Research Article

Population-Level Effects of Wind Farms on a Desert Lizard

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ABSTRACT Renewable forms of energy production can have major societal benefits including reduced carbon pollution and decreased dependence on fossil fuels but are not without associated costs. For example, habitat degradation at renewable energy production sites may affect the persistence of wildlife populations. We assessed the effects of wind farms in the San Gorgonio Wind Resource Area near Palm Springs, California, 2013–2015, on local populations of the side-blotched lizard (*Uta stansburiana*). The side-blotched lizard is a common and ubiquitous desert reptile that is a major consumer of invertebrates and, in turn, represents a key prey base for many avian, reptilian, and mammalian predators. We used spatially explicit capture-recapture methods to compare a comprehensive set of population-level vital signs (i.e., abundance, population growth rate, survival, recruitment, body condition, age structure, activity area size, movement rates) among populations at 4 wind farms and at 5 reference areas. Although our models indicate that wind facilities have a weak negative effect on side-blotched lizard survival, our overall results suggest that wind farms do not substantially influence the demography or behavior of these small lizards. Population response to general anthropogenic disturbance (quantified as an index of road type and density) was more pronounced, with lower population growth rates, adult-skewed age structure, and reduced body condition at highly disturbed wind farm and reference sites. We therefore conclude that wind-power facilities can support healthy populations of side-blotched lizards, indicating that wind energy development is compatible with a native Mojave Desert species. However, our results show that anthropogenic disturbance, as measured by the type and density of roadways, has a negative effect on lizard populations, and should be carefully planned whether associated with energy development or not. Our study demonstrates a methodological approach that can be applied to other species, including those with lower tolerances to disturbance, to measure their response to renewable energy development. © 2018 The Wildlife Society.

KEY WORDS anthropogenic disturbance, recruitment, renewable energy, side-blotched lizard, spatially explicit capture-recapture (SECR), survival, *Uta stansburiana*, wind turbine.

Climate change, influenced by fossil fuel use, is an unintended consequence of developed human societies that stands to significantly alter global patterns of biodiversity (Vitousek 1994). Slowing the rate of extinction from climate change will require substantial financial and political investment in renewable energy production (Bilgen et al. 2004). However, the widespread development of new renewable energy infrastructure might still result in local biodiversity loss during facility construction and operation, and may also compete with existing land-use priorities such as maintaining habitat for wildlife (Pearce-Higgins et al. 2009, Lovich and Ennen 2013, Jones et al. 2015). The magnitude of wildlife habitat loss from energy infrastructure varies among renewable technologies (Evans et al. 2009). For

example, wind turbine spacing requirements and associated access roads demand large tracts of land to accommodate energy production needs (Denholm et al., 2009, Evans et al. 2009), greatly exceeding project area size for alternative technologies such as solar or geothermal energy (Evans et al. 2009). However, wind energy developments are unique among renewable energy technologies because the actual footprint of a wind farm (1 ± 0.7 ha for each MW of installed capacity) may be small (Denholm et al. 2009). Most of the physical footprint of wind energy developments is from road infrastructure to access wind turbines; the remaining land can be left in a natural state (Denholm et al. 2009). Hence, if organisms can maintain viable populations within the turbine-habitat matrix, wind energy may be a sustainable form of renewable energy production with minimal loss of wildlife habitat (Kelcey 1975, Menzel and Pohlmeyer 1999).

Studies that address environmental consequences of wind energy for wildlife focus primarily on direct mortality risk for birds and bats (Barclay et al. 2007, Kuvlesky et al. 2007,

Baerwald et al. 2009, Cryan and Barclay 2009). However, the potential for loss of habitat, avoidance, and other behavioral changes at wind farm sites may result in greater biodiversity loss than turbine-induced mortality alone (Drewitt and Langston 2006, Pearce-Higgins et al. 2009, Helldin et al. 2012). Habitat loss may have a disproportionately negative effect on sensitive or native species and benefit more disturbance-tolerant or invasive species, an effect with potentially dire consequences including altered patterns of ecosystem structure and function (Gordon 1998, Finke and Denno 2004, Hansen et al. 2005). Researchers have begun to address whether wind farms can support viable populations of terrestrial mammals, including small mammals (Menzel and Pohlmeyer 1999, de Lucas et al. 2005, Rabin et al. 2006, Łopucki and Mróz 2016, Łopucki et al. 2017), ungulates (Flydal et al. 2004, Walter et al. 2006, Reimers et al. 2007, Colman et al. 2008, Veiberg and Pedersen 2010), and carnivores (Menzel and Pohlmeyer 1999, Flagstad and Tovmo 2010, Álvares et al. 2011, Agha et al. 2017, Łopucki et al. 2017). However, information is lacking for most other groups, with only a handful of studies on the effects of wind energy on reptiles (Lovich and Daniels 2000, Santos et al. 2010, Lovich et al. 2011b, Ennen et al. 2012, Agha et al. 2015), amphibians (Santos et al. 2010), and plants (Keehn and Feldman 2018a).

Reptiles are key components of desert food webs as important predators of invertebrates and other small vertebrates (Spiller and Schoener 1990, Polis 1991, Vitt 1991, Brown et al. 1994). Thus, a change in abundance or absence of reptiles from wind energy sites may alter species interactions, community composition, diversity, and ecosystem function.

To date, population-level responses of reptiles to wind farms have only been documented in the desert tortoise (*Gopherus agassizii*). Differences in habitat use and novel causes of mortality were identified at a single wind farm site (Lovich and Daniels 2000, Lovich et al. 2011a). When compared with nearby natural areas, tortoises at wind farms had slightly larger activity areas, and significantly higher survival (Agha et al. 2015). These effects may have been due to reduced mortality from predators and traffic, increased resource availability, and ease of movement at wind farms (Agha et al. 2015). More research is needed to better understand the generality of these effects at other wind farm sites, and the long-term effects of energy infrastructure on recruitment, which may greatly affect population persistence (Agha et al. 2015).

Few studies have addressed the population-level responses of short-lived terrestrial vertebrates at wind farms. Short-lived species may respond more quickly to changes in habitat composition and patch size resulting from anthropogenic activity at wind farm developments (Bossuyt and Honnay 2006, Morris et al. 2008, Krauss et al. 2010). Side-blotched lizards (*Uta stansburiana*) are ideal focal organisms for population-level studies because they maintain large populations across small areas, are relatively easy to capture, and have high site fidelity, making it easy to follow individuals over time (Tanner 1972). In addition, the side-blotched lizard is one of the most well-studied reptiles of North American deserts, providing useful context for understanding the ecological conditions and selective pressures that determine population persistence (Tinkle 1967a, Fox 1978, Turner et al. 1982, Wilson and Cooke 2004). As a nearly ubiquitous lizard in the arid west, this species provides a quick meal to a diverse group of predators, such as loggerhead shrikes (*Lanius ludovicianus*), roadrunners (*Geococcyx californianus*), collared lizards (*Crotophytus bicinctores*), leopard lizards (*Gambelia wislizenii*), rattlesnakes (*Crotalus* spp.), and scorpions (Tinkle et al. 1962, Tanner and Jorgensen 1963, Tinkle 1967a, Parker and Pianka 1975, Wilson 1991). As such, side-blotched lizards are considered important species in desert food webs across the western United States (Tinkle 1967a, Parker 1974, Wilson 1991).

In this study, we examined the population-level responses of the side-blotched lizard (*Uta stansburiana*), to wind energy development. Our objective was to assess the suitability of wind farms as habitat for the side-blotched lizard. We hypothesized that increased anthropogenic disturbance at wind farms would alter or degrade the quality of lizard habitat at these sites. For example, higher road densities may facilitate exotic plant introductions, reducing native prey density, increasing cost of movement (Newbold 2005, Pearson 2009, Rieder et al. 2010), and reducing survival and reproduction for lizards with poor energy reserves and high exposure to predators (Nussbaum and Diller 1976, Fox et al. 1981, Zani 2005, Keehn and Feldman 2018b). Thus, we predicted that disturbance associated with wind farms would negatively affect rates of survival, recruitment (and associated population age structure), movement, average activity area size, and body condition for local lizard populations (Johnson et al. 1975, Polis et al. 1998, Gosselink et al. 2007). In addition, fragmentation and loss of habitat can result in reduced carrying capacity and increased local extinction risk (Thomas et al. 2001); therefore, we predicted smaller population sizes and altered trends in abundance over time at wind farm sites.

STUDY AREA

Southern California's San Gorgonio Wind Resource Area (SGWRA) is 1 of 3 major wind resource areas in California and includes the lands in and around the San Gorgonio Pass (or Banning Pass), mainly between Cabazon and Palm Springs, at the northwestern edge of the Coachella Valley. The pass is one of the windiest places in California because air currents are forced through the narrow divide between the San Jacinto Mountains (Peninsular Ranges) to the south and the San Bernardino Mountains (Transverse Ranges) to the north. The area is rugged and varied, including steep mountain pitches, boulder strewn washes, and sandy basins. Our sites ranged in elevation from 318 m to 823 m, and average precipitation during the study period (Jul 2013 to Jun 2015) ranged from 16.8 cm/year to 46.7 cm/year. The study area also lies in a transition zone between the Mojave and Colorado deserts (Schoenherr 2017); the region experiences 2 distinct seasons, with mild late fall and winter weather driven by cool and humid air (and storms) from the

Pacific Ocean (average daily low temperatures below 10°C from mid-Nov through Feb), giving way to hot and dry spring and summer weather (average daily high temperatures in excess of 38°C from Jun through Sep). Dominant flora species at our sites are characteristic of Mojave Desert creosote-bush (*Larrea tridentata*) scrub communities, including creosote bush, white bur-sage (*Ambrosia dumosa*), cheesebush (*Ambrosia salsola*), and brittlebush (*Encelia farinosa*). Common fauna at our sites included side-blotched lizards, western whiptail lizards (*Aspidoscelis tigris*), common ravens (*Corvus corax*), loggerhead shrikes, coyotes (*Canis latrans*), and bobcats (*Lynx rufus*).
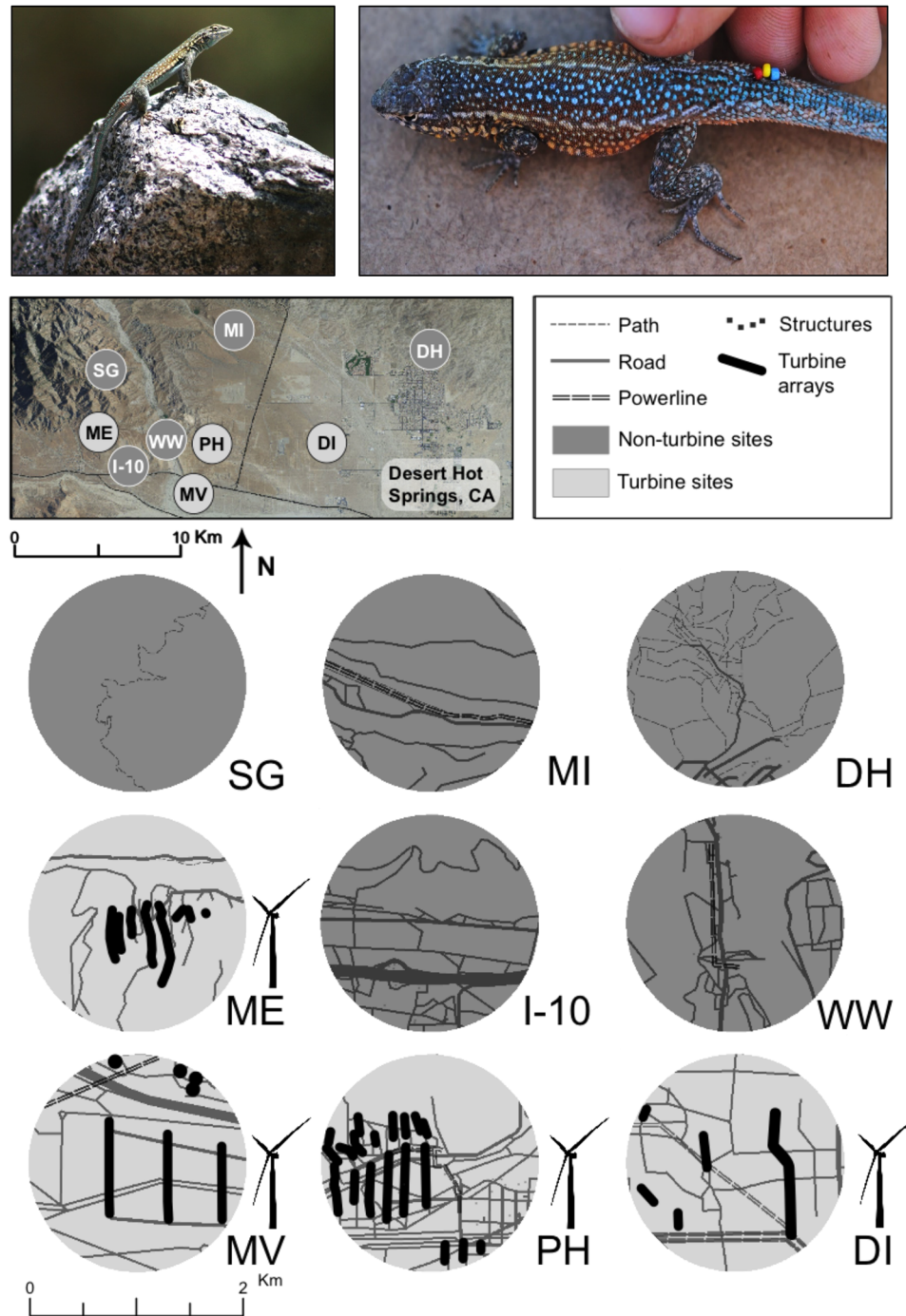

Figure 1. Side-blotched lizard and study sites in the San Gorgonio Wind Resource Area in Southern California, near Desert Hot Springs, north of Palm Springs, USA, 2013–2015. Image at top left illustrates an alert lizard defending its territory and allowing for visual recapture (photo: W. C. Flaxington), and image at top right shows a mature, adult male with color-coded bead tags used to mark lizards (photo: J. E. Keehn). We conducted mark-recapture surveys at 9 study sites; 5 reference sites lacked turbines (dark gray), and 4 treatment sites contained turbines (light gray). Insets show land-use at each study area: 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.

Table 1. Facility characteristics for each of the 4 wind farm study areas within the San Gorgonio Wind Resource Area near Palm Springs, California, USA, 2013–2015.

Wind farm	Wind farm size (km^2)	Number of turbines	Hub height (m)	Structure type	Turbine density	Installation date
ME	1.7	460	20–25	Lattice frame	High	1983
PH	0.7	168	20–25	Lattice frame	High	1984
MV	0.9	45	60–70	Monopole-mounted	Low	2002
DI	2.5	21	60–70	Monopole-mounted	Low	2007

We established 9 study plots (roughly 60 m × 60 m) across a gradient of land cover types within the SGWRA (Fig. 1). We selected study plots at 4 different wind farm sites with active turbines (sites ME, PH, DI, and MV). 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 (Table 1).

We established reference plots at 5 sites on Bureau of Land Management (BLM) lands (BLM permit number 6500 CT-063.50) without wind turbines (sites MI, SG, WW, DH, and I-10; Fig. 1). Sites MI and SG were low-disturbance areas ≥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 grazing. 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.

METHODS

Mark-Recapture Field Surveys

For each of the 9 study plots, we tracked the fates of adult and sub-adult lizards (>35 mm snout-to-vent length [SVL]; Tanner 1972) from July 2013 to June 2015. During this period, we conducted 10 primary capture sessions at semi-regular intervals throughout the main activity period of side-blotched lizards in the area: early spring, late spring, early summer, mid-summer, and late summer. Within each primary session, we visited each of the 9 sites on 2 to 3 consecutive days (capture occasions; hereafter, secondary occasions) except during the late spring survey period, which consisted of 1 rather than 2 secondary occasions. We added a final turbine site (PH) in late spring of 2014 (surveyed for 7 primary capture sessions).

During each site visit, a group of 1 to 4 observers searched for lizards during their activity periods, usually mornings or evenings, and occasionally all day when lizards remained active because of mild or cloudy weather (we recorded person-hours for each survey). At the start and end of each survey we recorded time of day, wind speed, cloud cover, substrate temperature, air temperature, and relative humidity (Table 2, S1). We avoided surveying on days that were unsuitable for lizard activity (i.e., rainy, high winds, cold temperatures). We thoroughly and evenly searched the entire study plot area and captured any unmarked adult or sub-adult lizards within the survey plot by hand-held noose or by hand. We continued to catch lizards from the time of emergence, until lizards retreated, typically around mid-morning or mid-day from high temperatures, or at dusk. On average, surveys took 2.92 ± 1.04 (SD) hours to complete. We recorded global positioning system (GPS) coordinates for all marked lizards encountered. Prior to analyses we used GPS locations and scale patterns of lizards from field photos (when available) to verify recaptures across years.

Table 2. Description of survey-level measurements used as covariates for estimating capture probabilities of side-blotched lizards in the spatially explicit capture-recapture model, and site-level measurements used as covariates in additive linear regression models explaining observed variation in population-level vital signs (abundance, population growth rate, survival, recruitment, body condition, age structure, activity area size, movement rates) from 2013 to 2015 at wind farms and reference areas in Southern California, USA.

Scope of measurement	Variable	Description
Secondary sampling session (measured at time of each survey)		
	Activity period	Categorical variable indicating morning vs. evening surveys
	Cloud cover	Categorized as low (0–24%), moderate (25–49%), high (50–75%), or very high (75–100%)
	Relative humidity	Humidity at breast height, measured with a Kestrel meter
	Survey effort	Time from first adult lizard emergence to end of survey, adjusted for (multiplied by) number of surveyors
	Temperature	Temperature (°C) of substrate in direct sunlight
	Wind speed	Average wind speed at time of survey, measured with a Kestrel meter
Site-level (unique characteristic of each site)		
	Disturbance	Physical human disturbance, measured as total road length and road type within a 1,000-m radius of the study site polygon
	Bare-ground cover	Bare ground cover at each site measured using a random-point-intercept survey protocol
	Noise	Average A-weighted decibel reading (dB$_A$) from a random sample of 10 readings taken at plots in June and July (2015) when turbines were running and wind was ≤5.6 km/hr
	Precipitation	Total winter precipitation (mm; PRISM Climate Group 2015)
	Turbine presence	Categorical variable indicating the presence of wind turbines

For each newly captured lizard, we recorded mass, total length (TL), and SVL (Table S2). We determined sex, palpated females for developing follicles, identified whether the lizard had previously lost a tail, noted any additional injuries, and counted the number of external parasites. In 2013, we individually marked lizards by removing combinations of up to 3 toes/lizard to create unique permanent identifiers (Bogert 1947) and to provide a source of DNA for future studies. We then applied temporary numbers on the dorsum with paint markers to allow re-sighting without recapture. In the early summer 2014, to facilitate visual re-sighting, we began marking lizards using a unique combination of 3 plastic beads secured with surgical steel to the base of the tail posterior, and in the case of males, just posterior to the hemipenes (Fisher and Muth 1989). All animal capture and handling protocols were approved by The Institutional Animal Care and Use Committee at the University of Nevada, Reno, USA (protocol number 00586), and with authorization from the California Department of Fish and Wildlife (scientific collecting permit numbers SC-012775 and SC-000814).

Analyses

Spatially explicit capture recapture (SECR).—We used a SECR study design to estimate 8 population-level vital signs —survival rate, recruitment rate, population densities, trends in abundance, size of activity areas, movement propensity (probability of selecting new core activity areas), age structure (fraction of subadults), and body condition—at replicated treatment (active turbines present) and reference (no turbines present) locations (Efford 2004, Borchers and Efford 2008, Royle et al. 2014). Given the intrinsic link between population status and habitat condition, the use of population vital parameters to assess the value of wind farms as wildlife habitat is a valuable approach that can aid efforts to identify and mitigate the environmental consequences of wind farms.

We estimated population vital signs using a custom SECR model, modified from Royle and Dorazio's (2008:248) formulation for closed-population abundance estimation and their data-augmented Schwarz-Arnason formulation for estimating survival and recruitment (Royle and Dorazio 2008:337–345; both in BUGS language). The raw data and the R/JAGS code needed to reproduce these analyses and a detailed description of the JAGS model are available at https://github.com/kevintshoemaker/UTA_secr.

We modeled capture probability as a logit-linear function of individual lizard characteristics (sex, presence of visual marking) and survey characteristics (person-hours spent surveying, wind speed, evening vs. morning; Table 2). Wind speed may reduce surface activity of reptiles by increasing the rate of heat and water loss (Stevenson 1985). We distinguished between evening surveys (initiated from 1310 to 1815), relative to morning surveys (initiated from 0625 to 1030) because evening surveys may be characterized by warmer and less variable substrate temperatures, potentially suppressing lizard activity (Grant 1990). Additional survey-condition variables that were measured but not included in our final capture probability model included substrate temperature (which can affect surface activity; Huey 1982), cloud cover, and humidity (which can affect evaporative water loss and prey activity levels; Norris 1953, Tanner 1972, Holm and Edney 1973, Jaworski and Hilszczański 2013). We assumed capture probability was related to the spatial location of individuals (based on the movement sub-model; see below) in the following manner: individuals present in the surveyed area were captured with a finite probability, whereas individuals present in the population but not present in the surveyed area had a zero probability of capture (Royle and Dorazio 2008). We assumed perfect population closure during sampling occasions (each of 1 to 3 consecutive-day surveys) following a standard robust design framework (Kendall et al. 1995).

We estimated mean monthly survival probability separately for each study site and assumed survival rates did not vary substantially by sex and age class (subadult or adult). We developed this model structure based on preliminary Huggins robust-design models conducted in Program MARK version 8.0 (Huggins 1991, White and Burnham 1999). We did not account for variation in survival across lizard throat color morphs (Sinervo and Lively 1996) because we could not reliably assess this trait in the field. We accounted for differences in the interval between primary sampling occasions (varying from ~2 weeks to 7 months) using the formula, $\phi_t = \phi_s^{interval_t}$, where ϕ_t is the survival rate from session t to $t+1$, ϕ_s is the estimated monthly site-level survival, and $interval_t$ is the interval between t and session $t+1$ in months.

We estimated entry probability (probability of entering the population from the pool of individuals living in the population at some point during the study period; hereafter, super-population), reflecting reproduction and immigration separately for each site and for each primary sampling period. We estimated the number of recruits for each site-period combination as a derived parameter. For subsequent processing, we ignored recruits from the initial sampling period, which, in the data-augmentation framework, represent individuals already alive and in the studied population upon initiation of sampling. Finally, we divided the estimated number of recruits by the estimated lizard abundance for each site-period combination, and treated site-level averages as a metric of site-level differences in *per capita* recruitment.

For the movement sub-model, we assumed each individual maintained a unique activity center within each primary session. We assumed each individual was most likely to be captured at its current activity center, with probabilities dropping off isotropically with distance from activity center according to a half-normal distribution (Royle and Dorazio 2008). We allowed individuals to relocate their activity centers among primary sessions according to a monthly movement probability that was corrected for different survey intervals using the same method as for survival. We modeled movement probability using the formula $\gamma_t = \gamma_s^{interval_t}$, where γ_t is the movement rate from session t to $t+1$, γ_s is the estimated monthly site-level movement probability, and

$interval_t$ is the interval between t and session $t+1$ in months. For those individuals we found to have shifted activity centers in our algorithm, we drew movement directions randomly from 0 to 2π radians, and drew movement distances from a uniform distribution ranging from 4 m (radius within which most normal daily movement occurs, determined from our preliminary analyses) and 20 m (arbitrarily determined as 5 times the radius of normal daily movements).

The movement process accounted for temporary emigration outside the study area, and partially accounted for permanent emigration (assuming that permanent and temporary emigration are manifestations of the same movement process). Therefore, we interpreted survival rates estimated from our model as true survival, rather than apparent survival (i.e., the survival estimates do not conflate true survival and permanent emigration). As further evidence for this interpretation, common side-blotched lizards have limited dispersal rates, with lifetime migration rates estimated at 12% (Tinkle 1967a, b) and a radius of activity estimated at ≤24 m from territory center points for 90% of observations (Spoecker 1967).

We computed population size and density estimates in each plot as derived terms using standard data-augmentation methods (Royle and Dorazio 2008). In preparation for evaluating site-level effects (see below), we computed mean population density, mean monthly survival, mean *per capita* recruitment rate (estimated recruits divided by abundance), size of activity area (standard deviation of the half-normal function describing probability of capture vs. distance from core activity area), and mean monthly movement probability for each study plot. We computed the abundance trend for each site as the slope of a linear regression of population density on time (days since study initiation).

We estimated all parameters with Markov chain Monte Carlo (MCMC) methods using JAGS version 4.2.0 (Plummer 2015), which was called from R version 3.4.0 (R Foundation for Statistical Computing, Vienna, Austria) using the runjags package (Denwood 2016). We assigned vague priors to all free parameters (Table S3). After an adaptive period of 1,000 samples, we ran 20,000 iterations of the MCMC sampler, discarding the first 10,000 MCMC samples as a burn-in, and retained every tenth sample thereafter to represent a joint posterior distribution. We ran 3 chains and assessed convergence with the Gelman-Rubin diagnostic (Gelman et al. 2014). We standardized all continuous covariates in units of standard deviation prior to analysis.

Site-level effects on population vital signs.—We used additive linear regression models (lm function in R), coupled with a standard information-theoretic (Akaike's Information Criterion; AIC) model-selection procedure (Burnham and Anderson 2002), to evaluate whether turbines, disturbance (quantified as a road index, which includes road type and straight-line road density), or other site-level factors (% bare ground, mean annual precipitation, sub-adult fraction) could explain substantial variation in key population-level vital rates. We logit-transformed proportional or probability-scale

data (survival, movement probability) prior to analysis, and log-transformed *per capita* recruitment to improve normality of residuals.

We derived several key population-level vital signs (survival, recruitment, size of activity area, movement probability, mean density, abundance trend) directly from the SECR analysis. We chose a 2-stage analysis (summary statistics from the SECR analysis used as input for linear regression models) rather than a single integrated model (effects of site-level covariates included directly within the SECR analysis) for practical reasons—primarily, the ability to harness a powerful and widely used information-theoretic approach for model selection. We acknowledge that such 2-stage approaches can introduce subtle biases or loss of precision because the variance–covariance structure associated with the point estimates (e.g., site-level mean survival rates) cannot be included in the final regression models. However, we allowed the vital signs to vary freely across sites within the SECR model, and the resulting point estimates exhibited substantial variation. If this variation represents true among-site differences, then modeling this variation using standard regression-based approaches is valid and powerful.

We derived 2 additional vital signs (mean body condition and sub-adult fraction) directly from field data (not summarized from the SECR analysis). We computed body condition as the residuals from a non-linear regression (smoothing spline fit using loess function in R) of body mass on body length, fitted separately for males and females. Low mass relative to body size may indicate low fat reserves for reproduction, high stress, or high parasite loads (Hahn and Tinkle 1965, Wilson 1991, Moore et al. 2000, Klukowski and Nelson 2001). We did not correct for the influence of female reproductive condition on body condition because we lacked reliable data on female reproductive state (i.e., gravid or non-gravid). We computed subadult fraction as the fraction of captured individuals at each site that were below the size threshold for adulthood in this species (42 mm SVL for females and 46 mm SVL for males; Tinkle 1967a).

We estimated winter precipitation, bare ground cover, human disturbance, and noise level for each of the 9 study sites (Table 2, Table S4). We averaged mean winter precipitation across November through February (2012 to 2015) on the basis of data retrieved from PRISM climate models (PRISM Climate Group 2015). Winter precipitation may increase annual plant growth, resulting in more abundant invertebrate prey, and influencing survival probability, growth rate, and reproductive output of lizards in the following spring (Turner et al. 1973, 1974; Worthington 1982). We estimated average bare-ground cover using field data collected in July of 2014 at 100-m point-line-intercept plant transect surveys (3 per site; Herrick et al. 2005). We calculated bare-ground cover as the proportion of random points at each 1-m interval that did not intersect any plant canopy during the 100-m point-line-intercept plant transect surveys. In deserts, total plant cover is often correlated with habitat quality (i.e., resource abundance, or vulnerability to predators; Ayal 2007). For each site, we estimated human

land-use disturbance as the linear road footprint (digitized in ArcMap [Environmental Systems Research Institute, Redlands, CA, USA] from 1-m resolution California National Agriculture Imagery Program imagery) within 1,000 m of the established study plots. Following the approach of Vos and Chardon (1998), we then adjusted our measures of road densities by weighting our straight-line measures by 0.5 for footpaths, 1.0 for dirt roads, 3.0 for residential roads, 5.0 for secondary roads, and 10.0 for primary highways. This road index creates a disturbance metric that increases with traffic volume and road width (Vos and Chardon 1998). Finally, we measured anthropogenic noise disturbance as an average A-weighted decibel reading (scale of loudness as perceived by human hearing; dB_A) taken with a MS6708 digital sound level meter (Mastech, Coral Gables, FL, USA) from a random sample of 10 readings at plots in June and July (2015) when turbines were running and wind was ≤ 5.6 km/hour. However, the noise variable was highly correlated with overall anthropogenic disturbance level and was not included in the final analyses.

We selected the most competitive additive model structure for linking each of the 8 population-level vital signs to site-level covariates using stepwise model selection (step function in R) on the basis of AIC (Burnham and Anderson 2002). We interpreted parameters that were statistically significant at the 95% confidence level as strong evidence for an effect,
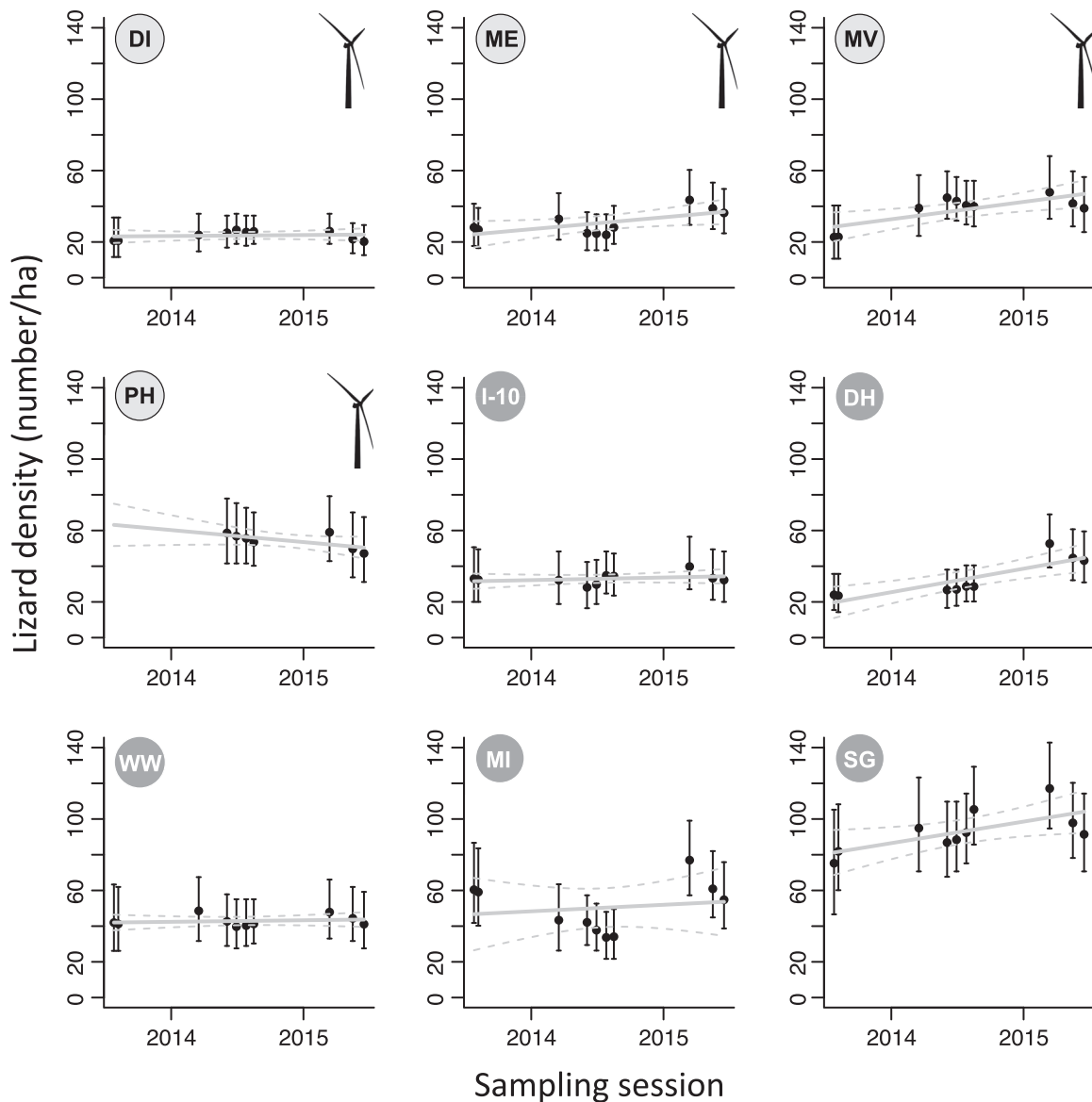

Figure 2. Estimates of side-blotched lizard densities (abundance/ha) over time for 9 study sites located within the San Gorgonio Wind Resource Area (SGWRA), Southern California, USA, derived from a Bayesian spatially explicit capture-recapture (SECR) model. Solid dots indicate posterior mean lizard density estimates, and error bars indicate 95% confidence intervals on lizard densities. The solid gray line represents a linear regression of density over time, and the dotted lines represent 95% confidence intervals for the linear relationship. We visited survey plots repeatedly from 2013–2015 in the SGWRA (10 sessions, 1–3 occasions each). Sites DI, ME, MV, and PH had active wind turbines (indicated with turbine and light gray box), whereas sites I-10, DH, WW, MI, and SG were outside of active wind-energy areas (indicated with dark gray box). Site PH was not visited on sessions 1–3, and site DH was not visited on session 3.

whereas we interpreted parameters that were not statistically significant at the 95% confidence level (95% CI overlapping 0) as weak evidence for an effect. We interpreted the biological importance of each of the parameters included within the most competitive models on the basis of regression coefficients and partial-dependence plots.

RESULTS

Over 3 years (10 capture periods), we recorded 1,172 observations of 394 unique lizards ($n = 25–88$ per site) across the 9 study sites (Fig. S1 depicts capture locations and surveyed area for each site). On average, we observed 8.4 lizards at each site per secondary capture occasion, with per-site mean captures ranged from 4 to 16 (Table S2). We observed some variation in age structure and sex ratio across sites, adult body size, and mass (Table S2).

SECR Model

Population densities estimated from the SECR model (computed as the abundance in each survey plot divided by the area of the survey plot) fluctuated among sites and periods (Fig. 2; Table S5). The SECR model indicated high mean capture probability per secondary capture occasion ($P = 0.49$, 95% credible interval = 0.32 to 0.49). Capture and recapture probabilities were influenced by (standardized) local wind speed ($\beta = -0.19$ on logit scale, 95% credible interval = -0.30 to -0.08), survey effort ($\beta = -0.15$, 95% CI = -0.30 to -0.08), sex (β [effect of being male] = 0.43, 95% CI = 0.16 to 0.70), and presence of visual markings (paint marks or bead tags; $\beta = 1.27$ [effect of being visually marked], 95% CI = 0.97 to 1.60). Capture efficiency was not affected by time of day ($\beta = -0.09$ [effect of being an evening survey], 95% CI = -0.33 to 0.17). Mean monthly survival was estimated at 0.90 (95% CI = 0.88 to 0.93), with moderate site-to-site variation (logit-scale SD = 0.26, 95% CI = 0.076 to 0.61; Fig. 3a). Annual survival projections for side-blotched lizards in this study were 20–41% (converted from monthly estimates). Entrance probabilities (recruitment; probability of an individual entering the study population from the super-population in each primary sampling occasion) varied among sites and periods (Table S6), resulting in site-to-site fluctuations in expected *per capita* recruitment ranging from 0.10 to 0.25 (Fig. 3b). Mean monthly probability of shifting core activity area (across all sites) was estimated at 0.08 (95% CI = 0.04 to 0.14), with weak evidence for a positive effect of being male ($\beta = 0.19$ on logit scale, 95% CI = -0.35 to 0.78; Fig. 3c). Sizes of core activity areas (measured as the SD of the half-normal distribution of capture probability around the activity center) were larger for males than for females and varied from 1.65 m for females at site ME to 4.10 m for males at site MI (Fig. 3d).

Site-Level Effects on Population-Level Vital Signs

Multiple linear regression of mean survival rate on site-level covariates indicated that side-blotched lizard survival rates were influenced by percent bare ground (Fig. 4a; 95% CI = 0.0095 to 0.033; $P = 0.005$), presence of wind turbines (Fig. 4b; 95% CI = -0.38 to -0.02; $P = 0.04$), and winter rainfall (Fig. 4c; 95% CI = -0.048 to -0.002; $P = 0.04$). No site-level covariates influenced *per capita* recruitment or mean population densities. Activity-area size was generally lower for sites with a greater percentage of bare ground (95% CI = -0.1 to -0.025; $P = 0.008$), and the probability of establishing a new core activity area was generally higher for sites with more bare ground (95% CI = 0.00 to 0.04;
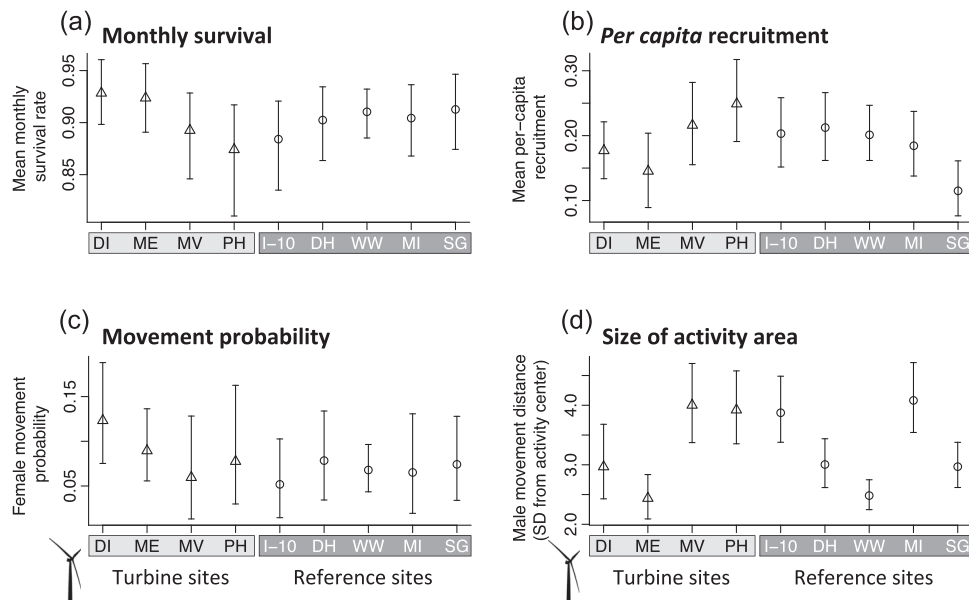

Figure 3. Estimates of key demographic and movement rates of side-botched lizards, Southern California, USA, 2013–2015: a) monthly survival, b) *per capita* recruitment, c) female movement probability, and d) size of male activity area. Estimates are derived from a spatially explicit capture-recapture (SECR) model of side-blotched lizard demography within the San Gorgonio Wind Resource Area. Sites DI, ME, MV, and PH had active wind turbines (light gray), whereas sites I-10, DH, WW, MI, and SG were outside of active wind-energy areas (dark gray).
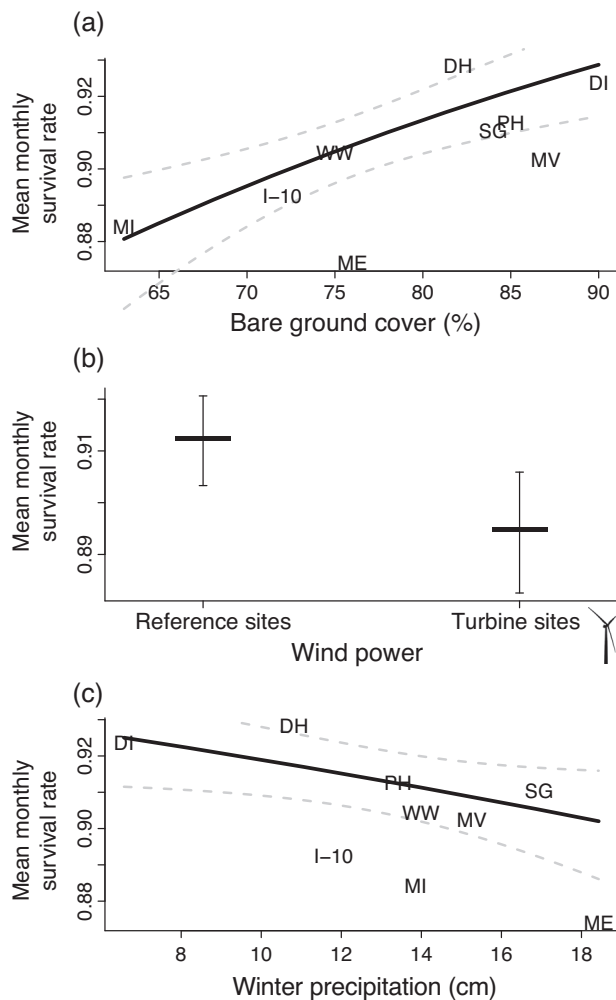
Figure 4. Mean monthly survival rates for side-blotched lizards at 9 study sites within the San Gorgonio Wind Resource Area, Southern California, USA, 2013–2015, derived from a Bayesian spatially explicit capture-recapture (SECR) model, as a function of 3 site-level covariates: a) percent bare ground cover, b) presence or absence of wind turbines, and c) mean winter rainfall. Sites DI, ME, MV, and PH had active wind turbines, whereas sites I-10, DH, WW, MI, and SG were outside of active wind-energy areas.

$P = 0.05$). We found weak evidence that density trends were affected by disturbance (i.e., road index), with highly disturbed sites generally experiencing reduced population growth (Fig. 5a; 95% CI = −0.001 to 0.001; $P = 0.06$). We also found weak evidence that movement distances, measured as the standard deviation in movement distance from the activity center, increased with disturbance levels (Fig. 5b; 95% CI = −0.003 to 0.030; $P = 0.09$). Age structure and body condition were influenced by anthropogenic disturbance, with highly disturbed sites corresponding to more adult-skewed age structure (Fig. 5c; 95% CI = −0.01 to −0.002; $P = 0.01$) and lower body conditions (Fig. 5d; 95% CI = −0.007 to 0.000; $P = 0.04$).

DISCUSSION

We evaluated the effects of renewable energy developments on wildlife habitat by comparing population-level vital signs for side-blotched lizards at wind farms versus nearby reference sites. Demographic metrics were not systematically different between side-blotched lizard populations at wind farms and at reference sites. Our models supported only a weak effect of wind farms on survival probability for common side-blotched lizards; the combined effects of the cover, precipitation, and wind farm parameters resulted in similar levels of survival across all sites. Overall, annual survival projections for side-blotched lizards in this study (20–41%, converted from monthly estimates) were within the range of values reported for this species, and were higher than average for southern populations (Tinkle 1967a, Parker 1974, Turner et al. 1974).

Wind farms introduce novel disturbances to local wildlife populations, including flickering shadows, subsonic vibrations, and fast-moving turbine blades (Lovich and Ennen 2013) and yet, our results highlight the not-so-novel threat of development as a more reliable indicator of population-level change in response to wind farm development. Site-level variation in anthropogenic disturbance (measured as a traffic-weighted road footprint; road index) was more important in explaining population growth, age structure, and body condition than wind farms alone. Human activity is pervasive in the San Gorgonio Pass of Southern California (Lovich and Bainbridge 1999), and although road disturbance was higher at wind farm sites on average, disturbance was not absent from reference sites and varied in severity across all sites, allowing us to assess the role of disturbance on population vital signs.

At wind farm sites, roads comprise most of the development footprint, relative to other infrastructure (Denholm et al. 2009). The negative effects of roads on wildlife are well documented (Gibbs and Shriver 2002, Fahrig and Rytwinski 2009, Benítez-López et al. 2010, van der Ree et al. 2011), including a number of studies specific to reptiles (Andrews et al. 2008). Desert reptiles may be especially vulnerable to road mortality because many are adapted to open land cover types and lack road avoidance behaviors (Brehme et al. 2013), or even seek out roads to thermoregulate (Andrews et al. 2008).

Beyond direct road mortality, roads fragment landscapes, reduce habitat patch size, and increase habitat edges (Andrews 1990, Saunders et al. 2002). Roads can also create barriers to animal movement (Andrews and Gibbons 2005), potentially affecting genetic diversity within isolated patches (Epps et al. 2005). In addition, the increased traffic and activity on and near roadways provides opportunities for exotic and invasive species introductions, further contributing to the degradation and loss of adjacent habitat (Gelbard and Belnap 2003). Indeed, in the SGWRA, wind farm and reference sites with greater road density were less ecologically diverse and contained more invasive species than sites with fewer roads and traffic (Keehn and Feldman 2018a). We found across all study sites, that increasing road density and traffic was correlated with lower body condition, adult-skewed age structure, and ultimately, reduced population growth in side-blotched lizards.
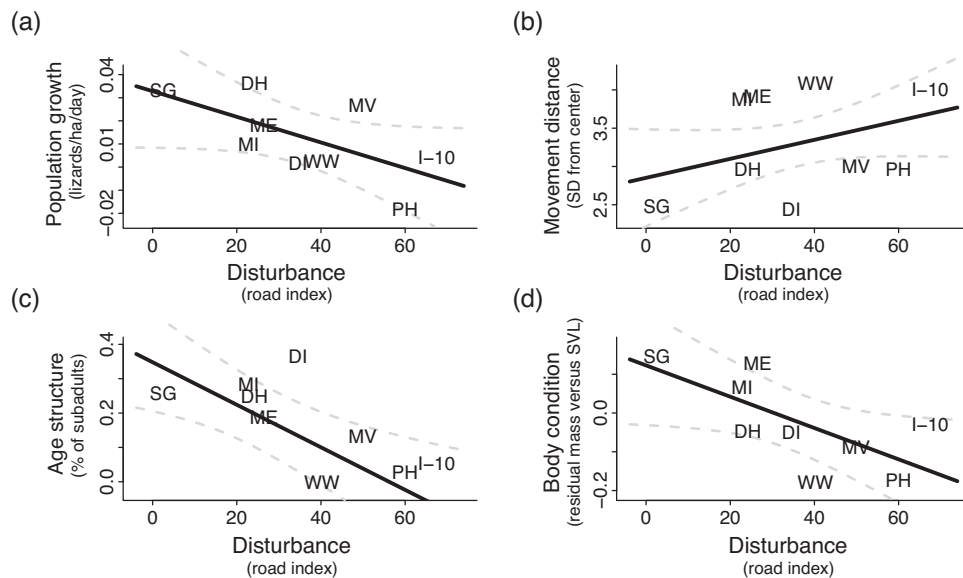
Figure 5. Effects of anthropogenic disturbance, quantified as a road index (which includes road density and a weighted measure of straight-line road distance to account for road width and traffic volume; after Vos and Chardon 1998) on 4 key population-level vital signs for side-blotched lizards within the San Gorgonio Wind Resource Area, Southern California, USA, 2013–2015: a) population growth trend (lizards/ha/day), b) size of core activity area (SD of relationship between capture probability and distance from activity center), c) age structure (% of subadult captures), and d) mean body condition (residual of non-linear regression between body mass and snout-vent length [SVL]). We derived population growth trends and movement distances from a Bayesian spatially explicit capture-recapture (SECR) model. Sites DI, ME, MV, and PH had active wind turbines, whereas sites I-10, DH, WW, MI, and SG were outside of active wind-energy areas.

Body condition declined at sites with high road density. Suboptimal conditions in fragmented and disturbed habitat patches can increase physiological stress in small vertebrates (Janin et al. 2011), which is generally inversely correlated with body condition (Sapolsky et al. 2000). Traffic noise alone may increase physiological stress (Blickley et al. 2012). In addition, roads can facilitate the invasion of exotic plants species, especially annual grasses (Gelbard and Belnap 2003, Brooks and Berry 2006), which can decrease the habitat condition for lizards in several ways. First, the increased abundance of exotic grass near roadsides can reduce thermal and structural diversity relative to undisturbed areas (Hacking et al. 2014). Second, areas overgrown with annual grasses may be difficult for small vertebrates to navigate, with increased costs of movement during foraging bouts (Fitch 1955, Newbold 2005, Rieder et al. 2010). Lastly, changes in plant communities associated with disturbed roadsides might influence the availability of preferred prey items, which could also lead to reduced body condition (Bury and Busack 1974, Vitt and Ohmart 1974, Jones 1981).

We also found that sites with high levels of road disturbance tended to have larger (and presumably older) individuals, with very few subadult captures. A higher fraction of adults at more disturbed sites could indicate lower recruitment the prior year (Walkup et al. 2017), or perhaps lower turnover of lizard territories with more dispersal of juveniles to new areas. Alternatively, dispersing juveniles may be more prone to road mortality (Andrews et al. 2008).

Ultimately, poor body condition and adult-skewed age structure may have significant demographic consequences for local populations (Wilson 1991, Hoare et al. 2006, Kight and

Swaddle 2007). Indeed, we found a significant, negative relationship between levels of road disturbance and population growth. Additional research is needed to better understand whether populations responded directly to road development, or rather the associated and likely cumulative effects of anthropogenic stressors associated with road development at more disturbed sites. Regardless, our research indicates that wind farms are similar to other disturbed areas because roads and other anthropogenic disturbance can influence local wildlife populations. Wind farms, relative to other renewable energy technologies, have low land-use intensity and a small physical footprint; however, our results suggest that this land-use strategy can still influence population vital statistics, as a consequence of increase road development to access infrastructure.

The significance of road disturbance and associated development effects in desert ecosystems cannot be overstated because deserts recover slowly from human activity (Lovich and Bainbridge 1999, Abella 2010). Renewable energy development in deserts is nearly inevitable (Pocewicz et al. 2011) and developed areas in arid regions may have altered community structure and function for centuries after human activities have ceased (Lovich and Bainbridge 1999). Responsible wind energy development requires an understanding of the inherent risks to biota from changing habitat conditions at energy production sites, including the effects of access roads on local wildlife populations.

MANAGEMENT IMPLICATIONS

Our results showed that roads and associated human disturbance at wind farm sites are detrimental to local

side-blotched lizard populations. However, side-blotched lizards are moderately tolerance of disturbance (Castellano and Valone 2006) and may be more resilient than other terrestrial vertebrate taxa to potential negative effects of wind farms. In the absence of similar research on other taxa, a conservative management approach would be to encourage mitigation measures that minimize road disturbance at wind farms (e.g., avoid new road construction, decommission unused roads, or limit road traffic speed and volume) to improve the quantity and condition of the remaining habitat matrix for local wildlife.

ACKNOWLEDGMENTS

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Associate Editor: John Maerz.

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