Note

Mammalian Mesocarnivore Visitation at Tortoise Burrows in a Wind Farm

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ABSTRACT There is little information on predator–prey interactions in wind energy landscapes in North America, especially among terrestrial vertebrates. Here, we evaluated how proximity to roads and wind turbines affect mesocarnivore visitation with desert tortoises (*Gopherus agassizii*) and their burrows in a wind energy landscape. In 2013, we placed motion-sensor cameras facing the entrances of 46 active desert tortoise burrows in a 5.2-km^2 wind energy facility near Palm Springs, California, USA. Cameras recorded images of 35 species of reptiles, mammals, and birds. Counts for 4 species of mesocarnivores at desert tortoise burrows increased closer to dirt roads, and decreased closer to wind turbines. Our results suggest that anthropogenic infrastructure associated with wind energy facilities could influence the general behavior of mammalian predators and their prey. Further investigation of proximate mechanisms that underlie road and wind turbine effects (i.e., ground vibrations, sound emission, and traffic volume) and on wind energy facility spatial designs (i.e., road and wind turbine configuration) could prove useful for better understanding wildlife responses to wind energy development. © 2017 The Wildlife Society.

KEY WORDS burrow symbionts, *Gopherus agassizii*, meso-predator, predator–prey interactions, renewable energy, roads, trail camera.

Mesocarnivores (Mammalia: Carnivora) occupy diverse habitats in North America, including anthropogenic landscapes (Ray 2000). Although fragmented landscapes may increase extinction vulnerability of large mammalian carnivores, small to medium-sized mesocarnivores expand home ranges in the face of some anthropogenic changes (Crooks and Soulé 1999, Crooks 2002, Urquiza-Haas et al. 2009). A new cause of habitat alteration in the desert southwest, USA, is renewable energy development (Lovich and Ennen 2011, 2013). Habitat disturbance caused by wind energy facilities creates unique challenges and opportunities for wildlife (Lovich and Ennen 2013, Agha et al. 2015b). Although wind energy facilities and associated infrastructure

may create potential hazards for many species (Kuvlesky et al. 2007), these facilities may also benefit others by restricting public access and limiting cultivation (Kelcey 1975, Lovich and Daniels 2000). Additionally, infrastructure associated with wind energy facilities (e.g., roads, culverts) create movement corridors through disturbed habitat that may be preferred by mesocarnivores (Tigas et al. 2002, Ng et al. 2004, Frey and Conover 2006, Alonso et al. 2014). However, there is little published research about the effects of wind energy facilities on mesocarnivores and other groups of non-volant vertebrates (Lovich and Ennen 2013).

Mesocarnivores can be highly social or solitary and can influence community structure in diverse habitats, including anthropogenic landscapes (Roemer et al. 2009). As apex predator populations decrease from human hunting pressure or habitat loss, mesocarnivore populations can increase (Sterner and Shumake 2001, Prugh et al. 2009, Brashares et al. 2010). Population increase of mesocarnivores can have

measurable consequences on lower trophic levels (i.e., mesopredator release; Crooks and Soulé 1999). For example, increased numbers of mesocarnivore predators resulting from decreased trapping pressures on fur-bearing mammals (i.e., collapse of fur market) have been suggested as a cause of increased nest predation in several taxa (e.g., reptiles and birds; Congdon et al. 1993, 1994; Crooks and Soulé 1999; Ritchie and Johnson 2009).

In the desert southwest region of the United States, population declines of federally threatened desert tortoises (*Gopherus agassizii*) are attributed to several factors, including predation by carnivores (Lovich et al. 2014*b*) and ravens (*Corvus corax*; Boarman 2003), renewable energy development (Lovich and Ennen 2011, 2013), road mortality (Von Seckendorff Hoff and Marlow 2002), and fire (Lovich et al. 2011, U.S. Fish and Wildlife Service 2011). Predation of adult desert tortoises by subsidized mesocarnivores like coyotes (*Canis latrans*) can negatively affect populations of tortoises locally and regionally (Peterson 1994, Esque et al. 2010, Lovich et al. 2014*b*). However, instances of predation of desert tortoises for any age-class are notoriously difficult to observe and quantify (Peterson 1994), and therefore, evidence for most reported predation events by mammals is circumstantial (Table 1).

The objective of our study was to evaluate how proximity to anthropogenic infrastructure associated with wind energy facilities, such as roads and wind turbines, affected mesocarnivore visits to desert tortoise burrows and encounters with desert tortoises. We asked 3 questions: what meso-carnivore species visit desert tortoises or their burrows at a wind energy facility in the desert southwest; how frequently do these events occur; and does prey availability (i.e., birds, rodents, reptiles, lagomorphs using burrows), age of the burrow, distance to the nearest wind turbine, and distance to the nearest dirt road influence the likelihood of mesocarnivore visitation? For the latter question, we predicted that total mesocarnivore counts would decrease as tortoise burrow distance to wind turbines and dirt roads decreased because earlier research suggested a potential variance in carnivore occurrence across the wind energy facility resulting from associated infrastructure (Agha et al. 2015*b*). Although some mesocarnivores are known to occasionally eat carrion found underneath wind turbines (Smallwood et al. 2010).

STUDY AREA

We conducted our study at a wind energy facility, the Mesa wind energy facility (hereafter Mesa), near Palm Springs, Riverside County, California, USA (33°57′06″ N, 116°40′02″ W, WGS84). The facility includes 460 wind turbines, 51 electrical transformers, and a network of dirt roads (∼16 km total linear distance, and ∼6 m average width) on 2 sections of public land administered by the Bureau of Land Management (T2S, R3E, section 33, 34). These 2 sections constitute just under 5.2 km^2. Mesa is located at the western edge of the Sonoran Desert and is bordered on the north and west by the San Bernardino Mountains. Elevation ranges from approximately 300–900 m and long-term mean winter precipitation was 15.2 cm (Agha et al. 2015*b*). Plant species at Mesa are a mixture of Mojave and Sonoran desert ecosystem assemblages, and coastal and montane plant assemblages (Lovich and Daniels 2000). For a more detailed description of the Mesa study site see Lovich et al. (2011) and Agha et al. (2015*b*).

METHODS

Data Collection
From 1 June to 14 November 2013, we deployed motion sensor cameras (models HC500 and PC800; Reconyx, Holmen, WI, USA) at the entrances of 46 active desert tortoise burrows at Mesa. We considered a burrow active if a tortoise occupied the burrow in 2012 or 2013. We deployed all cameras at approximately the same time, and straight-line distance between cameras ranged from approximately 8 m to 2,471 m. We mounted cameras on 1.5-m tall stakes positioned 1 m from desert tortoise burrow entrances. Consequently, the camera detection zone was approximately 2–4 m^2, allowing us to see the entrance of the burrow and a small extent of the surrounding landscape (Agha et al. 2015*a*). To avoid camera sensitivity bias, we set all cameras to motion activation via an infrared sensor with high motion sensitivity and programmed them to take a series of 3 high-definition photographs at a trigger speed of 0.2 seconds, following methods and procedures from Rovero et al. (2013). Camera models HC500 and PC800 only differed in their maximum illumination range at night (15.2 vs. 18.3 m). Because our cameras were close to burrows, we did not statistically assess distance of wildlife from the camera in this study. However, camera placement >1 m from a burrow increased false-detections (i.e., misfiring) caused by windblown grass or dust, even after controlling for camera sensitivity settings.

Every 15–30 days, an investigator checked each camera and downloaded photos. Using long-term desert tortoise data from Mesa (1997–2013; Lovich et al. 2011, Agha et al.

Table 1. Documented or suspected terrestrial predators of the desert tortoise in North America.

Terrestrial predator species	Sources
Domestic dog	Burge (1979), Peterson (1994), Boyer and Boyer (2006), Ernst and Lovich (2009), Esque et al. (2010)
Mountain lion (*Puma concolor*)	Field et al. (2007), Medica and Greger (2009)
Bobcat (*Lynx rufus*)	Woodbury and Hardy (1948), Field et al. (2007)
Gray fox (*Urocyon cinereoargenteus*)	Ernst and Lovich (2009)
Black bear (*Ursus americanus*)	Lovich et al. (2014*a*)
Kit fox (*Vulpes macrotis*)	Coombs (1977), Hohman and Ohmart (1980), Hampton (1981), Roberson et al. (1985), Baxter (1987), Turner et al. (1987), Bjurlin and Bissonette (2004)
Coyote (*Canis latrans*)	Coombs (1977), Hohman and Ohmart (1980), Roberson et al. (1985), Berry et al. (2013), Lovich et al. (2014*b*)
American badger (*Taxidea taxus*)	Emblidge et al. (2015), Smith et al. (2016)

2015a), we noted the date when the burrow was first recorded as occupied by a radio-telemetered desert tortoise, providing an approximate minimum time since first known occupation or rough approximation for age of the burrow. As a result of our methods for determining camera locations, all monitored burrows were occupied at some point in the past 2 years by tracked desert tortoises. We followed approved field methods under permits from the United States Fish and Wildlife Service (TE-198910-1), Bureau of Land Management, and the California Department of Fish and Wildlife (SC-1639). The study also conformed to American Society of Mammalogists guidelines, and no mammals were procured, handled, immobilized, marked, or transported because this was a passive camera-trapping study only (Sikes and Gannon 2011). The Institutional Animal Care and Use Committee, Northern Arizona University, approved our research procedures.

During our study, we frequently observed various animals triggering the motion-sensor camera within short time periods (1–5 min), creating multiple sets of photographs for a single individual. These consecutive records exhibited high temporal correlation (Agha et al. 2015b). Consequently, if the same species triggered the motion-sensor camera on multiple occasions within a 5-minute period, we classified the grouping of photos as a single camera trap event. For each camera trap event, we first recorded the date and time the photo was triggered, identified the species, and classified the posture or behavior using ethograms (mammals: Fox 1969, Lingle 2000, Way et al. 2006, MacNulty et al. 2007, Stanton et al. 2015; desert tortoise: Ruby and Niblick 1994). With our motion-sensor cameras, we quantified the total number of reptile events, and mesocarnivore, bird, and other small vertebrate events by species for each burrow. Using ArcGIS 10.1.1 (ESRI, Redlands, CA, USA) and a 10-m digital elevation model, we estimated 3-dimensional landscape distances (m) to the nearest wind turbine and dirt road for desert tortoise burrows with camera traps.

Statistical Methods
To examine variation in mesocarnivore visitation (mesocarnivore counts) at desert tortoise burrows at Mesa, we quantified the following explanatory variables for each desert tortoise burrow: turbine distance (distance of burrow to nearest wind turbine), road distance (distance of burrow to nearest dirt road), age (min. known age of burrow), and prey availability (no. visits by mesocarnivore prey, including birds, reptiles, and small mammals).

Using Program R (version 3.1.1), we performed a Welch's 2-sample t-test for unequal variances ($\alpha = 0.05$) to test whether desert tortoise burrows visited by mesocarnivores were closer to roads and turbines, as compared to unvisited burrows. Subsequently, we fit generalized linear models with a Poisson distribution and log link to test our explanatory variables on total counts of mesocarnivores (Cameron and Trivedi 2013). To equate scales and account for multicollinearity, we standardized all explanatory variables to have a mean of 0 and a standard deviation of 1 (Cade 2015). We used residual deviance to perform a chi-squared goodness-of-fit

test for the global model, and concluded that our global model fit sufficiently ($P = 0.63$). Although 2 predictors, dirt road distance and turbine distance, were moderately correlated (>0.6), inclusion of both variables in the global model did not adversely affect model stability or regression estimates (Cade 2015). In addition, using the HH package, we calculated variance inflation factor (VIF) values for each predictor in our global model to detect multicollinearity, and these values did not require exclusion of any independent variables from our analysis (O'brien 2007). Subsequently, we fit all possible combinations of our explanatory variables using the MuMin package (Barton 2013). To identify the most parsimonious model, we ranked models using Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2003). We used model averaging because there were multiple models that were ≤4 AIC$_c$ units from the top model (Burnham and Anderson 2003). Finally, we provided estimates from model averaging, unconditional standard error, and 85% confidence intervals for supported coefficients within our top models to ensure that model selection and parameter evaluation criteria were congruent (Arnold 2010).

RESULTS
Over the course of the 5.5-month camera-trapping study (7,968 total trap nights), our cameras detected 4,903 wildlife events (including mesocarnivores and their prey species) distributed across 46 tortoise burrows. We recorded approximately 900 wildlife events/month and an average of 106 wildlife events/burrow. We recorded 22 mesocarnivore visitations, an average of 4 events/month, by 4 species (bobcat [*Lynx rufus*], coyote, gray fox [*Urocyon cinereoargenteus*], and western spotted skunk [*Spilogale gracilis*]) at 16 different tortoise burrows that ranged approximately 0–158 m from roads and 21–574 m from wind turbines (Table 2). Burrows visited by mesocarnivores were closer to roads, as compared to unvisited, based on a 1-tailed t-test ($P = 0.002$), and an opposite relationship was documented for wind turbines ($P = 0.038$). Mesocarnivore visitations occurred from 0100–0700 and 1800–2300 hours and were evenly dispersed from mid-June to mid-November. During our study and across 46 tortoise burrows, we also observed 1 species of tortoise, 3 species of lizards, 4 species of snakes, 7 species of small mammals (rodents and lagomorphs), and 14 species of birds, visiting and using monitored tortoise burrows for various reasons (Table 3).

Table 2. Number of camera events recorded and mean distance (m) and standard deviation from camera to nearest dirt road and wind turbine for cameras placed at desert tortoise burrows at the Mesa wind energy facility near Palm Springs, California, USA, 2013.

Mesocarnivore	N	Road $\bar{x}$	Road SD	Wind turbine $\bar{x}$	Wind turbine SD
Bobcat	15	78.29	44.59	244.65	152.20
Gray fox	2	41.36	58.49	185.38	207.69
Coyote	4	88.39	52.53	208.79	107.21
Western spotted skunk	1	158.06		574.58	

Table 3. A list of vertebrate species (other than mesocarnivores) and their counts documented by trail cameras, inside or near the entrance of active desert tortoise burrows at the Mesa wind energy facility near Palm Springs, California, USA, 2013. Species are first ordered by class and then by number of events. Migratory species have an asterisk following the scientific species name.

Class and common name	Scientific name	No. events
Mammalia		
Desert kangaroo rat	*Dipodomys deserti*	231
Desert cottontail	*Sylvilagus audubonii*	175
Desert woodrat	*Neotoma lepida*	122
White-tailed antelope squirrel	*Ammospermophilus leucurus*	86
Desert pocket mouse	*Chaetodipus penicillatus*	41
Black-tailed jackrabbit	*Lepus californicus*	22
Nelson's big horn sheep	*Ovis canadensis nelsoni*	8
California ground squirrel	*Otospermophilus beecheyi*	3
Domestic cattle	*Bos taurus*	2
Black bear	*Ursus americanus*	1
Aves		
Rock wren	*Salpinctes obsoletus*	1,507
California towhee	*Melozone crissalis*	196
Cactus wren	*Campylorhynchus brunneicapillus*	114
Black-throated sparrow	*Amphispiza bilineata*	49
Greater roadrunner	*Geococcyx californianus*	38
Loggerhead shrike	*Lanius ludovicianus*	24
Chukar partridge	*Alectoris chukar*	17
Burrowing owl	*Athene cunicularia*	13
Bewick's wren	*Thryomanes bewickii*	8
California quail	*Callipepla californica*	7
White-crowned sparrow	*Zonotrichia leucophrys**	7
California thrasher	*Toxostoma redivivum*	4
Common raven	*Corvus corax*	3
Verdin	*Auriparus flaviceps*	1
Reptilia		
Desert tortoise	*Gopherus agassizii*	2,754
Great basin whiptail	*Aspidoscelis tigris tigris*	104
Western side-blotched lizard	*Uta stansburiana*	65
Desert spiny lizard	*Sceloporus magister*	36
Sagebrush lizard	*Sceloporus graciosus*	27
Coachwhip	*Masticophis flagellum*	5
Long-nosed snake	*Rhinocheilus lecontei*	1

Most mesocarnivore camera trap events ($n = 17$ of 22) lasted <30 seconds (time the same individual mesocarnivore was photographed). We provide additional descriptions of mesocarnivore interactions with desert tortoises and burrow visitation events that lasted >30 seconds elsewhere (Supplement I, available online in Supporting Information).

After model selection, we found support for 4 models ($\Delta AIC_c \leq 4$ units from top model; Arnold 2010) predicting mesocarnivore counts (Table 4). Using model averaging, we found that mesocarnivore counts increased with distance from a wind turbine but decreased with distance from a dirt road (Table 5). For example, for each 1 standard deviation (160.08 m) increase in distance from roads, estimated mesocarnivore counts decreased by 1.94 (85% CI = −2.82 to −1.05). Conversely, for each 1 standard deviation (258.87 m) increase in distance from wind turbines, estimated mesocarnivore counts increased by 1.06 (85% CI = 0.50–1.61). Additionally, we found that mesocarnivore counts increased with estimated minimum age of a desert

Table 4. The 4 top models predicting total mesocarnivore detections from cameras placed at desert tortoise burrows at the Mesa wind energy facility near Palm Springs, California, USA, 2013, including standardized explanatory effects: distance to nearest wind turbine (turbine), distance to nearest dirt road (road), known age of burrow (age), and number of mesocarnivore prey events (prey). All models are ranked by corrected Akaike's Information Criterion (AIC_c) and listed with number of model parameters (K), log-likelihood (LL), difference in AIC_c relative to the best model (ΔAIC_c), and Akaike weight (w_i).

Model	K	LL	AIC_c	ΔAIC_c	w_i
Road + turbine + age	4	−38.96	86.91	0.00	0.39
Road + turbine	3	−40.26	87.08	0.18	0.36
Road + turbine + prey	4	−39.97	88.91	2.00	0.14
Road + turbine + age + prey	5	−38.96	89.42	2.51	0.11

tortoise burrow. For example, for each 1 standard deviation increase in burrow age (2.58 yr), estimated mesocarnivore counts increased by 0.26 (85% CI = 0.04–1.01). However, prey availability failed to predict mesocarnivore counts.

DISCUSSION

Our modeling results support the hypothesis that anthropogenic infrastructure associated with wind energy facilities (i.e., roads and wind turbines) potentially affect mesocarnivore visitation rates at desert tortoise burrows in 2 ways. First, our model-averaged estimates suggest that the number of visitations observed at desert tortoise burrows increases as distance from nearest wind turbine increases (Table 5). Ground vibrations and sound emitted by wind turbines may act as deterrents to wildlife or adversely affect behavior (Rabin et al. 2006, Lovich and Ennen 2013). Bobcats and coyotes rely on visual, auditory, and olfactory cues (Wells 1978, Tewes et al. 2002), and the extent to which sound and vibration produced by wind turbines affect prey detection for these mesocarnivores is unknown. However, prey species show heightened vigilance and increased caution because turbine noise masks their ability to detect predators through auditory cues (Rabin et al. 2006). Therefore, it is likely that mesocarnivores are also affected by noise from wind facilities.

Second, our model-averaged estimates suggest that the number of mesocarnivore visitations observed at desert tortoise burrows increases as distance to dirt roads decreases (Table 5). Dirt roads at Mesa may act as funnels for

Table 5. Model-averaged estimates of generalized linear models for predicting mesocarnivore detections from cameras placed at desert tortoise burrows at the Mesa wind energy facility near Palm Springs, California, USA, 2013, including the standardized effects of distance to nearest wind turbine (turbine), distance to nearest dirt road (road), known age of burrow (age), and total number of mesocarnivore prey events (prey). Effects with an 85% confidence interval not overlapping zero are significant (marked with asterisk).

Fixed effects	Parameter estimates	SE	Lower 85% CL	Upper 85% CL
Intercept	−0.97	0.30	−1.42	−0.52
Age*	0.26	0.35	0.04	1.01
Road*	−1.94	0.60	−2.82	−1.05
Turbine*	1.06	0.38	0.50	1.61
Prey	0.03	0.12	−0.23	0.44

mesocarnivores because they are potential corridors through the wind energy facility and direct efficient animal movement (Kelly et al. 2012). For instance, Frey and Conover (2006) reported that meso-predators incorporate more roads in their home ranges than expected by chance. Furthermore, Atwood et al. (2004) suggested that traveling corridors such as roads are critical to movement of coyotes in areas with human activity like Mesa. Thus, increased visits to desert tortoise burrows closer to roads may correspond to high use of dirt roads by mesocarnivores at Mesa. Alternatively, earlier research at the study site reported that tortoise burrows were more likely to be closer to roads than random points, likely for the same reason. For example, tortoises can move more easily on dirt roads and desert washes than highly vegetated landscapes (Lovich and Daniels 2000, Todd et al. 2016). The relationship between mesocarnivores and roads may be an artifact of this effect, because visited burrows were closer to roads as compared to unvisited burrows.

Additionally, our study found that mesocarnivore counts increased as the minimum age of the tortoise burrow increased. The relationship between burrow age and mesocarnivore visits may be linked to specific mesocarnivore behavioral observations made during our study. For example, we recorded a bobcat scent marking (i.e., spraying urine) at a 3-year-old burrow, which may be a significant mode of communication among bobcats (Bailey 1974). Scent marking a landmark may indicate a mesocarnivore's long-term presence in an area (i.e., territoriality; Bailey 1974). At our study site, older, more stable desert tortoise burrows may also represent essential resources for an individual mesocarnivore (i.e., prey availability, resting, denning places), and thus demarcation by scent marking may increase the number of reoccurring visits.

Desert tortoises provide shelter to many species with their burrows (Woodbury and Hardy 1948, Burge 1979, Luckenbach 1982, Haug et al. 1993, Walde et al. 2015), a phenomenon shared with other *Gopherus* species (Jackson and Milstrey 1989, Kent and Snell 1994, Heinrich et al. 1995, Kinlaw 1999, Engeman et al. 2009), and summarized in Ernst and Lovich (2009). Because tortoise burrows provide protection from high temperatures in harsh environments (Morafka and Berry 2002, Mack et al. 2015), they can be suitable for a variety of commensal species (Walde et al. 2009). These and other burrow symbionts may attract mesocarnivores (Coombs 1979, Winegarner 1985, Toland 1991). Our modeling results, however, did not detect a significant effect of prey availability on mesocarnivore visitation. It is possible that our camera traps missed predator–prey interactions adjacent to desert tortoise burrows, or that some of our recorded birds, reptiles, or small mammals are not commonly predated by mesocarnivores. For example, several mesocarnivore records were nocturnal, whereas most of our bird observations were diurnal. Furthermore, although birds accounted for 40% of wildlife observations, rock wrens (*Salpinctes obsoletus*; Table 3) in particular made up approximately 78% of our bird observations, which may have biased our prey availability variable towards the occurrence of rock wrens as compared to other prey species.

Finally, we did not detect or record any predation on adult desert tortoises by mesocarnivores close to burrows. Failure to detect predation could suggest that mesocarnivore species observed in our study do not actively depredate adult desert tortoises near burrows, or that spatial structure of the wind energy landscape may affect predator encounter rates with prey. Mesocarnivores are reported to be predators or scavengers of adult desert tortoises at other less fragmented (i.e., homogenous) study sites (Table 1). Additionally, reptiles are important prey items for mesocarnivores in desert ecosystems (Hernández et al. 1994, Delibes et al. 1997, Paltridge 2002). Because adult tortoises have been reported in the diet of mesocarnivores at other study sites suggests that predation or scavenging may occur during times when tortoises are more vulnerable (i.e., away from burrows) or other prey species are less abundant, as during droughts (Peterson 1994, Esque et al. 2010, Lovich et al. 2014b). Alternatively, variation in predator encounter rates with prey may be caused by spatial structure of the wind energy landscape (e.g., landscape heterogeneity). For example, wind energy facility spatial design (i.e., placement of wind turbines and roads) may control animal aggregation patterns across landscapes, thus influencing the nature of predator–prey interactions (Fortin et al. 2015).

Our sparse mesocarnivore observations and non-detection of predation may be related to study design, camera trap constraints, and spatial and temporal limitations (Meek et al. 2015). For instance, the proximity of our cameras to tortoise burrows and the use of a single camera directed towards each tortoise burrow likely limited detection of predator–prey interactions occurring away from burrows and our inferences on mesocarnivore behavior, orientation, and identification. Our study was conducted over a single year and only within the extent of the wind energy facility; therefore, our inferences do not include seasonal variation, nor do they account for comparisons to reference conditions (i.e., undisturbed habitat). Finally, our interpretations may not fully represent behaviors shared by the wider mesocarnivore population living in proximity to wind energy facilities because of the small number of detections (Rowcliffe et al. 2014).

MANAGEMENT IMPLICATIONS

Our study highlights that anthropogenic infrastructure associated with wind energy facilities potentially influences the general behavior of terrestrial vertebrates, such as mesocarnivores. For example, our results suggest that mesocarnivore counts increase closer to dirt roads. Dirt roads may facilitate movements of mesocarnivores. Furthermore, our results provide evidence that mesocarnivore counts increase with distance from wind turbines. In devising management plans, managers could potentially assess wind energy facility spatial design, particularly spacing between turbines and the number of roads, to provide habitat for sensitive terrestrial wildlife. Future investigations could compare terrestrial wildlife behavior among wind energy facilities and on undisturbed public land, and record proximate mechanisms that might underlie the effects of

roads and wind turbines (i.e., ground vibrations, sound emission, and traffic volume).

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LITERATURE CITED

Agha, M., B. Augustine, J. E. Lovich, D. Delaney, B. Sinervo, M. O. Murphy, J. R. Ennen, J. R. Briggs, R. Cooper, and S. J. Price. 2015a. Using motion-sensor camera technology to infer seasonal activity and thermal niche of the desert tortoise (*Gopherus agassizii*). Journal of Thermal Biology 49:119–126.

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, M. Austin, S. V. Madrak, and S. J. Price. 2015b. 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 55:1–10.

Alonso, R. S., L. M. Lyren, E. E. Boydston, C. D. Haas, and K. R. Crooks. 2014. Evaluation of road expansion and connectivity mitigation for wildlife in southern California. Southwestern Naturalist 59:181–187.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Atwood, T. C., H. P. Weeks, and T. M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. Journal of Wildlife Management 68:1000–1009.

Bailey, T. N. 1974. Social organization in a bobcat population. Journal of Wildlife Management 38:435–446.

Barton, K. 2013. MuMIn: multi-model inference. R package version, 1.5. http://cran.r-project.org/web/packages/MuMIn/index.html. Accessed 3 Jan 2016.

Baxter, R. J. 1987. Analyses of the population and spatial distribution of the desert tortoise (*Gopherus agassizii*) at the Twentynine Palms Marine Corps Base. Thesis, California State Polytechnic University, Pomona, USA.

Berry, K. H., J. L. Yee, A. A. Coble, W. M. Perry, and T. A. Shields. 2013. Multiple factors affect a population of Agassiz's desert tortoise (*Gopherus agassizii*) in the northwestern Mojave Desert. Herpetological Monographs 27:87–109.

Bjurlin, C. D., and J. A. Bissonette. 2004. Survival during early life stages of the desert tortoise (*Gopherus agassizii*) in the south-central Mojave Desert. Journal of Herpetology 38:527–535.

Boarman, W. I. 2003. Managing a subsidized predator population: reducing common raven predation on desert tortoises. Environmental Management 32:205–217.

Boyer, T. H., and D. M. Boyer. 2006. Turtles, tortoises, and terrapins. Pages 78–99 in D. R. Mader, editor. Reptile medicine and surgery. Second edition. Saunders Elsevier, Philadelphia, Pennsylvania, USA.

Brashares, J. S., L. R. Prugh, C. J. Stoner, and C. W. Epps. 2010. Ecological and conservation implications of mesopredator release. Pages 221–240 in J. Terborgh and J. A. Estes, editors. Trophic cascades. Island Press, Washington, D.C., USA.

Burge, B. 1979. Survey of the present distribution of the desert tortoise, *Gopherus agassizii*, in Arizona: additional data. Pages 36–60 in E. St. Amant, editor. Desert Tortoise Council Proceedings of 1979 Symposium. Desert Tortoise Council, Long Beach, California, USA.

Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Cade, B. 2015. Model averaging and muddled multimodel inferences. Ecology 96:2370–2382.

Cameron, A. C., and P. K. Trivedi. 2013. Regression analysis of count data. Second edition. Cambridge University Press, Cambridge, United Kingdom.

Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoology 34:397–408.

Coombs, E. M. 1977. Status of the desert tortoise, *Gopherus agassizii*, in the state of Utah. Pages 95–101 in M. Trotter, editor. Desert Tortoise Council Proceedings of 1977 Symposium. Desert Tortoise Council, Long Beach, California, USA.

Coombs, E. M. 1979. Food habitats and livestock competition with the desert tortoises on the Beaver Dam Slope. Pages 132–147 in E. St. Amant, editor. Desert Tortoise Council Proceedings of 1979 Symposium. Desert Tortoise Council, Long Beach, California, USA.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Delibes, M., S. C. Zapata, M. C. Blázquez, and R. Rodríguez-Estrella. 1997. Seasonal food habits of bobcats (*Lynx rufus*) in subtropical Baja California Sur, Mexico. Canadian Journal of Zoology 75:478–483.

Emblidge, P. G., K. E. Nussear, T. C. Esque, C. M. Aiello, and A. D. Walde. 2015. Severe mortality of a population of threatened Agassiz's desert tortoise: the American badger as a potential predator. Endangered Species Research 28:109–116.

Engeman, R. M., B. Constantin, M. Christie, and P. Hall. 2009. *Ctenosaura similis* (black spiny-tailed iguana), *Gopherus polyphemus* (gopher tortoise) concurrent burrow use. Herpetology Review 40:84.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Esque, T. C., K. E. Nussear, K. Drake, A. D. Walde, K. H. Berry, R. C. Averill-Murray, P. Woodman, W. I. Boarman, P. A. Medica, M. Jeremy, and J. Heaton. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research 12:167–177.

Field, K. J., C. R. Tracy, P. A. Medica, R. W. Marlow, and P. S. Corn. 2007. Return to the wild: translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). Biological Conservation 136:232–245.

Fortin, D., P. L. Buono, O. J. Schmitz, N. Courbin, C. Losier, M. H. St-Laurent, P. Drapeau, S. Heppell, C. Dussault, V. Brodeur, and J. Mainguy. 2015. A spatial theory for characterizing predator-multiprey interactions in heterogeneous landscapes. Proceedings of the Royal Society B 282:99–108.

Fox, M. 1969. Ontogeny of prey-killing behavior in Canidae. Behaviour 35:259–272.

Frey, S. N., and M. R. Conover. 2006. Habitat use by meso-predators in a corridor environment. Journal of Wildlife Management 70:1111–1118.

Hampton, A. M. 1981. Field studies of natality in the desert tortoise. Pages 128–138 in K. A. Hashagen, editor. Desert Tortoise Council Proceedings of 1981 Symposium. Desert Tortoise Council, Long Beach, California, USA.

Haug, E. A., B. A. Millsap, and M. S. Martell. 1993. Burrowing owl (*Speotyto cunicularia*). Account 61 in A. Poole and F. Gill, editors. The birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Heinrich, G., L. A. MacDonald, and J. D. McMurtray. 1995. *Gopherus polyphemus* (gopher tortoise) burrow associate. Herpetology Review 26:204.

Hernández, L., M. Delibes, and F. Hiraldo. 1994. Role of reptiles and arthropods in the diet of coyotes in extreme desert areas of northern Mexico. Journal of Arid Environments 26:165–170.

Hohman, J. P., and R. D. Ohmart. 1980. Ecology of the desert tortoise on the Beaver Dam Slope, Arizona. U.S. Bureau of Land Management, St. George, Utah, USA.

Jackson, D. R., and E. G. Milstrey. 1989. The fauna of gopher tortoise burrows. Proceedings of the Gopher Tortoise Relocation Symposium State of Florida, Game and Freshwater Fish Commission 86:86–98.

Kelcey, J. G. 1975. Industrial development and wildlife conservation. Environmental Conservation 2:99–108.

Kelly, M. J., J. Betsch, C. Wultsch, B. Mesa, and L. S. Mills. 2012. Noninvasive sampling for carnivores. Pages 47–69 in L. Boitani and R. A. Powell, editors. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, United Kingdom.

Kent, D., and E. Snell. 1994. Vertebrates associated with gopher tortoise burrows in Orange County, Florida. Florida Field Naturalist 22:8–10.

Kinlaw, A. 1999. A review of burrowing by semi-fossorial vertebrates in arid environment. Journal of Arid Environments 41:127–145.

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.

Lingle, S. 2000. Seasonal variation in coyote feeding behavior and mortality of white-tailed deer and mule deer. Canadian Journal of Zoology 78:85–99.

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

Lovich, J. E., D. Delaney, J. Briggs, M. Agha, M. Austin, and J. Reese. 2014a. Black bears (Ursus americanus) as a novel potential predator of Agassiz's desert tortoises (Gopherus agassizii) at a California wind energy facility. Bulletin of the South California Academy of Sciences 113:34–41.

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. Journal of Applied Energy 103:52–60.

Lovich, J. E., J. R. Ennen, S. Madrak, K. Meyer, C. Loughran, C. Bjurlin, T. R. Arundel, W. Turner, C. Jones, and G. M. Groenendaal. 2011. Effects of wind energy production on growth, demography, and survivorship of a desert tortoise (Gopherus agassizii) population in Southern California with comparisons to natural populations. Herpetological Conservation Biology 6:161–174.

Lovich, J. E., C. B. Yackulic, J. Freilich, M. Agha, M. Meulblok, K. P. Meyer, T. R. Arundel, J. Hansen, M. S. Vamstad, and S. A. Root. 2014b. Climatic variation and tortoise survival: has a desert species met its match? Biological Conservation 169:214–224.

Luckenbach, R. A. 1982. Ecology and management of the desert tortoise (Gopherus agassizii) in California. North American tortoises: conservation and ecology. U.S. Fish and Wildlife Service Wildlife Research Report 12, Washington, D.C., USA.

Mack, J. S., K. H. Berry, D. M. Miller, and A. S. Carlson. 2015. Factors affecting the thermal environment of Agassiz's desert tortoise (Gopherus agassizii) cover sites in the central Mojave Desert during periods of temperature extremes. Journal of Herpetology 49:405–414.

MacNulty, D. R., L. D. Mech, and D. W. Smith. 2007. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. Journal of Mammalogy 88:595–605.

Medica, P. A., and P. D. Greger. 2009. Gopherus agassizii (desert tortoise), predation by mountain lion. Herpetological Review 40:75–77.

Meek, P. D., G. A. Ballard, and P. J. Fleming. 2015. The pitfalls of wildlife camera trapping as a survey tool in Australia. Australian Mammalogy 37:13–22.

Morafka, D. J., and K. H. Berry. 2002. Is Gopherus agassizii a desert-adapted tortoise, or an exaptive opportunist? Implications for tortoise conservation. Chelonian Conservation Biology 4:263–287.

Ng, S. J., J. W. Dole, R. M. Sauvajot, S. P. Riley, and T. J. Valone. 2004. Use of highway undercrossings by wildlife in southern California. Biological Conservation 115:499–507.

O'brien, R. M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality and Quantity 41:673–690.

Paltridge, R. 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. Wildlife Research 29:389–403.

Peterson, C. C. 1994. Different rates and causes of high mortality in two populations of the threatened desert tortoise Gopherus agassizii. Biological Conservation 70:101–108.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. Bioscience 59:779–791.

Rabin, L. A., R. G. Coss, and D. H. Owings. 2006. The effects of wind turbines on antipredator behavior in California ground squirrels (Spermophilus beecheyi). Biological Conservation 131:410–420.

Ray, J. C. 2000. Mesocarnivores of northeastern North America: status and conservation issues. Wildlife Conservation Society Working Paper 15:1–82.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Roberson, J. B., B. L. Burge, and P. Hayden. 1985. Nesting observations of free-living desert tortoises (Gopherus agassizii) and hatching success of eggs protected from predators. Pages 91–99 in M. W. Trotter, editor. Desert Tortoise Council Proceedings of 1985 Symposium. Desert Tortoise Council, Long Beach, California, USA.

Roemer, G. W., M. E. Gompper, and B. Van Valkengurgh. 2009. The ecological role of the mammalian mesocarnivore. Bioscience 59:165–173.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. Which camera trap type and how many do I need? A review of camera features and study designs for a range of wildlife research applications. Hystrix, the Italian Journal of Mammalogy 24:148–156.

Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen. 2014. Quantifying levels of animal activity using camera trap data. Methods in Ecology and Evolution 5:1170–1179.

Ruby, D. E., and H. A. Niblick. 1994. A behavioral inventory of the desert tortoise: development of an ethogram. Herpetological Monographs 8:88–102.

Sikes, R. S., and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Smallwood, K. S., D. A. Bell, S. A. Snyder, and J. E. DiDonato. 2010. Novel scavenger removal trials increase wind turbine-caused avian fatality extimates. Journal of Wildlife Management 74:1089–1096.

Smith, A. L, S. R. Puffer, J. E. Lovich, L. A. Tennant, T. R. Arundel, M. S. Vamstad, and K. D. Brundige. 2016. A potential predator-prey interaction of an American badger and an Agassiz's desert tortoise with a review of badger predation on turtles. California Fish and Game 102:131–144.

Stanton, L. A., M. S. Sullivan, and J. M. Fazio. 2015. A standardized ethogram for the felidae: a tool for behavioral researchers. Applied Animal Behavior Science 173:3–16.

Sterner, R. T., and S. A. Shumake. 2001. Coyote damage control research: a review and analysis. Pages 297–325 in M. Bekoff, editor. Coyotes: biology, behavior, and management. Blackburn Press, Caldwell, New Jersey, USA.

Tewes, M. E., J. M. Mock, and J. H. Young. 2002. Bobcat predation on quail, birds, and mesomammals. National Quail Symposium 5:65–70.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation 108:299–306.

Todd, B. D., B. J. Halstead, L. P. Chiquoine, J. M. Peaden, K. A. Buhlmann, T. D. Tuberville, and M. G. Nafus. 2016. Habitat selection by juvenile Mojave Desert tortoises. Journal of Widlife Management 80:720–728.

Toland, B. 1991. Spotted skunk use of a gopher tortoise burrow for breeding. Florida Scientist 54:10–12.

Turner, F. B., K. H. Berry, D. C. Randall, and G. C. White. 1987. Population ecology of the desert tortoise at Goffs, California, 1983–1986. Southern California Edison, Rosemead, California, USA.

Urquiza-Haas, T., C. A. Peres, and P. M. Dolman. 2009. Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatán Peninsula, Mexico. Biological Conservation 142:134–148.

U.S. Fish and Wildlife Service. 2011. Revised recovery plan for the Mojave population of the desert tortoise (Gopherus agassizii). U.S. Fish and Wildlife Service, Pacific Southwest Region, Sacramento, California, USA.

Von Seckendorff Hoff, K., and R. W. Marlow. 2002. Impacts of vehicle road traffic on desert tortoise populations with consideration of conservation of tortoise habitat in southern Nevada. Chelonian Conseration Biology 4:449–456.

Walde, A. D., A. Currylow, and A. M. Walde. 2015. Discovery of a new burrow associate of the desert tortoise (Gopherus agassizii), the long-nosed leopard lizard (Gambelia wislizenii). Herpetological Notes 8:107–109.

Walde, A. D., A. M. Walde, D. K. Delaney, and L. L. Pater. 2009. Burrows of desert tortoises (*Gopherus agassizii*) as thermal refugia for horned larks (*Eremophila alpestris*) in the Mojave Desert. Southwestern Naturalist 54:375–381.

Way, J. G., D. L. M. Szumylo, and E. G. Strauss. 2006. An ethogram developed on captive eastern coyotes *Canis latrans*. Canadian Field Naturalist 120:263–288.

Wells, M. C. 1978. Coyote senses in predation: environmental influences on their relative use. Behavarioul Processes 3:149–158.

Winegarner, M. S. 1985. Bobcat family utilizes tortoise burrow. Flordia Field Naturalist 13:32–33.

Woodbury, A. M., and R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecological Monographs 18:145–200.

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