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PREDATOR ATTACK RATES AND ANTI-PREDATOR BEHAVIOR OF SIDE-BLOTCHED LIZARDS (*UTA STANSBURIANA*) AT SOUTHERN CALIFORNIA WIND FARMS, USA

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***Abstract.*—The development of renewable wind energy farms changes land-use patterns at a landscape scale. Wind energy sites are characterized by high levels of anthropogenic disturbance (e.g., noise, roads, structures, etc.) that can facilitate the use of wind farms by some species, while fragmenting and degrading habitat for others. We lack an understanding of how these species-specific responses to changes in habitat quality will affect patterns of species interactions. Here, we test whether changes in habitat quality alter predator attack rates and anti-predator behavior in Side-blotched Lizards (*Uta stansburiana*) at wind farms relative to reference sites in the San Gorgonio Wind Resource Area (SGWRA) of Southern California, USA. We use clay models of Side-blotched Lizards to show that predator attack rates on these lizards appear lower at turbine sites (though total number of predation attempts precludes robust statistical analysis). We then use flight-initiation-distance (FID) trials to show that Side-blotched Lizards are also less wary to approaching predators at turbine sites. These data suggest that Side-blotched Lizards have responded to changes in predator community composition and abundance at disturbed wind farms by becoming less wary. Additional work is needed to better understand how other species will respond to changes in community structure at wind farm developments, and whether wind farm habitats are truly suitable for a wide variety of terrestrial taxa.**

Key Words.—anthropogenic disturbance; clay models; flight-initiation-distance (FID); predation; renewable energy; reptile; roads; wind turbines

INTRODUCTION

Renewable energy development (e.g., geothermal, hydroelectric, wind, and solar) is a way to sustainably support growing energy demands, while also addressing global climate change driven by fossil fuel consumption (Panwar et al. 2011). The benefits of renewable energy are clear: by investing in non-finite methods of energy production, we reduce carbon extraction and consumption, increase energy security, reduce greenhouse gas emissions responsible for global climate change, improve public health, and create high-quality jobs (Frondel et al. 2010). Renewable wind energy, in particular, is thought to be one of the most benign alternatives to fossil fuels (Harte and Jassby 1978; Evans et al. 2009). However, the ecological costs of renewable wind energy are not easily understood. It is clear that wind turbines are responsible for the direct mortality of volant species such as birds and bats (Kuvlesky et al. 2007; Cryan and Barclay 2009; Smith and Dwyer 2016). Yet, the indirect effects of habitat alteration, degradation, and loss may have many additional unintended and hard-to-measure consequences for both aerial and terrestrial species (Santos et al. 2010; Lovich and Ennen 2013; Northrup and Wittemyer 2013).

In the deserts of Southern California, USA, there is substantial overlap between the demands for renewable energy development and the needs to meet wildlife habitat conservation objectives (Spencer et al. 2010; Stoms et al. 2013). Areas with high potential for renewable wind and solar energy production also support a high diversity of native and endemic and species, as well as those of high conservation priority (McLaughlin 1986; Dobson et al. 1997; Vandergast et al. 2013; Wood et al. 2013; Baldwin et al. 2017). In addition, desert habitats are exceptionally sensitive to disturbance (Abella 2010), and extensive anthropogenic activity in Southern California has already caused substantial habitat loss and degradation for a number of species throughout the region (Lovich and Bainbridge 1999). Additional development for renewable energy may further jeopardize limited wildlife habitat for native desert species.

Effective mitigation measures for wind energy development in the desert southwest of North America necessitate an understanding of species-specific responses to wind farms. For a number of species, wind farm development may not impact habitat quality (Devereux et al. 2008; Ennen et al. 2012) and may even increase the suitability of habitat (Agha et al.

2015). Concrete pads, raw material yards, buildings, and storage areas may provide refuge for reptiles (Lovich and Daniels 2000) and mammals (Hethcoat and Chalfoun 2015). New structural features including buildings, roads, powerlines, and wind turbines may facilitate dispersal and foraging for disturbance-tolerant predators and scavengers (Agha et al. 2017; Smith and Dwyer 2016; but see Smith et al. 2017). Powerline supports and turbine lattice towers appear to create novel hunting perches and nest sites for some avian species (Howe et al. 2014; Smith and Dwyer 2016), particularly in desert systems where natural vertical structures and shade may be limited. On the other hand, wind turbines have caused extensive mortalities of some bird and bat species (Kuvlesky et al. 2007; Cryan and Barclay 2009; Smith and Dwyer 2016), with potential population-level declines of resident species (Hunt et al. 1998). Wind farms may also reduce the fitness for some bird species due to increased foraging costs and poorer quality nesting sites (Pearce-Higgins et al. 2009; Mahoney and Chalfoun 2016). Some reptile species may experience greater mortality and lower survival due to increases in hunting perches for avian predators (Barrows et al. 2006; Hawlena et al. 2010). Such demographic effects may eventually lead to population declines of certain species on wind farms, while other changes in abundance could reflect avoidance behaviors and displacement by other species (Leddy et al. 1999; Santos et al. 2010; Villegas-Patraca et al. 2012; Tanis 2013). Thus, the direct and indirect effects of wind turbines on local ecological communities remain uncertain (Lovich and Ennen 2013; Northrup and Wittemyer 2013).

Varying sensitivities of wildlife species to changes in habitat suitability at wind farms (relative to pre-development site conditions) may alter patterns of community structure and assemblage (Tanis 2013). In disturbed landscapes, changes in species interactions are often related to changes in predator activity, which influences top-down regulation of prey species (Fischer et al. 2012). Predator activity is an important driver of terrestrial vertebrate diversity and abundance in desert systems (Finke and Denno 2004; Ayal 2007; Hawlena et al. 2010; Fischer et al. 2012). If wind farms create poor habitat conditions for predators, then prey species may experience reduced predation pressure and higher survival in wind farm habitats (Winder et al. 2014). For example, mortality of avian predators or avoidance of wind farms by terrestrial predators could improve survival of ground-nesting birds at wind farms (Smith et al. 2017). However, if wind farms attract predators, prey species may experience increased risk of predation (Barrows et al. 2006; Hawlena et al. 2010), creating an ecological trap in otherwise suitable habitats (Hethcoat and Chalfoun 2015).

In this study, we test whether wind farms influence predation intensity for common terrestrial vertebrates. We focus on populations of Side-blotched Lizards (*Uta stansburiana*) at wind farms relative to reference areas within the San Gorgonio Wind Resource Area (SGWRA) of Southern California, USA. Side-blotched Lizards are moderately tolerant of disturbance, tend to maintain large populations over small areas (Tinkle 1967), and are found in abundance at sites across the SGWRA. In addition, Side-blotched Lizards are prey for a host of vertebrate and invertebrate predators, and thus, considered an important species in desert food webs (Tinkle 1967; Parker and Pianka 1975; Wilson 1991).

First, we estimated predation intensity on Side-blotched Lizards from avian, reptilian, and mammalian guilds. We compared attack rates on clay model Side-blotched Lizards at wind farm sites (turbine sites) against attack rates on clay models placed in nearby reference sites without energy development (non-turbine sites) in the SGWRA. Next, we determined anti-predator behavior of Side-blotched Lizards at turbine and non-turbine sites by quantifying the distance that lizards would initiate flight from an approaching predator (human observer). Behavior in this species is affected by predation environment (Zani et al. 2013), and previous work has documented variation in anti-predator flight behavior for Side-blotched Lizards in response to differing levels of predator abundance (Wagner and Zani 2017). We expect that if predators are more abundant at wind farms, we will find more clay model attacks at wind farms relative to reference sites. This would coincide with increased wariness as expressed by a greater distance from an approaching predator at which Side-blotched Lizards take flight (Lima and Dill 1990). Alternatively, lower predator abundance at wind farms would result in fewer clay model attacks relative to reference sites. Under this scenario, lizards at turbine sites would instead exhibit increased boldness as expressed by less distance from the predator to take flight and be less wary of potential predators (Lima and Dill 1990). Thus, measures of attack rates and anti-predator behavior in a common desert lizard may shed light on the ecological impacts of anthropogenic disturbance at wind farms on desert communities.

MATERIALS AND METHODS

Study sites.—We established nine study plots across a gradient of habitats within the SGWRA in Southern California, USA (Fig. 1). We selected four study plots from populations at wind farms: Mesa (ME), Painted Hills (PH), Dillon (DI), and Mountain View (MV).

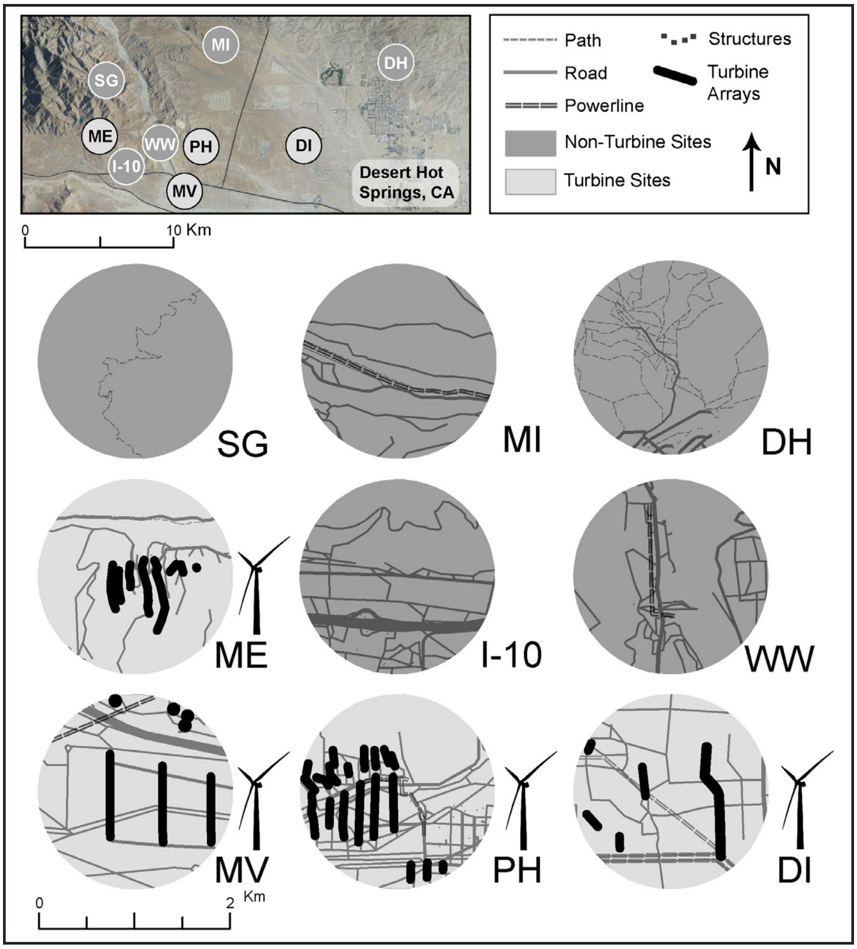

Figure 1. Nine study sites in the San Gorgonio Wind Resource Area (SGWRA) in southern California, near Desert Hot Springs, north of Palm Springs, USA, where predation rates and anti-predator behavior were surveyed for Side-blotched Lizards (*Uta stansburiana*). Five study areas lack turbines (dark gray) and were used as reference sites, while four sites contained turbines (light gray) and were considered as treatments. Insets (centered on 100 × 10 m model array locations) show land-use within a 1 km radius that defined the flight-initiation-distance study area for each population. Paths (dashed line), roads (gray lines; thickness reflects road traffic volume), transmission lines (double-dashed line), buildings (squares) and turbine arrays (black) indicate the types of human disturbances present at each site.

Sites ME and PH were developed in the mid-1980s; these sites have high densities of smaller turbines with lattice tower bases. Sites DI and MV were developed in the mid-2000s; these sites have tall, tubular turbines at lower densities.

We selected five plots from sites without wind turbines as reference populations: Mission (MI), San Gorgonio (SG), Whitewater (WW), Desert Hot Springs (DH), and I-10 Corridor (I-10). Sites MI and SG were low-disturbance areas at least 2.4 km away from any paved road disturbances, with limited human activity. However, site SG experienced substantial erosion and soil disturbance over the course of the study from illegal livestock grazing, and we removed data from this reference site from further analyses (see below). Sites WW and DH were moderately disturbed areas, with nearby paved roads used frequently for access to recreation opportunities (WW), and substantial human activity such as hiking and dog walking (DH). Finally, site I-10 was highly disturbed, 420 m north of a rest stop on a major interstate (I-10) with substantial traffic noise, off-road vehicle use, human activity, and multiple transmission line corridors (Fig. 1).

Estimating rates of predation.—To test the hypothesis that anthropogenic disturbance has altered predation rates at wind turbine sites relative to reference sites, we created clay lizard replicas to record predation attempts. Clay models have been successfully used in a range of studies to infer predation pressure on different reptile color morphs, sexes, subpopulations, and within different habitats (Husak et al. 2006; Vervust et al. 2007; Gifford et al. 2008). We used Sculpey polymer clay (Sculpey Products, Stockbridge, Georgia, USA), a sculpting medium that remains soft unless baked. Using a vouchered specimen of an adult male Side-blotched

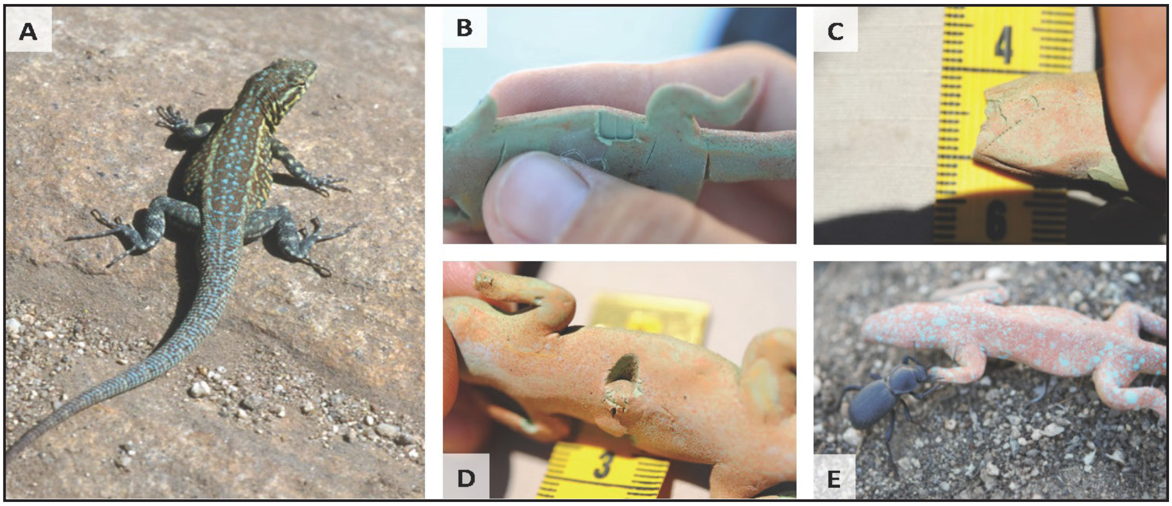

Figure 2. A Side-blotched Lizard (*Uta stansburiana*) in life, and clay model replicas deployed in the field at the nine study sites to estimate predation rates. (A) An adult male Side-blotched Lizard was used to create model lizard replicas (Photographed by Gary Nafis). (B) Attack on *Uta* model by a mammal; note incisor marks and size of teeth marks relative to model torso and human hand, indicative of a modest-sized rodent such as a Desert Woodrat (*Neotoma lepida*) or White-tailed Antelope Squirrel (*Ammospermophilus leucurus*). (C) Attack by a reptile; note the small teeth marks and shape of mouth, suggestive of a larger lizard such as a whiptail (*Aspidoscelis tigris*). (D) Attack by bird; note narrow and deep marks indicative of a smaller passerine. (E) Some models were molested by arthropods such as ants and beetles. (Photographed by Jade Keehn).

Lizard from the Museum of Natural History of the University of Nevada Reno, USA (UNR 5028), we created a plaster mold of the body and tail. We pressed softened clay into the mold to form the body of the model, and then added clay to form arms and legs by hand, shaping them into a natural alert stance (Fig. 2). We used orange, blue, and yellow spray paint to color the models in a pattern similar to the adult breeding colors of males. However, it should be noted that the colors approximated a Side-blotched Lizard to our (human) eyes, and may not have accurately matched the colors perceived by non-human predators (Osorio et al. 1999; Jacobs 1981, 2009).

In June of 2014, we deployed models in open, visible areas at each of the four turbine and five non-turbine study plots. We placed 333 models (37 per study plot; 148 in the four turbine sites; 185 in the five reference sites) at least 10 m apart along four parallel 100 m rows, oriented in a random cardinal direction. At turbine plots, we deployed models within 50 m of a turbine array. We retrieved models after 10–13 d; however, high substrate temperatures (up to 55° C) likely hardened the clay preventing additional imprints after 4–5 d.

After retrieving all the models, we used the impressions left in the clay (e.g., beak marks, tooth patterns, etc.) to categorize predation attempts as those from birds, reptiles, rodents, and mammalian carnivores. We tallied the total number of attacks, and the number of attacks by predator guild for reference and treatment sites. We then compared differences in total predator attack rates between turbine and non-turbine sites, as well as differences in rates by the predator classes between turbine and non-turbine sites using Mann-Whitney U (two-sided Wilcoxon rank sum) tests ($\alpha < 0.05$; $n_{turbine} = 4$, $n_{reference} = 4$) in R v3.2.2 (R Core Team 2015).

Quantifying anti-predator behavior.—We hypothesized that changes in the richness and diversity of predators at wind farms might lead to changes in the anti-predator behavior of Side-blotched Lizards. We quantified anti-predator behavior as the average flight-initiation-distance (FID) of individual lizards (Cooper and Whiting 2007), which is the distance at which a lizard flees from an approaching predator (human). In August 2014, we conducted FID trials on unmarked lizards at each of the nine study sites within a 1 km radius of the model deployment area (Fig. 1), and no greater than 0.25 km from the nearest wind turbine array for turbine sites.

For each FID trial, an observer simulated a predator approach by walking a standardized approach pace of approximately 0.4 m/sec towards a lizard from a starting point of within 45 degrees of the snout (i.e., facing the lizard) at a distance of 4 m from the lizard. The approach ended when the target lizard fled from the observer. At the end of the approach, we recorded FID as the linear distance, to the nearest cm, between the starting perch of the lizard and the observer at the time of flight. We noted the age class (adult, subadult, hatchling, or unknown) and sex (male, female, or unknown) of the fleeing lizard based on size, coloration, and appearance. We also recorded perch type (rock or bare ground), perch height (cm), perch (substrate) temperature (Enviro-safe Pocket Thermometer, Thomas

Scientific, Swedesboro, New Jersey, USA; ° C), time of day, sun exposure (full sun, partial sun, cloudy), canopy cover above perch (none or shrub cover above a perch that would obscure a top-down view of lizard from directly above), date, site, treatment (wind farm or reference site), and observer. We targeted lizards perched on rocks or bare ground so that lizards had a clear view of approaching observers, and we did not conduct trials on lizards perched in shrubs or otherwise obscured from the approaching observer. We only conducted trials during the morning activity period between 0700–1100, with substrate temperatures between 30–45° C. To minimize potential differences in FID resulting from differences in observer appearance (i.e., conspicuousness, perceived threat, etc.), each of the four possible observers dressed in similar colors during trials (white shirt, blue jeans, hardhat, and sun glasses).

We then used a Student's *t*-test in R to compare differences in mean FID between turbine and non-turbine sites ($\alpha < 0.05$). In addition, a number of surveys could not be completed because lizards fled (initiated a flight response) before surveyors were within trial distance (4 m). For each site, we calculated the number of trials not completed relative to the total number of trials and compared the percentage of FIDs > 4 m between turbine and non-turbine sites using a Mann-Whitney U (two-sided Wilcoxon rank sum) test in R ($\alpha < 0.05$; $n_{turbine} = 4$, $n_{reference} = 4$).

Finally, we used multiple regression to explore potential relationships between FID (response variable) and lizard traits (age class, sex) and various abiotic and trial conditions (perch height, perch temperature, site, treatment, observer, etc.). To assess the most appropriate model for multiple linear regression and avoid over-parameterization, we performed a model fitting procedure in R using the glmulti package v1.0.7 (Calcagno and de Mazancourt 2010). The method exhaustively tests every combination of explanatory variables in contributing to the response variable under a general linear model, ranking models via AICc (Burnham and Anderson 2002). We then used the top-ranking model for inference, conducting a linear regression in R.

RESULTS

Estimating rates of predation.—We deployed 333 clay lizard models at each of the nine study sites in the SGWRA (37 models per site). Unfortunately, we were forced to discard data from site SG; many of our clay models were trampled by cattle prior to retrieval because of illegal grazing at this site. Of the 296 remaining lizard models (148 per treatment with four sites each), only 32 models were attacked (10.8%). Of the 32 attacks, nine were from birds (28.1%), three from reptiles (9.4%), 16 from rodents (50%), one from a carnivore (3.1%), and three could not be assigned to any taxon (9.4%) due to ambiguous imprint marks (Fig. 2). In total, models at wind farm sites with turbines were attacked 11 times, while models at non-turbine reference sites were attacked 21 times. Nonetheless, these differences were not statistically significant ($W = 12$, $P = 0.309$), nor were any differences in predator attack rates between treatments by particular predator groups (birds: $W = 12$, $P = 0.285$; reptiles: $W = 12$, $P = 0.186$; rodents: $W = 9$, $P = 0.882$; carnivores: $W = 10$, $P = 0.453$; unknown: $W = 10$, $P = 0.608$).

Quantifying anti-predator behavior.—We recorded data from 638 completed FID trials at the nine study sites (51–80 trials per site). However, we noted inconsistencies in FID measurements among observers at site SG, possibly related to the presence of introduced cattle on some occasions. Thus, we excluded data from site SG, leaving 540 FID trials to compare the behavioral responses of *Uta* between four sites with and four sites without wind turbines.

Lizards had a lower FID at wind farms ($\bar{x} = 2.080$, SD = 0.84 m) than lizards at reference sites ($\bar{x} = 2.259$, SD = 0.81 m), and this nearly 20 cm difference in FID is significant ($t = 2.527$, df = 538, $P = 0.012$; Fig. 3). We also recorded 213 incomplete FID trials (FID > 4 m), or nearly one incomplete trial for every two complete trials. The proportion of incomplete trials ranged from 0.08 to 0.56 per survey. The proportion of incomplete FID trials per survey was slightly lower, on average, at turbine sites ($\bar{x} = 0.29$, SD = 0.11) relative to non-turbine sites ($\bar{x} = 0.32$, SD = 0.11), indicating a trend of increased wariness (flight before initiating approach) at reference sites; however, the difference was not significant ($W = 10$, $P = 0.686$; Fig. 3).

Because flight responses were so variable, we sought to explore the potential correlates between FID and a number of possible explanatory variables: age class, sex, perch height, perch temperate, perch type (rock or bare ground), canopy cover (none or shrub), sun exposure (full partial, or cloudy) time of day, date, site, treatment (turbine or non-turbine), and observer. Our best-fit model (Table 1) included site, treatment, sex, and canopy cover as predictors of FID ($F_{9,453} = 4.434$, $P < 0.001$), but explained only 8% of the variance in FID ($r^2 = 0.081$). In this multiple regression, only canopy cover and site I-10 were significant predictors of FID (Table 1); lizards perching under shrub cover displayed lower FID ($\beta = -0.401$, $P < 0.001$) and lizards from site I-10 displayed higher FID ($\beta = 0.525$, $P = < 0.001$).

DISCUSSION

Anthropogenic disturbance can affect the richness and total abundance of predators, changing the intensity of predation experienced by prey species in altered

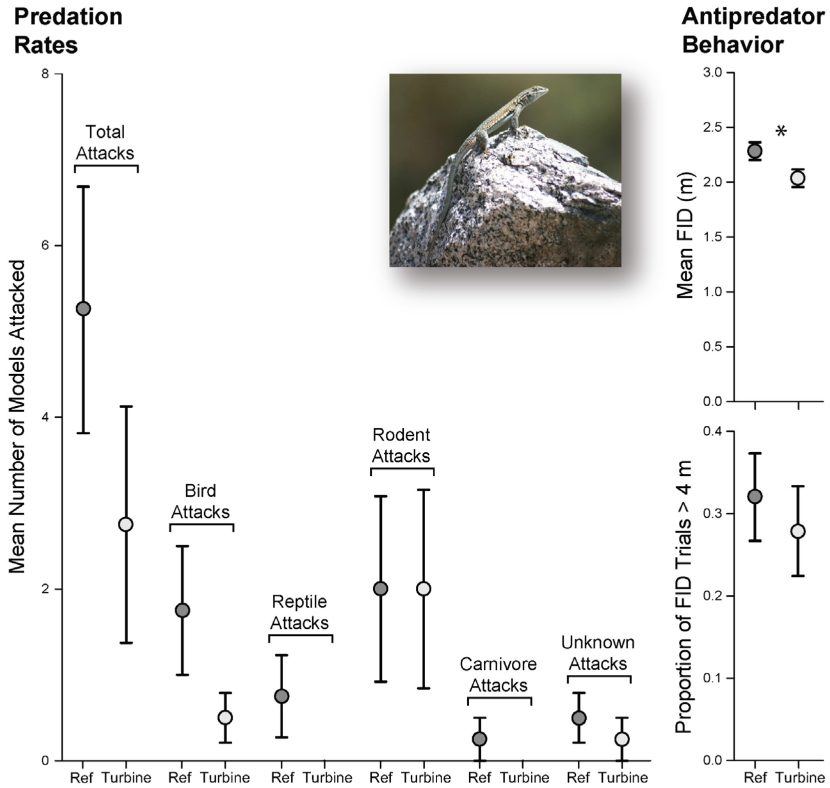

Figure 3. Estimates of predation rates (left) and anti-predator flight-initiation-distance (FID; right) of Side-blotched Lizards (*Uta stansburiana*) surveyed at reference sites without turbines (ref; dark gray) and at sites with wind turbines (turbines: light gray) in the San Gorgonio Wind Resource Area (SGWRA) in southern California, near Desert Hot Springs, north of Palm Springs, USA. Symbols represent mean values, with bars indicating standard error values, and significant differences noted with an asterisk. Inset shows an alert male Side-blotched Lizard perched on a rock in the open. (Photographed by William Flaxington).

Table 1. Summary of the multiple linear regression of the best-fit model of predictors contributing to variation in flight-initiation-distance (FID) in Side-blotched Lizards (*Uta stansburiana*) across the San Gorgonio Wind Resource Area (SGWRA) in southern California, near Desert Hot Springs, north of Palm Springs, USA, with site DH as reference. The best-fit model included site, treatment, sex, and shrub canopy cover as predictor variables of FID ($F_{9,453} = 4.434$, $r^2 = 0.81$, $P < 0.001$).

Factor	β Estimate	Std. Error	*t*-value	*P*-value
Intercept	2.182	0.119	18.347	< 0.001
Site DI	-0.134	0.143	-0.936	0.350
Site I-10	-0.526	0.147	3.574	< 0.001
Site ME	-0.194	0.143	-1.354	0.176
Site MI	0.179	0.157	1.137	0.256
Site MV	-0.254	0.149	-1.711	0.088
Site PH	0.195	0.157	1.241	0.215
Site WW	0.076	0.148	0.512	0.609
Treatment (wind farm)	0.195	0.157	1.241	0.215
Sex (male)	-0.036	0.078	-0.459	0.646
Canopy (cover)	-0.401	0.095	-4.219	< 0.001

habitats (Fischer et al. 2012). At the SGWRA, renewable wind energy sites are characterized by greater levels of anthropogenic disturbance than nearby reference sites without wind turbines (Keehn 2016). Thus, we expected that changes in habitat quality would influence community composition and species interactions, especially predation. Specifically, we predicted that Side-blotched Lizards, a common and abundant prey species, would experience altered predation intensity and change their behavior accordingly at disturbed wind turbine sites relative to reference sites. Indeed, we found that predator attacks on lizard models were less frequent at turbine sites (though not significantly so), and that these lizards were also measurably less wary. Thus, our study suggests that anthropogenic disturbance at wind farms has indirectly influenced Side-blotched Lizards, and this species has responded to through behavioral changes that best suit local biotic conditions.

We found that attack rates on lizard models were nearly half as frequent at turbine sites than those at reference sites. However, our results lacked statistical robustness because of the paucity of attacks per location and overall preclude us from fully assessing the strength and significance of differences between treatment groups. Of 296 models deployed, only 32 experienced attacks, making inferences of predator activity and predation pressure across sites and predator groups difficult.

Our overall, average avian attack rate of 3.0% was within the range of documented clay model attack rates, albeit on the low end (Brodie 1993; Hinman et al. 1997). We noted that most beak prints were small and narrow, characteristic of smaller species such as the Rock Wren (*Salpinctes obsoletus*) or the Loggerhead Shrike (*Lanius ludovicianus*). Other potential predators were easily identified, including larger lizard predators of *Uta*, and local rodents, many of which are omnivorous (such as White-tailed Antelope Squirrels, *Ammospermophilus leucurus*) and known to depredate small lizards opportunistically (Bradley 1968). However, many predators, such as snakes and large invertebrates, are less visually oriented than other predators such as birds or diurnal mammals. Thus, predation intensity by these guilds is poorly approximated using a model lizard attack rate proxy (Baird et al. 1997; Husak et al. 2006). In addition, we observed beetles and ants disturbing the clay models, and it is unclear whether this activity drew the attention of additional predators.

Side-blotched Lizards also appeared less predator-averse at wind farm sites compared to reference sites. Lizards at turbines sites showed a significantly lower flight-initiation-distance (FID) than those at reference sites without turbines. These results are consistent with data from biotic surveys that document fewer encounters of most potential Side-blotched Lizard predators (especially birds) at the same wind farm and reference sites studied here. There were fewer arachnids, mammals, raptors, and songbirds encountered per search hour at turbine sites compared to reference sites, and turbine sites contained lower predator richness overall (Keehn 2016). Taken together, our data on attack rates and anti-predator behavior, along with ecological information on these sites (Keehn 2016), suggest that predation pressure may be lower on Side-blotched Lizards at wind farms in the SGWRA, despite the lack of resolution from our estimates using clay models.

We also observed tremendous variation in anti-predator behavior between individual lizards, much more than between sites or treatment. This variation was not explained by sex (Lailvaux et al. 2003), size class (López et al. 2005), or thermal environment (Bulova 1994). We did find that lizards perched under a shrub canopy were less wary (lower FID) than lizards that perched in the open. We observed that shrubs were often closer to burrowing and refuge sites than other perches, which is consistent with other work demonstrating that lizards closer to potential refuges (burrows and cover sites in shrubs) tend to be less wary (Cooper 2003a; Zani et al. 2009), and that open habitats may also increase visibility of prey to foraging predators (Cooper 2006). Individual variation in flight responses may be influenced by a number of additional underlying and unmodeled factors, including prior experience with a predator (Olla and Davis 1989) or physical and physiological condition (Bauwens and Thoen 1981; Johnson et al. 1996; Cooper 2003b; López et al. 2005). Such individual level variation, if heritable, would create an opportunity for lizards to adapt to differences in predation pressure between sites (Storfer and Sih 1998).

While differences in predation pressure may explain the significance of the treatment effect on wariness behavior, it is possible that a number of other selective pressures may be influencing the behavior of Side-blotched Lizards at wind farm sites. For example, lizards could experience habituation to higher levels of human activity at wind farms (McGowan et al. 2014; but see Amo et al. 2006). Habituation has been documented in geese (Madsen and Boertmann 2008); however, it is unclear whether animals are responding to infrastructure or human activity. Our results do not support a habituation effect, as wariness was not related to magnitude of human activity among reference sites (e.g., heightened wariness at disturbed reference site I-10).

Wind infrastructure may directly influence animal wariness in ways that are unrelated to actual predation intensity. For example, California Ground Squirrels (*Otospermophilus beecheyi*) display increased wariness behavior (measured as foraging activity, alertness, and time spent away from predator refuge sites) in noisy wind farm environments (Rabin et al. 2006). The effect was attributed to masking of anti-predator vocalizations by wind turbines, as control and treatment sites had similar levels of predator abundance (Rabin et al. 2006). We documented fewer clay model attacks at wind farms, which supports our conclusion that lower wariness behavior at wind farms is a consequence of reduced predator activity (or foraging efficiency).

Wind farms may affect frequency of interactions between predators and prey species by reducing predator abundance (through increased mortality or habitat displacement) at wind farms. While a predator refuge effect has been suggested as a mechanism for higher survival rates of Greater Prairie-chickens (*Tympanuchus cupido*; Smith et al. 2017), Desert Tortoises (*Gopherus agassizii*; Agha et al. 2015), and for European Hamster (*Cricetus cricetus*) persistence (Łopucki and Perzanowski 2018) at wind farms, we are not aware of any studies that directly quantify this effect. Predators (as well as prey) will likely exhibit species- and site-specific responses to wind farm development (Smith and Dwyer 2016), and additional research is also needed to better predict the cumulative effects on wildlife community composition. For example, terrestrial or disturbance-tolerant avian predators and scavengers may compensate for the absence of other more sensitive avian predator species at wind farms.

Wind farms are a sustainable energy solution with minimal direct disturbance and associated habitat loss compared to other means of energy production (Denholm et al. 2009). However, wind farms have one of the largest spatial footprints (Mega Watts produced per acre) and require expansive total project areas (Kiesecker et al. 2011). Dispersed infrastructure can cause habitat fragmentation and disturbance over large areas that can significantly alter habitat quality, especially when facilities are sited in previously undisturbed habitats. As seen with urban development, loss of habitat connectivity and associated disturbance at wind farm sites may alter the diversity and function of affected natural systems (Rapport et al. 1985; Sullivan et al. 2017). In our study, wind farm developments appear to have altered ecologically relevant predator-prey interactions and their attendant behaviors in a common lizard species. We suggest that wind farms may indirectly impact habitat quality in other prey species by similarly modifying patterns of species interactions and associations. Continued research on the use or avoidance of wind farms by prey and predators alike will assist land managers charged with mitigating the negative effects of wind energy development on wildlife.

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LITERATURE CITED

Abella, S.R. 2010. Disturbance and plant succession in the Mojave and Sonoran deserts of the American Southwest. International Journal of Environmental Research and Public Health 7:1248–1284.

Agha, M., J.E. Lovich, J.R. Ennen, B. Augustine, T.R. Arundel, M.O. Murphy, K. Meyer-Wilkins, C. Bjurlin, D. Delaney, J. Briggs, et al. 2015. Turbines and terrestrial vertebrates: variation in tortoise survivorship between a wind energy facility and an adjacent undisturbed wildland area in the desert southwest (USA). Environmental Management 56:332–341.

Agha, M., A.L. Smith, J.E. Lovich, D. Delaney, J.R. Ennen, J. Briggs, L.J. Fleckenstein, L.A. Tennant, S.R. Puffer, A. Walde, et al. 2017. Mammalian mesocarnivore visitation at tortoise burrows in a wind farm. Journal of Wildlife Management 81:1117–1124.

Amo, L., P. López, and J. Martín. 2006. Nature-based tourism as a form of predation risk affects body condition and health state of *Podarcis muralis* lizards. Biological Conservation 131:402–409.

Ayal Y. 2007. Trophic structure and the role of predation in shaping hot desert communities. Journal of Arid Environments 68:171–187.

Baird, T.A., S.F. Fox, and J.K. McCoy. 1997. Population differences in the roles of size and coloration in intra- and intersexual selection in the Collared Lizard, *Crotaphytus collaris*: influence of habitat and social organization. Behavioral Ecology 8:506–517.

Baldwin, B.G., A.H. Thornhill, W.A. Freyman, D.D. Ackerly, M.M. Kling, N Morueta-Holme, and D. D. Mishler. 2017. Species richness and endemism in the native flora of California. American Journal of Botany 104:487–501.

Barrows, C.W., M.F. Allen, and J.T. Rotenberry. 2006. Boundary processes between a desert sand dune community and an encroaching suburban landscape. Biological Conservation 131:486–494.

Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. Journal of Animal Ecology 50:733–743.

Bradley, W.G. 1968. Food habits of the antelope ground squirrel in southern Nevada. Journal of Mammalogy 49:14–21.

Brodie, E.D. III. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution 47:227–235.

Bulova, S.J. 1994. Ecological correlates of population and individual variation in anti-predator behavior of two species of desert lizards. Copeia 1994:980–992.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd Edition. Springer, New York, New York, USA.

Calcagno, V., and C. de Mazancourt. 2010. glmulti: an R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34:1–29.

Cooper, W.E., Jr. 2003a. Risk factors affecting escape behavior by the Desert Iguana, *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. Canadian Journal of Zoology 81:979–984.

Cooper, W.E., Jr. 2003b. Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the Keeled Earless Lizard (*Holbrookia propinqua*). Behavioral Ecology and Sociobiology 54:179–187.

Cooper, W.E., Jr. 2006. Risk factors affecting escape behaviour by Puerto Rican Anolis lizards. Canadian Journal of Zoology 84:495–504.

Cooper, W.E., Jr. and M.J. Whiting. 2007. Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. Ethology 113:661–672.

Cryan, P.M., and R.M. Barclay. 2009. Causes of bat fatalities at wind turbines: hypotheses and predictions. Journal of Mammalogy 90:1330–1340.

Denholm, P., M. Hand, M. Jackson, and S. Ong. 2009. Land-use requirements of modern wind power plants in the United States. Technical Report NREL/TP-6A2-45834. National Renewable Energy Laboratory, Golden, Colorado, USA. 46 p.

Devereux, C.L., M.J. Denny, and M.J. Whittingham. 2008. Minimal effects of wind turbines on the distribution of wintering farmland birds. Journal of Applied Ecology 45:1689–1694.

Dobson, A.P., J.P. Rodriguez, W.M. Roberts, and D.S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science 275:550–553.

Ennen, J.R., J.E. Lovich, K.P. Meyer, C. Bjurlin, and T.R. Arundel. 2012. Nesting ecology of a population of *Gopherus agassizii* at a utility-scale wind energy facility in Southern California. Copeia 2012:222–228.

Evans, A., V. Strezov, and T.J. Evans. 2009. Assessment of sustainability indicators for renewable energy technologies. Renewable and Sustainable Energy Reviews 13:1082–1088.

Finke, D.L., and R.F. Denno. 2004. Predator diversity dampens trophic cascades. Nature 429:407–410.

Fischer, J.D., S.H. Cleeton, T.P. Lyons, and J.R. Miller. 2012. Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. Bioscience 62:809–818.

Frondel, M., N. Ritter, C.M. Schmidt, and C. Vance. 2010. Economic impacts from the promotion of renewable energy technologies: the German experience. Energy Policy 38:4048–4056.

Gifford, M.E., A. Herrel, and D.L. Mahler. 2008. The evolution of locomotor morphology, performance, and anti-predator behaviour among populations of *Leiocephalus* lizards from the Dominican Republic. Biological Journal of the Linnean Society 93:445–456.

Harte, J., and A. Jassby. 1978. Energy technologies and natural environments: the search for compatibility. Annual Review of Energy 3:101–146.

Hawlena, D., D. Saltz, Z. Abramsky, and A. Bouskila. 2010. Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. Conservation Biology 24:803–809.

Hethcoat, M.G., and A.D. Chalfoun. 2015. Towards a mechanistic understanding of human-induced rapid environmental change: a case study linking energy development, nest predation and predators. Journal of Applied Ecology 52:1492–1499.

Hinman, K.E., H.L. Throop, K.L. Adams, A.J. Dake, K.K. McLauchlan, and M.J. McKone. 1997. Predation by free-ranging birds on partial coral snake mimics: the importance of ring width and color. Evolution 51:1011–1014.

Howe, K.B., P.S. Coates, and D.J. Delehanty. 2014. Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem. The Condor 116:35–49.

Hunt, W.G., R.E. Jackman, T.L. Hunt, D.E. Driscoll, and L. Culp. 1998. A population study of Golden Eagles in the Altamont Pass Wind Resource Area: a population trend analysis 1994–1997. National Resource Energy Laboratory SR-500-26092, Golden, Colorado, USA. 43 p.

Husak, J.F., J.M. Macedonia, S.F. Fox, and R.C. Sauceda. 2006. Predation cost of conspicuous male coloration in Collared Lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. Ethology 112:572–580.

Jacobs, G.H. 1981. Comparative Color Vision. Academic Press, New York, New York, USA.

Jacobs, G.H. 2009. Evolution of colour vision in mammals. Philosophical Transactions of the Royal Society B: Biological Sciences 364:2957–2967.

Johnsson, J.I., E. Petersson, E. Jönsson, B.T. Björnsson, and T. Järvi. 1996. Domestication and growth hormone alter anti-predator behaviour and growth patterns in juvenile Brown Trout, *Salmo trutta*. Canadian Journal of Fisheries and Aquatic Sciences 53:1546–1554.

Keehn, J.E. 2016. Persistence of wildlife populations in low-diversity renewable wind-energy landscapes. M.Sc. Thesis, University of Nevada, Reno, Nevada, USA. 146 p.

Kiesecker, J.M., J.S. Evans, J. Fargione, K. Doherty, K.R. Foresman, T.H. Kunz, D. Naugle, N.P. Nibbelink, and N.D. Niemuth. 2011. Win-win for wind and wildlife: a vision to facilitate sustainable development. PLoS One 6, 1–8. https://doi.org/10.1371/journal.pone.0017566.

Kuvlesky, W.P., L.A. Brennan, M.L. Morrison, K.K. Boydston, B.M. Ballard, and F.C. Bryant. 2007. Wind energy development and wildlife conservation: challenges and opportunities. Journal of Wildlife Management 71:2487–2498.

Lailvaux, S.P, G.J. Alexander, and M.J. Whiting. 2003. Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. Physiological and Biochemical Zoology 76:511–521.

Leddy, K.L., K.F. Higgins, and D.E. Naugle. 1999. Effects of wind turbines on upland nesting birds in Conservation Reserve Program grasslands. Wilson Bulletin 111:100–104.

Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

López, P., D. Hawlena, V. Polo, L. Amo, and J. Martín. 2005. Sources of individual shy-bold variations in anti-predator behaviour of male Iberian rock lizards. Animal Behaviour 69:1–9.

Łopucki, R., and K. Perzanowski. 2018. Effects of wind turbines on spatial distribution of the European Hamster. Ecological Indicators 84:433–436.

Lovich, J.E., and D. Bainbridge. 1999. Anthropogenic degradation of the Southern California desert ecosystem and prospects for natural recovery and restoration. Environmental Management 24:309–326.

Lovich, J.E., and R. Daniels. 2000. Environmental characteristics of Desert Tortoise (*Gopherus agassizii*) burrow locations in an altered industrial landscape. Chelonian Conservation and Biology 3:714–721.

Lovich, J.E., and J.R. Ennen. 2013. Assessing the state of knowledge of utility-scale wind energy development and operation on non-volant terrestrial and marine wildlife. Applied Energy 103:52–60.

Madsen, J., and D. Boertmann. 2008. Animal behavioral adaptation to changing landscapes: spring-staging geese habituate to wind farms. Landscape Ecology 23:1007–1011.

Mahoney, A., and A.D. Chalfoun. 2016. Reproductive success of Horned Lark and McCown's Longspur in relation to wind energy infrastructure. Condor 118:360–375.

McGowan, M.M., P.D. Patel, J.D. Stroh, and D.T. Blumstein. 2014. The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. Ethology 120:1081–1089.

McLaughlin, S.P. 1986. Floristic analysis of the southwestern United States. Great Basin Naturalist 46:46–65.

Northrup, J.M., and G. Wittemyer. 2013. Characterizing the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecology Letters 16:112–125.

Olla, B.L., and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared Coho Salmon (*Oncorhynchus kisutch*) juveniles. Aquaculture 76:209–214.

Osorio, D., A. Miklósi, and Z. Gonda. 1999. Visual ecology and perception of coloration patterns by domestic chicks. Evolutionary Ecology 13:673–689.

Panwar N.L., S.C. Kaushik, and S. Kothari. 2011. Role of renewable energy sources in environmental protection: a review. Renewable and Sustainable Energy Reviews 15:1513–1524.

Parker W.S., and E.R. Pianka. 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. Copeia 1975:615–632.

Pearce-Higgins, J.W., L. Stephen, R.H. Langston, I.P. Bainbridge, and R. Bullman. 2009. The distribution of breeding birds around upland wind farms. Journal of Applied Ecology 46: 1323–1331.

Rabin, L.A., R.G. Coss, and D.H. Owings. 2006. The effects of wind turbines on anti-predator behavior in California Ground Squirrels (*Spermophilus beecheyi*). Biological Conservation 131:410–420.

Rapport, D.J., H.A. Regier, and T.C. Hutchinson. 1985. Ecosystem behavior under stress. American Naturalist 125:617–640.

R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org.

Santos, M., R. Bastos, P. Travassos, R. Bessa, M. Repas, and J.A. Cabral. 2010. Predicting the trends of vertebrate species richness as a response to wind farms installation in mountain ecosystems of northwest Portugal. Ecological Indicators 10:192–205.

Smith, J.A., M.B. Brown, J.O. Harrison, and L.A. Powell. 2017. Predation risk: a potential mechanism for effects of a wind energy facility on Greater Prairie-Chicken survival. Ecosphere 8:1–15. https://doi.org/10.1002/ecs2.1835.

Smith, J.A., and J.F. Dwyer. 2016. Avian interactions with renewable energy infrastructure: an update. Condor 118:411–423.

Spencer, W., S.R. Abella, C. Barrows, K. Berry, T.C. Esque, K Garrett, C.A. Howell, R. Kobaly, R, R.F. Noss, R.A. Redak, et al. 2010. Recommendations of independent science advisors for the California Desert Renewable Energy Conservation Plans (DRECP). Conservation Biology Institute, Corvallis, Oregon, USA.

Stoms, D.M., S.L. Dashiell, and F.W. Davis. 2013. Siting solar energy development to minimize biological impacts. Renewable Energy 57:289–298.

Storfer, A., and A. Sih. 1998. Gene flow and ineffective anti-predator behavior in a stream-breeding salamander. Evolution 52:558–565.

Sullivan, B.K., D.J. Leavitt, and K.O. Sullivan. 2017. Snake communities on the urban fringe in the Sonoran Desert: influences on species richness and abundance. Urban Ecosystems 20:199–206.

Tanis, B.P. 2013. Influence of wind turbines on mammalian occupancy patterns. M.Sc. Thesis, Fort Hays State University, Hays, Kansas, USA. 76 p.

Tinkle, D.W. 1967. The life and demography of the Side-blotched Lizard, *Uta stansburiana*. Miscellaneous Publications Museum of Zoology, University of Michigan 132:1–182.

Vandergast, A.G., R.D. Inman, K.R Barr, K.E. Nussear, T.C. Esque, S.A. Hathaway, D.A. Wood, P.A. Medica, J.W. Breinholt, C.L. Stephen, et al. 2013. Evolutionary hotspots in the Mojave Desert. Diversity 5:293–319.

Vervust, B., I. Grbac, and R. Van Damme. 2007. Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. Oikos 116:1343–1352.

Villegas-Patraca, R., I. Macgregor-Fors, T. Ortiz-Martínez, C.E. Pérez-Sánchez, L. Herrera-Alsina, and C. Muñoz-Robles. 2012. Bird-community shifts in relation to wind farms: a case study comparing a wind farm, croplands, and secondary forests in southern Mexico. Condor 114:711–719.

Wagner, E.A., and P.A. Zani. 2017. Escape behavior of side-blotched lizards in response to model predators. Canadian Journal of Zoology 95:965–973.

Wilson, B.S. 1991. Latitudinal variation in activity season mortality rates of the lizard *Uta stansburiana*. Ecological Monographs 61:393–414.

Winder, V.L., L.B. McNew, A.J. Gregory, L.M. Hunt, S.M. Wisely, and B.K. Sandercock. 2014. Effects of wind energy development on survival of female greater prairie-chickens. Journal of Applied Ecology 51:395–405.

Wood, D.A., A.G. Vandergast, K.R. Barr, R.D. Inman, T.C. Esque, K.E. Nussear, and R.N. Fisher. 2013. Comparative phylogeography reveals deep lineages and regional evolutionary hotspots in the Mojave and Sonoran deserts. Diversity and Distributions 19:722–737.

Zani, P.A., T.D. Jones, R.A. Neuhaus, and J.E. Milgrom. 2009. Effect of refuge distance on escape behavior of Side-blotched Lizards (*Uta stansburiana*). Canadian Journal of Zoology 87:407–414.

Zani, P.A., J.L. Tillman, and K.M. Scoular. 2013. Geographic variation of movement and display behavior of Side-blotched Lizards (*Uta stansburiana*) related to predation environment. Journal of Herpetology 47:85–92.

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