for studying the effects of wind farms because they are relatively easy to capture in high numbers, and they have limited dispersal and high site fidelity (Tinkle 1967; Wilson 1991; Doughty and Sinervo 1994; Keehn et al. 2019), such that individuals experience narrow local environments over their lifetime and are strongly influenced by localized disturbance (Tinkle 1967; Tanner and Hopkin 1972; Lucas and French 2012).

Here, we investigated oxidative balance and external parasite load in side-blotched lizards at three wind farms and three reference sites in the San Geronio Pass wind resource area (SGWRA) in the Mojave Desert in Southern California. Previous work on this system has shown that wind farms in the SGWRA have higher levels of noise pollution and human disturbance, as well as altered biotic communities that include reduced native plant richness and diversity and increased nonnative plant richness compared with undeveloped reference sites (Keehn and Feldman 2018a). Such changes in plant community composition may be associated with shifts in the richness and abundance of the arthropods these lizards rely on and might also impact behavior, foraging, thermoregulation, physiology, and other aspects of lizard life history (Durso et al. 2020). Indeed, side-blotched lizards display slightly lower survival at these wind farm sites compared with nearby reference sites (Keehn et al. 2019). However, wind turbine sites also possess fewer avian predators of lizards (Keehn and Feldman 2018a), and predator attack rates on side-blotched lizards appear lower on wind farms, resulting in less wary side-blotched lizards at these sites (Keehn and Feldman 2018b). Therefore, predicting the impacts of wind farms on the health and physiology of local lizards is not straightforward. On one hand, increases in noise, disturbance, and disruptions to native communities (and possible resource

availability and use) may increase signs of oxidative stress and parasite loads in lizards on wind farms. On the other hand, reductions in predation pressure (and perceived threats) may dampen stress levels (Clinchy et al. 2012; Graham et al. 2017; Thaker et al. 2018) and attendant parasitism rates in lizards at wind farms. By increasing our understanding of the multifaceted consequences of wind energy development on the health of local species, we anticipate that this study will inform management decisions to support wildlife conservation goals in renewable energy development. Such work is vital as renewable energy expands as a global industry.

## Methods

### Study Species

*Uta stansburiana* is a short-lived, oviparous lizard that inhabits arid parts of the western United States in high abundances (Tinkle 1967; Stebbins 2003). They can be found across a wide range of terrain types, including hillsides, rocky outcrops, sand dunes, grasslands, and sagebrush flats (Tinkle 1967), but they are most common in open landscapes with proximity to rocks and shrubs for basking and shelter (Tinkle 1967; Stebbins 2003). Mean life expectancy of side-blotched lizards is 1–1.5 yr at southern latitudes, so population turnover is roughly annual in southern deserts (Tinkle 1967; Parker and Pianka 1975; Wilson 1991; Sinervo et al. 2000b; Zani 2005; Keehn et al. 2019). Mating occurs in the spring, and most eggs hatch in late summer (Parker and Pianka 1975; Doughty and Sinervo 1994; Stebbins 2003).

The trombiculid mite, *Neotrombicula*, is the most prevalent external parasite of *U. stansburiana* (Goldberg and Bursley 1991b) and infects a diverse array of other western vertebrates (Walters et al. 2011). These chiggers occur mostly on the upper

eyelids, gular folds, and ventral surfaces and cause necrosis of the epidermis at the point of attachment. Infestations last approximately 1 wk and result in integumental lesions and a diffuse inflammatory response (Goldberg and Bursley 1991a). Infections occur on both male and female hosts at similar densities and are highest between February and June but persist in lower densities through November (Goldberg and Bursley 1991b).

### Study Sites

We examined lizards and their external parasites from three wind farm sites and three undeveloped reference sites in the SGWRA of the Mojave Desert in Southern California (fig. 1). The SGWRA was first developed for wind energy production in the mid-1980s and is currently one of the largest wind production regions in the United States (Pasqualetti 2001), covering more than 18,000 ha. We selected three wind farm sites (Painted Hills, Mesa, and Mountain View) and three reference sites (Mission Preserve, Mesa Control, Mountain View Control) with comparable abiotic characteristics (e.g., elevation, slope, substrates) and biotic communities (table 1). All sites are also relatively disturbed, with trails, dirt roads, and human visitation by maintenance workers at wind farms and recreators at reference sites (located on public lands). Nevertheless, wind farms have greater levels of disturbance overall, with a higher density of roads and human traffic, as well as introduced plant species (Keehn and Feldman 2018a).

### Field and Live Animal Methods

We collected lizards ( $n = 180$ ) from our six study sites during a 6-d period (June 27–July 2, 2015), visiting two sites per day and sampling each site twice on different days (table S1; tables S1,

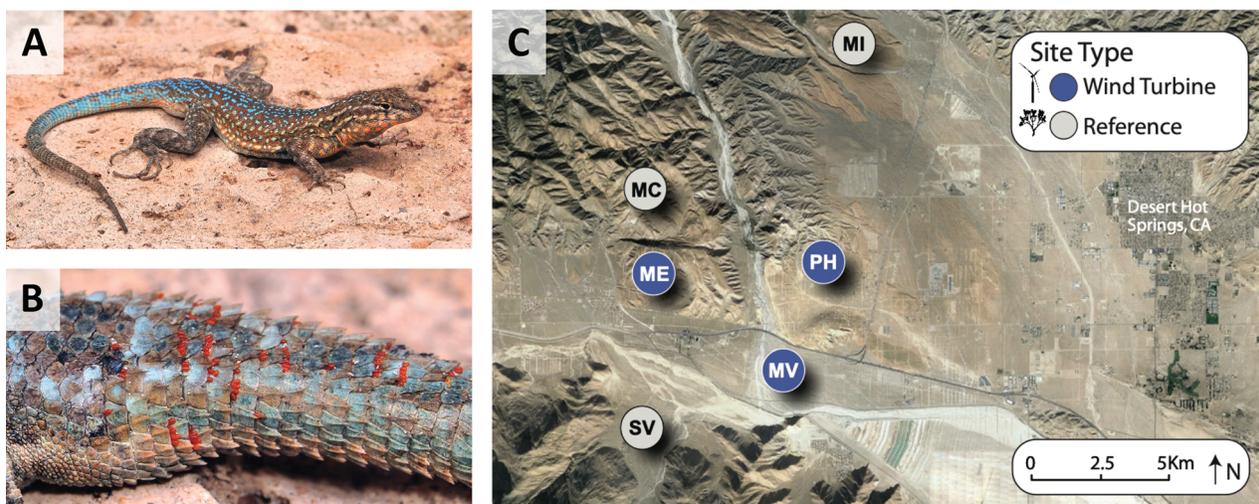


Figure 1. A, Male common side-blotched lizard (*Uta stansburiana*) displaying breeding colors. B, Close-up view of tail base of the same lizard, showing trombiculid mite (*Neotrombicula*) infestation; mites (bright red) are embedded at the base of the scales that encircle the tail. C, Six field sites located in the San Gorgonio Pass wind resource area in the Mojave Desert in Southern California. Wind farm sites: Painted Hills (PH), Mesa (ME), and Mountain View (MV). Reference sites without wind turbines: Mission Preserve (MI), Mesa Control (MC), and Mountain View Control (SV). We selected wind farm sites and reference sites that were generally similar in abiotic and biotic characteristics (table 1). Photo credits: R. W. Hansen.

Table 1: Study sites in the San Geronio Pass wind resource area in the Mojave Desert in Southern California along with location, disturbance levels, and some important abiotic and climate characteristics

Study site	Latitude, longitude	Disturbance index <sup>a</sup>	Avg noise levels (dBA)	Elevation (m)	Avg annual rainfall (cm)	<i>n</i> (female, male)	Avg mass $\pm$ SD (g)	Avg SVL $\pm$ SD (mm)
<b>Reference:</b>								
MI	34.0012, -116.6047	22.8	45.5	649.2	35.2	26, 1	3.57 $\pm$ .63	49.26 $\pm$ 2.26
MC	33.9614, -116.6766	40.2	40.7	468.8	35.5	22, 12	4.11 $\pm$ .86	50.64 $\pm$ 2.64
SV	33.8924, -116.6788	24.2	43.3	500.9	27.5	25, 5	3.74 $\pm$ .88	49.77 $\pm$ 3.19
Avg $\pm$ SD		29.1 $\pm$ 15.1	43.2 $\pm$ 2.4	539.6 $\pm$ 70.2	32.7 $\pm$ 6.0	73, 18	3.82 $\pm$ .83	49.94 $\pm$ 2.77
<b>Wind farm:</b>								
PH	33.9385, -116.6203	59.9	66.4	466.3	34.1	22, 0	3.25 $\pm$ .37	48.59 $\pm$ 2.28
ME	33.9441, -116.6757	26.5	47.9	715.1	46.8	23, 21	4.41 $\pm$ .84	51.20 $\pm$ 2.27
MV	33.9126, -116.6277	49.9	60.5	648.0	38.8	21, 0	3.21 $\pm$ .40	47.57 $\pm$ 1.53
Avg $\pm$ SD		45.7 $\pm$ 24.2	58.3 $\pm$ 9.5	609.8 $\pm$ 75.5	39.9 $\pm$ 12.7	66, 21	3.77 $\pm$ .85	49.67 $\pm$ 2.64

Note. Sample size and important physical measures (mass and body size reported as snout-vent length [SVL]) of the lizards (*Uta stansburiana*) examined from these sites are also given (additional information and raw data reported in table S1, available online). MI = Mission Preserve; MC = Mesa Control; SV = Mountain View Control; PH = Painted Hills; ME = Mesa; MV = Mountain View; avg = average.

<sup>a</sup>Total length of road (weighted by 0.5 for footpath, 1.0 for two track, 3.0 for residential, 5.0 for secondary, and 10.0 for highway) within a 1,000-m radius from plant richness study plots; digitized in ArcMap from 1-m-resolution imagery from the California National Agricultural Imagery Program. See Keehn and Feldman (2018a) for further details.

S2 are available online). Using a handheld “lizard loop,” we captured adult lizards, recorded exact capture locations for each individual with a GPS receiver (Garmin), quickly labeled animals with a unique code, then placed them in individual cloth bags for transport back to a field station (Boyd Deep Canyon Desert Research Center, University of California Reserve). At the field station, we measured body size (snout-vent length [SVL]), tail length, and mass. We noted whether individuals had a recent tail loss because tail loss may decrease immunocompetence (Kuo et al. 2013; Argaez et al. 2018). We also recorded sex, and if female, we palpated the abdominal region by hand to record the number of yolked follicles (1–4), because reproductive investment can influence stress and immunocompetence. Finally, we counted the number of external parasites for each individual using a handheld lens ( $\times 5$ ,  $\times 10$ , and  $\times 15$ ).

Following these field efforts, we transported animals to Utah State University to obtain measures of oxidative balance. We transported lizards on June 29, 2015 (after sampling all six sites once), and again on July 2, 2015 (again after visiting all sites). Within an hour of arrival, we collected blood samples from all individuals via retro-orbital sinus using a heparinized capillary tube. We immediately placed blood samples on ice, separated blood plasma from cells via centrifugation, and stored samples at  $-20^{\circ}\text{C}$ . Note that lizards were held in captivity (in a cool room at the field station) for 1–3 d before transport and blood sampling. However, acute stress of collection and short-term captivity should have no bearing on our measures of oxidative balance (described below), which are markers of long-term oxidative damage (Costantini et al. 2011). Research demonstrates significant increases in oxidative damage following only prolonged glucocorticoid treatment or stress exposure (i.e., multiple weeks) in most vertebrates, including lizards (Costantini et al. 2011; Voituron et al. 2017).

On completion of the study, we humanely euthanized all animals and preserved them as voucher specimens in the herpetology collection of the University of Nevada, Reno, Museum of Natural History (table S1). We followed Institutional Animal Care and Use Committee protocols (UNR 00586; USU 2068) for the safe care, handling, and use of live animals in this study.

### Oxidative Stress

To measure dROMs, we used a kit (Diacron, Grosseto, Italy) that detects the level of hydroperoxides, which are dROMs that signal both protein and lipid oxidative damage (Costantini and Dell’Omo 2006; Lucas and French 2012). We diluted 5  $\mu\text{L}$  of blood plasma into 100  $\mu\text{L}$  of the provided acidic buffered solution and followed the end point mode protocol, with modifications for use on a 96-well microplate. To measure OXY, we used an OXY-adsorbent test (Diacron, Grosseto, Italy), which measures blood antioxidant barrier by quantifying the oxidant action of hypochlorous acid ( $\text{HClO}$ ; Vassalle et al. 2008). Briefly, we diluted 2  $\mu\text{L}$  of blood plasma in 100  $\mu\text{L}$  of distilled water and followed manufacturer protocol but modified for microplate use. We then mixed a 5- $\mu\text{L}$  subsample of diluted plasma with 100  $\mu\text{L}$  of the  $\text{HClO}$  solution provided. All samples were run in singlicate. Interassay variation

was calculated using six replicate standards as the standard deviation of the standards divided by the average. Interassay variation was 4.6% and 2.3% for dROMs and OXY, respectively.

### Analyses

A biologically relevant assessment of oxidative stress includes both the levels of circulating dROMs and the absorbance capacity of the blood (OXY) within individuals, so we used an integrative index of oxidative stress to combine these complementary measures. We standardized dROM and OXY using the formula  $x_s = (x - m)/\text{SD}$ , where  $x_s$  represents a standardized value,  $x$  represents the corresponding original value, and  $m$  and SD represent the mean and standard deviation, respectively. We then consider the oxidative stress index as the difference between the standardized dROM and OXY values for each individual, such that higher values of our index correspond to a greater differential between dROM and OXY (Vassalle et al. 2008).

We calculated body condition for each individual using a scaled mass index ( $M_i$ ) and the equation  $M_i = M \times (\text{SVL}_0/\text{SVL})^b$ , where  $M$  is body mass,  $\text{SVL}_0$  is the mean SVL of the population (all samples), and  $b$  is calculated as the slope from an ordinary least squares regression of body mass on SVL divided by Pearson’s correlation coefficient (Peig and Green 2009).

We conducted all statistical analyses in R version 3.5.3 (R Development Core Team 2019) and assessed for multicollinearity of all variables using Pearson’s product-moment correlation (table S2). To test whether parasite loads varied between wind farm and reference sites, we used a generalized linear mixed model with a Poisson distribution, employing the lme4 package (Bates et al. 2015). We included fixed effects of sex, body condition, SVL, site type (wind farm or reference), and tail loss (binomial yes/no), because recent tail loss and active tail regeneration may cause physiological stress or decrease immunocompetence (Kuo et al. 2013; Argaez et al. 2018). We also tested for an effect of oxidative stress because environmental conditions that increase oxidative stress may simultaneously compromise immune function and result in higher levels of parasites. We compared models of increasing complexity by including interaction terms and selected a final model using Akaike information criterion (AIC) comparison and a maximum likelihood approach (table 2). Unique site ID was included as a random effect to control for site effects in all models. The lsmeans package in R (Lenth 2016) was employed to obtain Tukey-adjusted pairwise comparisons of significant predictors.

To test whether oxidative stress varied between wind farm and reference sites, we used a generalized linear mixed model employing the lme4 package (Bates et al. 2015). As in the previous model, we included fixed effects of sex, body condition, SVL, site type (wind farm or reference), and tail loss. We also include parasite load as a predictor because parasitic infection is likely to result in upregulation of an immune response and could explain variance in oxidative stress (Costantini and Møller 2009; Spence et al. 2017). In a second model, we limited our samples to females and included the number of yolked follicles (an estimate of clutch size) as a predictor because reproductive investment may also impose a

Table 2: Comparison of generalized linear mixed models to predict ectoparasite load in *Uta stansburiana* using maximum likelihood

Model, factor	Estimate	SE	Z	P	AICc
Parasites ~ site type + sex + body cond + SVL + tail loss					3,082.159
Site type	-1.768	.463	-3.821	<.001***	
Sex	.064	.046	1.395	.163	
SVL	.055	.008	7.067	<.001***	
Body cond	.004	.027	.143	.886	
Tail loss	-.199	.030	-6.658	<.001***	
Parasites ~ site type + sex + body cond + SVL + tail loss + stress					2,668.641
Site type	-1.824	.413	-4.418	<.001***	
Sex	.039	.049	.797	.425	
SVL	.062	.008	7.046	<.001***	
Body cond	.010	.028	.370	.711	
Tail loss	-.107	.034	-3.180	.001**	
Stress	.030	.012	2.507	.012*	
Parasites ~ site type + sex + body cond + SVL + tail loss + stress + site type × sex					2,670.674
Site type	-1.830	.409	-4.475	<.001***	
Sex	.025	.056	.460	.646	
SVL	.063	.009	7.021	<.001***	
Body cond	.011	.028	.407	.684	
Tail loss	-.107	.034	-3.186	.001**	
Stress	.030	.012	2.527	.011*	
Site type × sex	.042	.088	.481	.631	

Note. All models include site as a random effect. All models include fixed effects of site type (wind or reference), sex (male or female), snout-vent length (SVL), body condition (cond), and tail loss. Stress was calculated as a combined metric of reactive oxygen metabolites concentration and neutralizing capacity of antioxidants in blood plasma. AICc = corrected Akaike information criterion.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

\*\*\* $P < 0.001$ .

trade-off with self-maintenance and affect immunocompetence or susceptibility to physiological stress (Smith and French 2017). We also used generalized linear models to investigate whether variation in oxidative stress (i.e., stress index, as described above) was driven specifically by dROMs or OXY by testing raw values of dROMs (mg H<sub>2</sub>O<sub>2</sub>/dL) and OXY (HClO/mL). We compared models, keeping fixed effects constant but increasing complexity by including interaction terms, and selected a final model using AIC comparison and a maximum likelihood approach (table 3). Unique site ID was included as a random effect to control for site effects in all models. The lsmmeans package in R (Lenth 2016) was employed to obtain Tukey-adjusted pairwise comparisons of significant predictors.

## Results

Across all sites, we caught more females than males, but the proportions of males and females caught at reference sites and wind farms were similar; at wind farm sites, we caught 66 females and 21 males, and at reference sites, we caught 73 females and 18 males. Males were  $1.47 \pm 0.16$  g heavier (mean difference  $\pm$  SE;  $t = 9.208$ ,  $P \ll 0.001$ ) and  $4.50 \pm 0.25$  mm longer (mean difference SVL  $\pm$  SE;  $t = 8.055$ ,  $P \ll 0.001$ ) than females across

sites. There was no difference in body condition between sexes ( $t = 0.022$ ,  $P = 0.983$ ). There was no difference in individual mass ( $t = -0.835$ ,  $P = 0.405$ ), SVL ( $t = -0.740$ ,  $P = 0.460$ ), or body condition ( $t = -0.226$ ,  $P = 0.821$ ) between wind farms and reference sites. Summary statistics of mass and length of specimens at each site are included in table 1 (additional raw data provided in table S1). Collinearity of fixed effect variables is reported in table S2.

Our best-performing model of parasite load included no interaction terms (table 2). We found a significant effect of site type on parasite load (table 4; fig. 2A). Lizards at wind farm sites had lower parasite loads (mean  $\pm$  SE =  $8.18 \pm 2.69$ ) compared with reference sites (mean  $\pm$  SE =  $47.89 \pm 15.58$ ). There was a positive correlation between SVL and parasite load ( $\beta = 0.062$ , SE = 0.009, 95% confidence interval [CI] = 0.045–0.079,  $P < 0.001$ ). There were also significant effects of oxidative stress and tail loss on parasite load but no effects of sex or body condition (table 4).

Our best-performing model of oxidative stress included an interaction of site type and parasite load (table 3). There were no effects of site type (wind farm or reference), tail loss, body condition, or parasite load on oxidative stress in either sex (table 5; fig. 2B). There was a significant effect of sex (table 5),

Table 3: Comparison of generalized linear mixed models to predict oxidative stress levels in *Uta stansburiana* using maximum likelihood

Model, factor	Estimate	SE	<i>t</i>	<i>P</i>	AICc
Stress ~ site type + parasites + sex + body cond + SVL + tail loss					497.0817
Site type	.327	.418	.783	.458	
Parasites	.006	.005	1.243	.216	
Sex	-.681	.333	-2.049	.042*	
SVL	-.010	.058	-.177	.859	
Body cond	-.097	.193	-.501	.617	
Tail loss	.006	.211	.030	.976	
Stress ~ site type + parasites + sex + body cond + SVL + tail loss + site type × parasites					495.8393
Site type	-.076	.443	-.172	.866	
Parasites	.001	.005	.114	.909	
Sex	-.675	.329	-2.049	.042*	
SVL	-.004	.057	-.066	.947	
Body cond	-.117	.192	-.608	.544	
Tail loss	.011	.208	.055	.956	
Site type × parasites	.019	.010	1.911	.058	
Stress ~ site type + parasites + sex + body cond + SVL + tail loss + site type × parasites × sex					496.9708
Site type	-.099	.449	-.220	.829	
Parasites	.002	.006	.399	.690	
Sex	.062	.881	.070	.944	
SVL	-.019	.057	-.334	.739	
Body cond	-.162	.189	-.855	.394	
Tail loss	.008	.206	.038	.970	
Site type × parasites	.032	.012	2.671	.008**	
Site type × sex	.049	1.007	.049	.961	
Parasites × sex	-.008	.013	-.694	.490	
Site type × parasites × sex	-.032	.022	-1.491	.138	

Note. All models include site as a random effect. All models include fixed effects of site type (wind or reference), parasite load, sex (male or female), snout-vent length (SVL), body condition (cond), and tail loss. Stress was calculated as a combined metric of reactive oxygen metabolites concentration and neutralizing capacity of antioxidants in blood plasma. AICc = corrected Akaike information criterion.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

where females had higher oxidative stress than males (mean difference = 0.356, SE = 0.169,  $P = 0.037$ ), but this effect emerged in only two of our three top models (table 3). There was a slight interaction between site type and parasite load (table 5; fig. 3A), where oxidative stress tended to increase with parasite load at wind farms ( $\beta = 0.019$ , SE = 0.009, 95% CI = -0.002 to 0.039,  $P = 0.07$ ) but not at reference sites ( $\beta \leq 0.001$ , SE = 0.006, 95% CI = -0.012 to 0.013,  $P = 0.99$ ), but this relationship failed to achieve statistical significance. This trend was driven by a decrease in OXY absorbance capacity ( $\beta = -0.146$ , SE = 0.124, 95% CI = -0.392 to 0.100,  $F = 3.655$ ,  $P = 0.059$ ) as parasite load increased rather than by an increase in dROMs ( $\beta = 0.061$ , SE = 0.047, 95% CI = -0.026 to 0.155,  $F = 1.837$ ,  $P = 0.178$ ). The importance of this interactive term (i.e., effect size and significance) as a predictor of oxidative stress also varied across our three top models (table 3). For females, number of yolked follicles was a significant predictor of oxidative stress (fig. 3B;  $\beta = 0.565$ , SE = 0.176, 95%

CI = 0.264–0.981,  $F = 10.320$ ,  $P = 0.002$ ). There was no difference in yolked follicles among females between site types (mean difference = 0.013, SE = 0.077,  $t = -0.169$ ,  $P = 0.866$ ).

## Discussion

Clean energy infrastructure and technology are increasing worldwide to meet United Nations' sustainability goals by 2030 (United Nations 2019). Documenting the effects of these developments on local wildlife and informing efforts to expand alternative energy industries are therefore of immediate importance. Here, we examined the influence of wind turbine facilities on physiological stress and ectoparasitism rates in a common desert lizard of the southwestern United States. Our study is among the first investigations of the effects of wind turbine development on the physiology of local terrestrial fauna (Mikolajczak et al. 2013; Agnew et al. 2016; Łopucki et al. 2018; Thaker et al. 2018; Klich et al. 2020). Although our work is observational, we discuss potential

Table 4: Generalized linear mixed model predicting parasite load of side-blotched lizards (*Uta stansburiana*) using a Poisson distribution with site included as a random effect

Variable	Coef estimate	SE	95% CI	F	P
Sex	.039	.049	−.057 to .136	30.260	.425
Body condition	.010	.028	−.049 to .065	.257	.711
Snout-vent length	.062	.009	.045 to .080	89.557	<.001**
Tail loss	−.107	.034	−.173 to −.041	11.056	.001**
Site type	−1.824	.413	−2.794 to −.871	20.581	<.001**
Oxidative stress	.030	.012	.006 to .054	6.285	.012*

Note. Coef = coefficient; CI = confidence interval.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

mechanisms underlying the variation in parasite loads and advocate for more preemptive research approaches that will mitigate the ecological impacts of clean energy development.

We found that parasite loads were lower at wind farm sites than at reference sites, contrary to our original prediction. This might suggest that the biotic and abiotic conditions at wind farm sites are less habitable for trombiculids. Wind farm sites in the SGWRA tend to have greater human disturbance, more bare ground cover, less shrub canopy cover, and lower native plant diversity compared with nearby reference sites (Keehn and

Feldman 2018a). Soil and vegetation conditions at wind farms may be less productive for parasites; for example, areas with more vegetation may hold more soil moisture and be more suitable for the survival of trombiculid eggs and larva (Wharton and Fuller 1952). Curtis and Baird (2008) found higher rates of ectoparasitism in collared lizards (*Crotaphytus collaris*) at sites with more rock-vegetation interface and posit that lizards may acquire more parasites from making foraging strikes into vegetation. If wind farm sites consist of more cleared land and less regularly dispersed vegetation, then the prevalence of ectoparasites

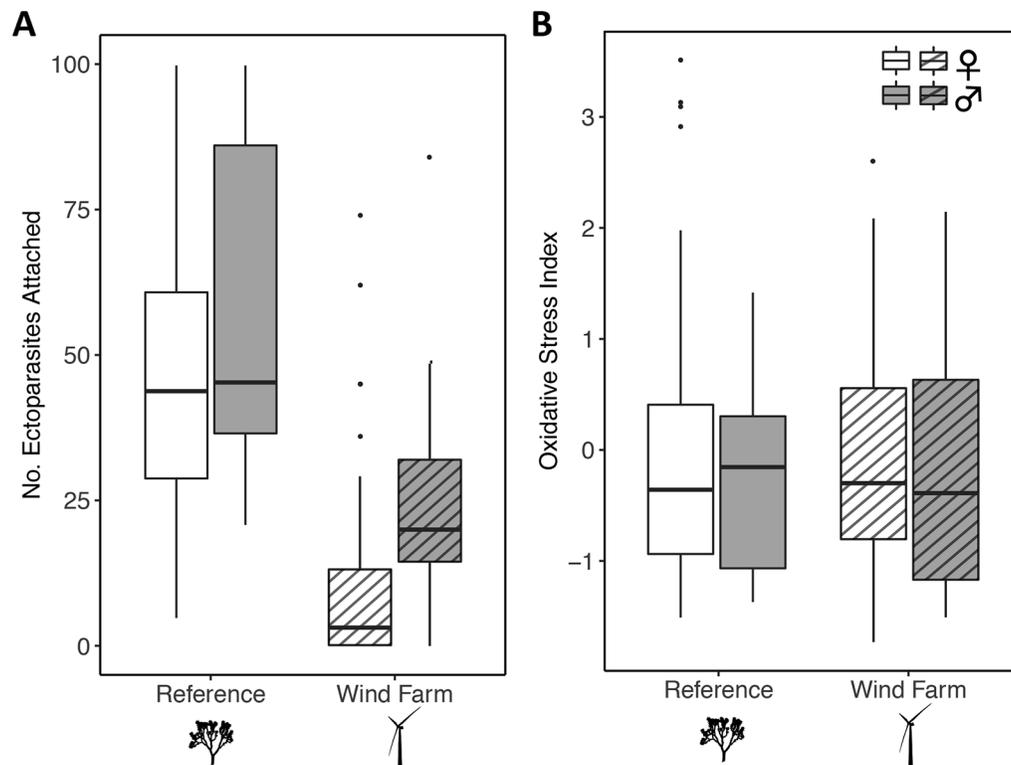


Figure 2. A, Parasite loads on side-blotched lizards ( $n = 174$ ) were higher at reference sites than at wind farm sites (Tukey pairwise comparison; mean difference = 34.66, 95% confidence interval = 26.54–46.80,  $P < 0.001$ ). B, There was no difference between oxidative stress levels at wind farms and reference sites for males (Tukey pairwise comparison; mean difference = 0.085,  $P = 0.99$ ) or females (Tukey pairwise comparison; mean difference = 0.119,  $P = 0.95$ ). A color version of this figure is available online.

Table 5: Generalized linear mixed model predicting oxidative stress in side-blotched lizards (*Uta stansburiana*)

Variable	Coef estimate	SE	95% CI	F	P
Sex	-.675	.329	-1.333 to -.010	4.472	.036*
Body condition	-.117	.192	-.499 to .269	.484	.488
Snout-vent length	-.004	.057	-.120 to .113	.048	.826
Tail loss	.011	.210	-.406 to .429	.004	.950
Parasites	-.096	.357	-.010 to .011	.009	.924
Site type	.001	.005	-1.021 to .882	.018	.899
Site type × parasites	.021	.010	-.001 to .038	.079	.079

Note. Oxidative stress was calculated as an integrative index of reactive oxygen metabolites concentration and antioxidant absorbance capacity in blood plasma. Site was included as a random effect. Coef = coefficient; CI = confidence interval.

\* $P < 0.05$ .

could be lower in these areas. An alternative explanation for greater parasite loads at reference sites could be that variation in host density plays a role in parasite transmission rates (Côté and Poulin 1995; Moore 2002). However, this is unlikely because population densities of *Uta stansburiana* at the SGWRA are similar between wind farm and reference sites (Keehn et al. 2019). Reduced parasite loads at wind farms could also be the result of variation in immunocompetence between sites. For example, individuals at wind farms could be investing more in self-maintenance and exhibit enhanced immunocompetence to promote survival, resulting in

lower rates of parasitism but also lower reproductive investment (Lucas and French 2012). However, we found no differences in ovarian follicle production across sites, and prior work suggests little differences in female reproductive investment or recruitment across sites (Keehn et al. 2019).

Despite lizards having lower parasite loads at wind farm sites, oxidative stress was not different from reference sites, and parasite load was not a significant predictor of oxidative stress. This is contrary to other studies that report a positive correlation between parasitic infection and oxidative damage

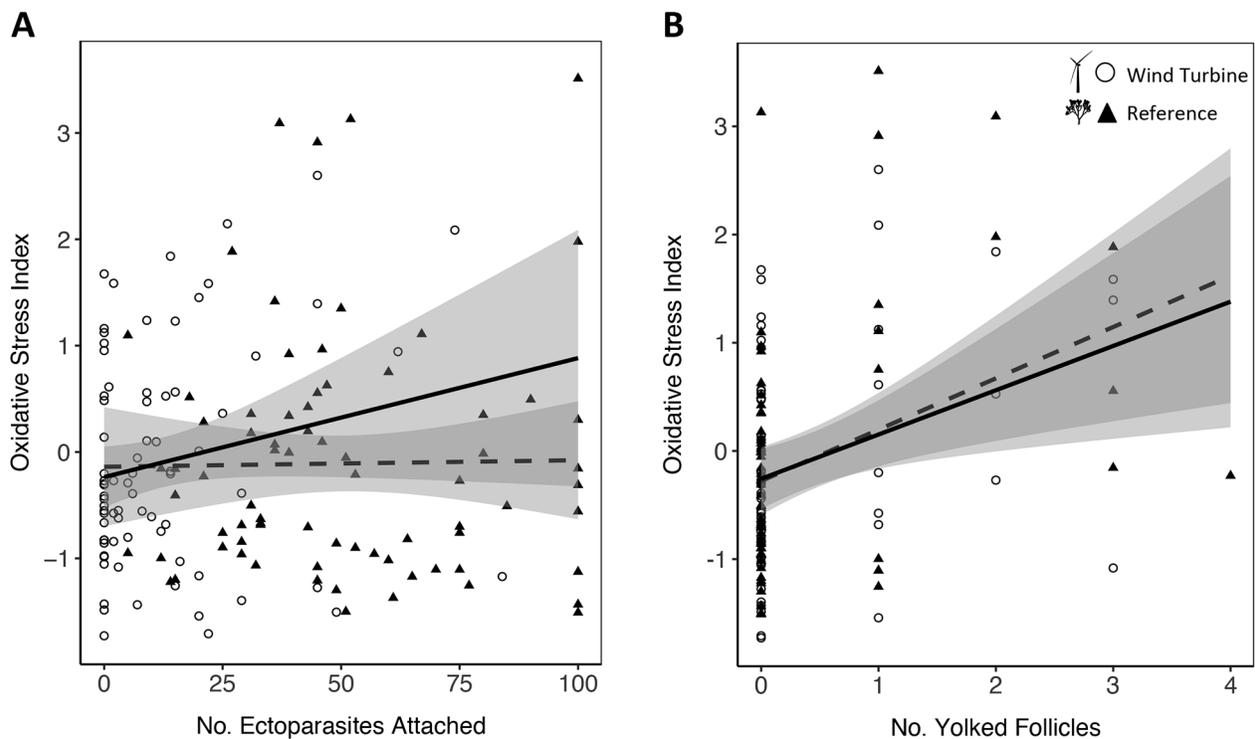


Figure 3. Oxidative stress was calculated as an integrative index of antioxidant absorbance capacity and concentrations of reactive oxygen metabolites in blood plasma. A, Oxidative stress is marginally correlated with parasite load for individuals at wind farm sites ( $n = 84$ ,  $\beta = 0.019$ ,  $SE = 0.009$ ,  $P = 0.07$ ) but not at reference sites ( $n = 90$ ,  $\beta \leq 0.001$ ,  $SE = 0.006$ ,  $P = 0.99$ ). B, Among females, oxidative stress is positively correlated with reproductive investment, measured as number of ovarian yolked follicles ( $n = 124$ ,  $\beta = 0.565$ ,  $SE = 0.176$ ,  $P = 0.002$ ). A color version of this figure is available online.

(Isaksson et al. 2013; López-Arrabé et al. 2015; Mészáros et al. 2019). One possibility is that the benefits of reduced parasite loads are offset by other environmental perturbations, such as noise pollution or human presence, that increase oxidative stress (French et al. 2017) at wind farms. Wind power sites at the SGWRA have more ambient noise (from turbines and vehicle traffic) and human disturbance from road traffic than reference sites (table 1; Keehn and Feldman 2018a). Indeed, some small mammals appear to be more vigilant on wind farms because of the increases in noise and human traffic (Rabin et al. 2006), and others display heightened corticosterone levels on wind farms (Łopucki et al. 2018). Alternatively, parasitism by trombiculids may simply be insufficient to effect oxidative balance in this system (Wegmann et al. 2015; Maronde et al. 2018). The relationship between parasitic infection and oxidative status in vertebrates is complex, and research on this topic shows mixed results (Marcogliese et al. 2005; Hanssen et al. 2013; Lilley et al. 2014; Delhayé et al. 2016). Furthermore, while parasite load was not a significant predictor of oxidative stress in our study, oxidative stress was a significant predictor of parasite load. This may suggest that presence or absence of parasites is related to oxidative status rather than to degree of parasitism, such that there is a threshold effect, or that the relationship between the two is indirect. For example, in red grouse (*Lagopus lagopus scoticus*), interindividual differences in carotenoid levels, sex, and parasite number before parasite removal treatment interacted to affect oxidative status (Mougeot et al. 2010).

While we found no significant difference in oxidative stress between site types, we did detect a slight (but not statistically significant) positive relationship between oxidative stress and parasite load at wind farm sites but not at reference sites (fig. 3A). It may be that the effect of parasite load on the oxidative status of individuals in this system is detectable only under other compounding stressful conditions. For example, in Seychelles warblers (*Acrocephalus sechellensis*) infected with malaria, oxidative damage increased only during the energetically demanding period of chick provisioning (van de Crommenacker et al. 2012). Similarly, a study on yellow perch (*Perca flavescens*) found a positive correlation between oxidative stress and parasite infection in a polluted river system but not at reference sites (Marcogliese et al. 2005). Alternatively, individuals that regularly experience high parasitism rates (e.g., at reference sites) might be better at coping physiologically and possess a less robust oxidative response compared with those that regularly experience less parasitism (e.g., at wind farm sites). High parasitism rates in early-life environments can result in increased immunocompetency in adulthood as a mechanism of preparing organisms for future stressful conditions (Sol et al. 2003; Martin 2009; Spence et al. 2017). However, we caution that the data collected here offer only weak support of an interaction between oxidative stress and parasite loads. The strength of this interaction as a predictor varied among our top three models (see table 3). Additionally, parasite loads are lower at wind farm sites overall, so there are few observations of individuals with high parasite loads and high oxidative stress at wind farms. Last, oxidative damage represents only one of many indices of physiological stress, and more comprehensive physiological measurements are necessary to detect variation in immunocompetency in this system.

Among females, oxidative stress was also positively correlated with reproductive investment (number of yolked follicles) at all sites. During follicle development, female fat stores are often depleted and baseline glucocorticoids are elevated (Hahn and Tinkle 1965; Wilson and Wingfield 1992), which can lead to oxidative stress (Lucas and French 2012; Webb et al. 2019). There may be a trade-off between investment in reproduction and self-maintenance, where females investing in larger clutches have more oxidative damage (Costantini 2008; Costantini et al. 2016). However, if reproduction imposes a trade-off, then we might have also expected a suppression of immune function. On the contrary, there was no relationship detected between number of follicles and parasite loads, although immunocompetence and other potential parasite types were not measured directly (Spence et al. 2017; Megía-Palma et al. 2020).

Oxidative stress is a general physiological response in free-living animals, and we cannot dismiss the potential effects of unmeasured variables. For example, the quality of carotenoid-based traits in males may be related to resistance oxidative stress and to parasite load because carotenoids function as both a pigment and an important antioxidant (Helfenstein et al. 2010; Mougeot et al. 2010). In Iberian green lizards (*Lacerta schreiberi*), structural-based ultraviolet coloration has also been negatively correlated with parasite load (Megía-Palma et al. 2017). Future work on this system may consider quantifying lizard coloration and scoring color morphs (e.g., Sinervo and Lively 1996), which are at least partially hormonally mediated (Sinervo et al. 2000a; Miles et al. 2007) and known to show differential physiological responses to stress (Comendant et al. 2003). Additionally, while oxidative stress is often correlated with long-duration physiological stress, acute stress can result in upregulation of the antioxidant response (Costantini et al. 2011), and events before capture likely account for some individual variation. Oxidative status also represents only one of many indices of physiological stress, and more comprehensive physiological measurements may be necessary to fully describe the complex relationships between environmental disturbance, physiological stress, and immune function.

Reliance on wind energy is increasing worldwide at unprecedented rates, offering promising reductions in CO<sub>2</sub> emissions, water consumption, and air pollution, all of which benefit societal and environmental health (US Department of Energy 2015). However, ambitious goals for power plant development come at the cost of widespread habitat alteration and downstream consequences for the health of local flora and fauna. This research represents one of the first efforts to document the consequences of wind farm development on the individual health of local reptiles. Our work reveals trends in a single species occupying one wind resource area in the desert southwest; clearly, more research on diverse taxa in a variety of settings is needed to understand the breadth of potential impacts wind farms may have on wildlife. Furthermore, our findings are correlative and do not infer causation. Research that documents physiological characteristics in populations before and after development is needed to infer mechanism and effectively predict impacts on wildlife. Nevertheless, such conservation physiology can provide an important first step toward understanding how anthropogenic developments affect the health of animals,

and we hope land managers will consider the potential physiological effects on wildlife when developing wind farms and other forms of renewable energy.

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