BRIEF COMMUNICATION

https://doi.org/10.1038/s41559-018-0707-z

Wind farms have cascading impacts on ecosystems across trophic levels

Maria Thaker 1,3*, Amod Zambre 1,2,3 and Harshal Bhosale1

Wind farms are a cleaner alternative to fossil fuels for mitigating the effects of climate change, but they also have complex ecological consequences. In the biodiversity hotspot of the Western Ghats in India, we find that wind farms reduce the abundance and activity of predatory birds (for example, Buteo, Butastur and Elanus species), which consequently increases the density of lizards, Sarada superba. The cascading effects of wind turbines on lizards include changes in behaviour, physiology and morphology that reflect a combination of predator release and density-dependent competition. By adding an effective trophic level to the top of food webs, we find that wind farms have emerging impacts that are greatly underestimated. There is thus a strong need for an ecosystem-wide view when aligning green-energy goals with environment protection.

Wind energy is the fastest-growing renewable energy sector in the world, with current capacity estimates at ~500,000 MW per year (4% of global energy demand)^{1,2}. With land requirement of as high as 34 hectares MW⁻¹, close to 17 million hectares of land is currently used for wind energy generation worldwide3. Despite the benefits of this renewable energy production, wind farms have ecological costs4. Wind turbines cause high mortality in birds and bats from direct impacts^{5,6}, impede bird migration routes⁷, and reduce the density and activity of terrestrial mammals^{8,9}. It is often assumed that the greatest impacts of wind turbines are restricted to volant species9, resulting in significant reduction in local population density (but see ref. 10). Here, we show that the effects of wind turbines are much larger and are akin to adding an apex predator to natural communities. By reducing the activity of predatory birds in the area, wind turbines effectively create a predation-free environment that causes a cascade of effects on a lower trophic level.

Predator-induced trophic cascades are most apparent in ecosystems where top predators are removed or added, and are often driven by numerical changes in predator densities¹¹. Changing predation pressure can affect the local density of prey through direct consumption^{12,13}, but predation risk can also cause nonconsumptive effects by altering the behaviour, physiology and morphology of prey that survive14-18. Our study area—the lateritic plateaus in the Western Ghats of India-is ecologically unique, with high endemism in flora and fauna¹⁹. Wind farms here have been functioning for 16-20 years²⁰. To detect legacy effects of wind farms on small vertebrates, we used a space-fortime substitution²¹ and compared areas with and without wind turbines on the same plateau (Supplementary Fig. 1). Apart from the presence or absence of wind turbines, the habitats of sites with $(n=3; \sim 0.5 \text{ km}^2 \text{ each})$ and without wind turbines $(n=3; \sim 0.5 \text{ km}^2 \text{ each})$ ~0.5 km² each) were indistinguishable (Supplementary Figs. 2 and 3, and Fig. 1a,b).

Many studies have demonstrated reduced avian density in areas with wind turbines^{22–26}, but this in itself would not affect lower trophic levels unless there is a concomitant decrease in predation pressure for prey. Raptors regularly prey on small terrestrial vertebrates and are among the most important diurnal lizard predators in this landscape. We found that both the abundance of predatory birds (Z=-13.91, P<0.001, Cohen's d=0.84; Fig. 1d) and the frequency of predation attempts (dive attacks) by raptors on ground-dwelling prey (Z=-4.45, P<0.001, Cohen's d=0.29; Fig. 1e) were almost four times lower in sites with wind turbines than those without. As expected from reduced predation pressure, the density of the most dominant terrestrial vertebrate species in this ecosystem, the endemic superb fan-throated lizard *Sarada superba* (Fig. 1c) was significantly higher in sites with wind turbines compared with those without (Z=8.93, P<0.001, Cohen's d=0.48; Fig. 1f).

However, predation is a strong selective force and terrestrial lizards in sites with wind turbines showed differences in physiology, behaviour and even morphology that were consistent with the nonconsumptive effects of predator release^{14,17,18}. Signatures of reduced predation pressure in sites with wind turbines compared with those without were detected in the lower stress-induced (t = -2.61, P = 0.05, Cohen's d = 0.43) but not baseline (t = -0.76, P = 0.48) levels of circulating corticosterone in free-ranging S. superba (Fig. 2a). Physiological stress coping strategies, especially those mediated by the steroid hormone corticosterone, are sensitive to changes in predation pressure and play a vital role in influencing energy mobilization, as well as behavioural and cognitive processes²⁷. In some terrestrial mammals, proximity to wind turbines causes an increase in glucocorticoid levels^{9,28}, presumably because of the stress and interference induced by mechanical noise and infrasound. In contrast with these findings, the downregulation of the hypothalamuspituitary-adrenal axis for stress reactivity, but not homoeostatic processes, in lizards from sites with wind turbines, is a good indicator of habituation to an environment with fewer intense (predation) stressors¹⁵. In response to controlled simulated 'predator attacks' by an approaching human, lizards at sites with wind turbines showed significantly lower approach distances (Z = -5.41, P < 0.001, Cohen's d = 0.12) and flight initiation distances (FIDs) compared with those without (Z=-5.86, P<0.001, Cohen's d=0.52). Lizards from sites with wind turbines had FIDs that were five times shorter than those from sites without, allowing researchers to approach within 3 m before fleeing (Fig. 2b). This reduction in the escape responsiveness of lizards in areas with wind turbines directly follows expectations from the low stress-induced levels of corticosterone^{29,30}. The study plateau is used for various anthropogenic activities besides clean energy production; local communities graze livestock and extract non-timber resources. Despite the prevalent human activity in the area, lizards showed relaxed physiological stress responses and

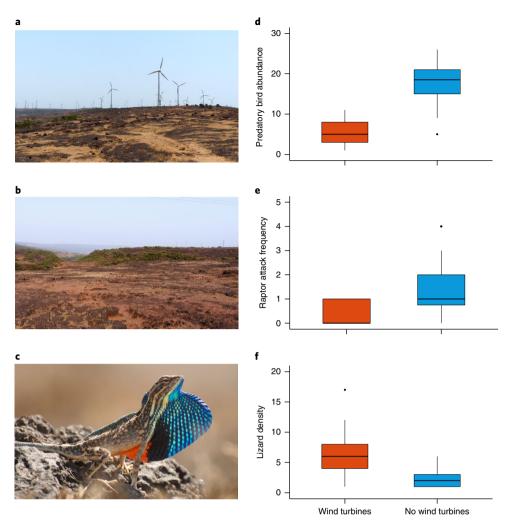


Fig. 1 Numerical effect of wind turbines on predatory birds and lizard prey. a,b, Lateritic habitat on the Chalkewadi plateau (a) with (n=3 sites) and (b) without wind turbines (n=3 sites). c, The endemic superb fan-throated lizard *S. superba*, which lives on the Chalkewadi plateau. **d-f**, Areas with wind turbines (red box plots) had (d) a significantly lower abundance of predatory birds (birds per 3 h), (e) a significantly lower frequency of raptor attacks on ground-dwelling prey (attacks per 3 h) and (f) significantly higher densities of lizards (lizards per 100 m belt transect) compared with areas with no wind turbines (blue box plots). Box plots show the medians, quartiles, 5th and 95th percentiles, and outliers.

anti-predator responses in sites with wind turbines, consistent with the perception of lower predation pressure.

The numerical effects on prey density, as well as shifts in the physiological and behavioural responses to stressors in lizards from sites with wind turbines, are typical effects of predator release on prey in many ecosystems³¹. However, prey can also experience indirect effects of reduced predation pressure mediated through other regulatory mechanisms. Lower predation risk allows for greater foraging opportunities by prey, which can enhance prey growth³². However, we found the opposite pattern; free-ranging *S. superba* from sites with wind turbines had lower body condition (that is, they were thinner) than those at sites without (scaled body mass index; t=24.5, P<0.001, Cohen's d=0.22; Fig. 2c). Although we found no differences in habitat or substrate structure, areas with wind turbines may still have lower per-capita food availability (arthropods) because of the higher local lizard densities³³, thereby reducing the body condition of individuals.

Notably, these density-dependent effects in areas with wind turbines not only affected body condition, but also influenced the expression of secondary sexual characteristics. Males of *S. superba* have highly conspicuous blue, black and orange patches on their

dewlaps, which are used during inter- and intrasexual communication³⁴. We found that males from sites with wind turbines had lower chroma and brightness of the blue (chroma: t=-3.995, P = 0.01, Cohen's d = 0.32; brightness: t = -3.40, P = 0.02, Cohen's d = 0.23) and orange (chroma: t = -2.23, P < 0.001, Cohen's d = 0.30; brightness: t = -5.40, P < 0.001, Cohen's d = 0.30) patches on their dewlap compared with those from sites without wind turbines (Supplementary Fig. 4). The intensity of colours is a signal of individual quality in many taxa³⁵; thus, a reduction in the chroma and brightness of colours in males from areas with wind turbines can have consequences for sexual selection in this population. Sexual ornamentation is known to be enhanced when predation risk decreases³⁶ and sexual selection increases³⁷. Instead, we found that density-dependent competition was a high cost of predator release. High lizard densities under low avian predation risk resulted in greater competition for potentially limiting resources (for example, beetles with high carotenoid content) that are needed to develop enhanced ornamentation.

Wind farms can affect ecological communities in ways that are unexpected and complex. Despite the fact that our study was restricted to a single plateau, we found multiple lines of evidence

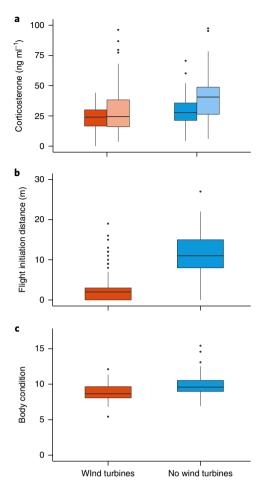


Fig. 2 | The presence of wind turbines influences the phenotypic trait responses of lizards. \mathbf{a} - \mathbf{c} , S. superba from sites with wind turbines (red box plots) had significantly (\mathbf{a}) lower stress-induced (light box plots), but not baseline (dark box plots), corticosterone levels (n = 81 from sites with wind turbines; n = 63 from sites without), (\mathbf{b}) lower anti-predator responses, as measured by FID (n = 106 in sites with wind turbines; n = 73 in sites without) and (\mathbf{c}) lower body condition, as measured by scaled body mass index (n = 89 from sites with wind turbines; n = 64 from sites without) compared with those from sites with no wind turbines (blue box plots). Box plots show the medians, quartiles, 5th and 95th percentiles, and outliers.

for a green-energy-induced trophic cascade. We found that wind turbines do not significantly alter habitat or substrate structure, but they do reduce avian predator abundance and hunting activity (see also refs ^{23,24}). This large reduction in predator activity lowered the predation pressure for small diurnal terrestrial vertebrates in that area. Numerical changes in prey population size are one of the most conspicuous and rapid consequences of predator release¹¹. Consistent with this, we found that densities of the most common lizard species were three times higher in sites with wind turbines compared with those without. We also found strong trait-mediated effects of predator release: lizards at sites with wind turbine not only had lower stress-induced corticosterone levels and anti-predator behavioural responses, but they also had lower body condition and intensity of sexual ornamentation. These population- and individual-level changes in lizards seem to be driven by both the direct (lowered predation pressure) and indirect (increased competition) effects of reduced predation pressure from the top predator guild.

Increasing evidence suggests that humans are an unchecked 'super predator' globally, through their removal of animals³⁸ and by their induction of fear³⁹. Our work shows that even without the

direct presence of humans, anthropogenic disturbances such as wind farms act as effective apex predators. By reducing the impact of predatory birds in the area, wind turbines cause a cascade of changes in terrestrial prey, driven primarily by the ecological processes of predator release and density-mediated competition. The loss of apex predators worldwide has resulted in far-reaching consequences for ecosystem processes and stability¹¹. Since the locations of wind farms are mainly determined based on economic rather than environmental considerations⁴⁰, we stress that the consequences of wind farms are greatly underestimated. While conservation efforts are a necessary global priority, wind farms in unique or biodiverse ecosystems illustrate an unexpected conflict between the goals from the United Nations Paris Agreement² for climate change mitigation and Aichi targets from the Convention on Biological Diversity⁴¹.

Methods

Study area. Lateritic plateaus, formed from intense physical and chemical weathering of basaltic rocks, are a unique feature of the northern Western Ghats¹⁹. These high-altitude (>1,000 m) flat table-topped mountains are characterized by low soil cover and exposed sheet rocks that are mostly devoid of large woody vegetation, giving them a barren appearance. This has led to lateritic plateaus being classified as 'category 22: barren rocky/stony waste' by the Department of Land Resources, India, even though they support a high diversity of endemic flora and fauna 19,20,26. The unique topographical features of these plateaus, primarily high elevation and absence of large woody vegetation, make them suitable for wind farms. As a consequence, many high-elevation lateritic plateaus in the northern Western Ghats already have wind farms, or are proposed sites for new wind farms²⁰. Our study site—the Chalkewadi plateau in Satara district in the northern Western Ghats—has one of the largest and longest-running (~16–20 years) wind farms in the region²⁰. Large parts of the Chalkewadi plateau and the adjacent valley lie within the Sahyadri Tiger Reserve and Koyna Wildlife Sanctuary, which are protected and harbour pristine forest habitats¹⁹ (see Supplementary Fig. 1 for a map). These protected areas do not have wind turbines 19,26. The close spatial proximity of wind farms and undisturbed habitats provides an excellent system for comparison. Although there are no large permanent settlements on the plateau itself, both the eastern and western slopes of the plateau are dotted with several small villages, supporting a substantial pastoralist population. These communities use the plateau as grazing grounds. Hence, there is high human and cattle activity on the plateau, in areas both with and without wind turbines20.

In this matrix of disturbed habitats (sites with wind turbines) and pristine plateau habitats, we selected six sites (Supplementary Fig. 1): three with wind turbines (13–15 wind turbines in each site) and three without. These sites were approximately 0.5 km² in size and about 2 km apart (except 'Enercon' and 'Medha', which were ~1 km apart)—the maximum distance that small-sized agamids (for example, superb fan-throated lizards with a snout-to-vent length (SVL) of <8 cm) are thought to disperse. During the summer months, when this study was conducted, all sites were similar in habitat structure, as determined by a classification of substrate types (see below).

All statistical analyses were done using R statistical software⁴². For all linear and generalized linear models, the model fit was assessed qualitatively, using the distribution of residual versus fitted values, and quantitatively, by comparing small-sample-size-corrected Akaike information criterion (AICc) values of all the competing models. Differences in AICc values (Δ AICc) between the best and second best models are reported for all tests.

Habitat classification. The habitat structure of sites with and without wind turbines was classified at two spatial resolutions. We used remote sensing data with supervised correction methods to classify land-cover types on the entire Chalkewadi plateau into three main categories: (1) rocks/bare ground, (2) vegetation and (3) anthropogenic built-up structures. A satellite image of the plateau containing three bands in the visible-light spectrum (red, blue and green) at a spatial resolution of approximately 5 m for April 2015 was downloaded from an open-source data platform (Bing Maps) and converted into a 'TIFF' format raster before processing in ArcGIS 10.3.1. Pixel reflectance values for bare ground and rocks were indistinguishable and were pooled. We calculated the percentage land cover for each type across the entire plateau and for the individual study areas, and used chi-squared tests to compare the relative proportions of land-cover type between sites with wind turbines and those without. The results from this analysis are reported in Supplementary Fig. 2.

Dry grass is particularly difficult to discriminate from bare ground during the dry summer season using satellite imagery. We therefore also classified substrate types at a finer scale, using sampling plots $(1\times 1\,\mathrm{m})$ that we placed randomly at each site $(n=10\,\mathrm{per}$ site; $n=60\,\mathrm{in}$ total) during the peak study period (Supplementary Fig. 3). Plots were photographed with a Canon 5D Mark III and Canon 17–55 mm lens. The open-source image-processing software ImageJ was used to measure the relative proportion of the three dominant substrates: (1) rocks,

which included boulders and lateritic sheet rocks; (2) bare ground, characterized as the absence of rocks and vegetation; and (3) vegetation (both green and dry). In most of our plots, vegetation was primarily senescent grasses (Supplementary Fig. 3). For each land-cover type, we ran separate generalized linear mixed models with site as a fixed effect and plot as a random effect with negative binomial distribution. To ensure that the six study sites within areas with and without wind turbines did not differ in substrate, we performed post-hoc Tukey's pairwise comparisons using the 'glht' function in the 'multicomp' package in R. The results from this analysis are reported in Supplementary Fig. 3.

Predation pressure. To determine whether small terrestrial vertebrates such as lizards experience lower predation risk in areas with wind turbines, we estimated the abundance of predatory birds and the frequency of raptor attacks on ground-dwelling prey. Predatory bird abundance was estimated from $500\,\mathrm{m}$ time-bound transects ($n\!=\!32\,3$ h transects) in areas with and without wind turbines over a period of 8 months from August 2012 to March 2013. We sampled four transects per month on two separate days (one day at the start of the month and another at the end). On each day, H.B. walked two transects (once during the morning from 09:00-12:00 and once in the evening from 16:00-19:00). Hence, we had a total of 96 h of observations for each of our treatments. We classified the birds observed during the transect walks as lizard predators based on information from published bird guides 13,44 .

Additionally, to get a more direct measure of predation risk, we conducted point counts over the same 8-month period (n = 32 sampling events) in areas with and without wind turbines. We followed a sampling protocol similar to the one used to measure bird abundances: we sampled each area four times per month on two separate days (one day at the start of the month and another at the end). Each day involved 3 h of observations in the morning (09:00-12:00) and 3 h in the evening (16:00-19:00). For this measure, we selected a vantage point that provided the best possible 360° view of the area with or without wind turbines, at a larger scale than for the replicate site sampling. H.B. counted the number of times an avian predator dived towards the ground. Predator species that were actively hunting mainly included buzzards (Buteo and Butastur species), eagles and kites (Elanus species). The success of avian predator attacks is difficult to ascertain and thus all attempted attacks were counted. We examined differences in bird abundances using a generalized linear mixed model with Poisson error distribution (Δ AICc=6.66), with treatment (with or without wind turbines) as a fixed effect and month as a random effect. Similarly, for raptor attack frequency, we ran a generalized linear mixed model with Poisson error distribution (Δ AICc = 3.20), with treatment (with or without wind turbines) as a fixed effect and month as a

Lizard densities. Study sites were far enough apart to restrict the movement of small territorial diurnal lizards between sites during the study period; thus, we were able to accurately estimate site-level lizard density during the peak activity period. At each of the 6 sites, we marked 100 m × 20 m parallel belt transects that were separated by 100 m. The number of transects per site depended on the size and shape of the site. Belt transect surveys are a widely used method for reptile density estimation⁴⁵, and work particularly well for non-cryptic species, such as the fan-throated lizard^{46,47}. Two observers (A.Z. and H.B.) walked all transects (n = 10transects in each site with wind turbines and 10-16 transects in each site without) during the field season in 2014, and recorded the number and sex of lizards that were observed within 10 m on both sides of the transect line. We alternated sampling between sites with wind turbines and those without across days; thus, sampling was done at a new site with new transect locations on each day (that is, there were no repeated measures of the same transect). The numbers of lizards from all transects at each site were analysed using a generalized linear mixed model with a Poisson error distribution (\triangle AICc=36.76), where treatment (with or without wind turbines) was a fixed effect and site as was a random effect.

Hormonal stress reactivity. To measure hormonal stress reactivity, we quantified corticosterone levels from two blood samples obtained from each lizard (n = 144in total). Lizards (n = 29-32 males from each site with wind turbines; n = 15-30males from each site without) were captured by hand and the first blood sample was collected within 3 min of sighting ('baseline'). The stress-induced level of corticosterone was determined from a blood sample obtained 30 min after capture, during which a standardized stress-inducing protocol was implemented where lizards were kept in dark cotton bags⁴⁸. All blood samples were taken within a two-month period during the peak breeding season for the species (April to May 2013), and sites with and without wind turbines were visited on alternate days while sampling. Blood samples (70–100 µl each) were collected from the retro-orbital sinus using a heparinized microhaematocrit tube—a standard sampling method that poses little subsequent risk to individuals²⁹. All captured individuals were marked on their ventral side with a permanent non-toxic marker and released at the capture site. Blood samples were stored on ice while in the field. Within 6h of collection, samples were centrifuged and the isolated plasma was stored in 100% ethanol (1:10 dilution). Corticosterone levels were measured from the plasma samples using enzyme immunoassay kits (DetectX; Arbor Assays) after optimization⁴⁹. Baseline and stressinduced samples were diluted at ratios of 1:20 and 1:40, respectively, and assayed

in duplicate across 14 plates. The intra-assay coefficient of variation was 4.81%, based on two standards run with each assay plate, and the interassay coefficient of variation was 5.93%. We ran separate linear mixed models (baseline: $\Delta AICc=52.65$; stress-induced: $\Delta AICc=4.76$), with treatment (with or without wind turbines) as a fixed effect and site as a random effect to examine the differences in baseline and stress-induced corticosterone levels.

Anti-predator behaviour. FID is a widely used assessment of anti-predator responsiveness in lizards and other animals 50,51 that directly reflects the economics of fleeing^{51,52}. Anti-predator behaviours of lizards were collected between 09:00 and 12:00 from all sites within a single week in April 2014. We alternated sampling between sites with wind turbines and those without on subsequent days, such that each site was sampled once, with no opportunity for habituation to our measurement protocol. We measured FID by approaching male and female lizards from the study sites (n = 31-43 lizards from each site with wind turbines; n = 15-34 lizards from each site without) at a constant pace, and recording the distance between the lizard and the researcher when the lizard initiated flight. For all lizards (n = 179 in total), we also recorded the approach distance as the distance between the lizard and observer when the lizard was first spotted and the approach was initiated. After the lizard initiated flight, approach distances and FIDs were measured with a tape measure (if less than 5 m) or range finder (if greater than 5 m). To determine whether FIDs and approach distances varied between treatments (with or without wind turbines), we ran separate generalized mixed models with negative binomial distribution (FID: ΔAICc=83.73; approach distance: ΔAICc=31.93), with treatment and site as fixed and random effects, respectively.

Morphology and colour measurements. We caught a total of 153 males (n=29-32 lizards) from each site with wind turbines; n=15-30 lizards from each site without) by hand and measured their mass and SVL using 10 or 20 g Pesola scales (least count = 0.1 g) and standard rulers (least count = 1 mm), respectively. Mass and SVL data were used to calculate a scaled mass index, which is a measure of body condition³³. To examine differences in body condition, we ran a linear mixed model (ΔAICc=124.24), with treatment (with or without wind turbines) as a fixed effect and site as a random effect.

To quantify the magnitude and intensity of sexual colouration on lizards34, we extended and photographed the dewlap of males (n = 29-32 lizards from each site with wind turbines; n = 15-30 lizards from each site without) under full sunlight in the field against a neutral grey standard. We used band ratios to classify dewlaps into 'blue', 'black', 'orange' and 'others' (in C++), and extracted red, green and blue (RGB) values for each patch. A linearization function for the camera, in the form of $y = a \times \exp(b \times x) + c \times \exp(d \times x)$, was derived from a photograph of a colour checker standard (X-Rite) taken under the same conditions. Here, a, b, c and d are empirically derived constants specific to the camera and depend on the response of the camera to known reflectance values of six grey scale standards under specific light conditions⁵⁴. Linearized RGB values were then corrected for possible variation in lighting conditions using grey standards in each of the photographs54. We used these linearized and equalized RGB values to derive a two-dimensional representation of the colour space, in which the x axis is the standardized difference between red and green channels, calculated as (R-G)/(R+G+B), and the yaxis is the difference between green and blue, calculated as (G - B)/ (R+G+B). In this colour space, the distance from the origin is the chroma, calculated as $r = (x^2 + y^2)^{1/2}$, and the hue is the angle relative to the axis, calculated as $\Theta = \tan^{-1}(y/x)^{55,56}$. Brightness is the sum of the red, green and blue values.

Despite some limitations, we chose the photographic method for colour quantification because it has clear advantages over spectrophotometry, especially for field studies \$4.57. Spectrophotometry only provides point measures of colour with no spatial or topographical information. The standardized photographic method of colour analysis enabled us to obtain multiple measures (hue, chroma and brightness) for all the colour patches on male dewlaps \$\mathbb{S}\$. We compared the chroma and brightness of the two colour patches on males between sites with and without wind turbines using linear mixed effect models (blue chroma: $\Delta \text{AICc} = 14.92$; blue brightness: $\Delta \text{AICc} = 9.78$; orange chroma: $\Delta \text{AICc} = 7.15$; orange brightness: $\Delta \text{AICc} = 31.65$), with colour measures as the response variable, and treatment and sites as fixed and random effects, respectively.

Ethical approval. This research was approved by the Institutional Animal Ethics Committee at the Indian Institute of Science (CAF/Ethics/396/2014).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available from the corresponding author upon request.

Received: 22 April 2018; Accepted: 1 October 2018; Published online: 05 November 2018

BRIEF COMMUNICATION

References

- 1. Global Wind Report (Global Wind Energy Council, 2017).
- Adoption of the Paris Agreement (United Nations Framework Convention on Climate Change, 2015).
- Denholm, P., Hand, M., Jackson, M. & Ong, S. Land Use Requirements of Modern Wind Power Plants in the United States Technical Report (National Renewable Energy Laboratory, Golden, 2009).
- 4. Schuster, E., Bulling, L. & Köppel, J. Environ. Manage. 56, 300-331 (2015).
- 5. Barrios, L. & Rodríguez, A. J. Appl. Ecol. 41, 72-81 (2004).
- Korner-Nievergelt, F., Brinkmann, R., Niermann, I. & Behr, O. PLoS ONE 8, e67997 (2013).
- 7. Desholm, M. & Kahlert, J. Biol. Lett. 1, 296-298 (2005).
- 8. Cryan, P. M. et al. Proc. Natl Acad. Sci. USA 111, 15126-15131 (2014).
- 9. Łopucki, R. & Mróz, I. Environ. Monit. Assess. 188, 122 (2016).
- 10. Stewart, G. B., Pullin, A. S. & Coles, C. F. Environ. Conserv. 34, 1-11 (2007).
- 11. Estes, J. A. et al. Science 333, 301-306 (2011).
- 12. Paine, R. T. Am. Nat. 103, 91-93 (1969).
- Sih, A., Crowley, P., McPeek, M., Petranka, J. & Strohmeier, K. Annu. Rev. Ecol. Syst. 16, 269–311 (1985).
- 14. Lima, S. L. Bioscience 48, 25-34 (1998).
- 15. Clinchy, M., Sheriff, M. J. & Zanette, L. Y. Funct. Ecol. 27, 56-65 (2013).
- 16. Peckarsky, B. L. et al. Ecology 89, 2416-2425 (2008).
- 17. Werner, E. E. & Peacor, S. D. Ecology 84, 1083-1100 (2003).
- 18. Sheriff, M. J. & Thaler, J. S. Oecologia 176, 607-611 (2014).
- 19. Watve, A. J. Threat. Taxa 5, 3935-3962 (2013).
- 20. Karandikar, M., Ghate, K. & Kulkarni, K. J. Ecol. Soc. 28, 45-62 (2015).
- Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T. & Ferrier, S. Proc. Natl Acad. Sci. USA 110, 9374–9379 (2013).
- 22. Miller, T. A. et al. Conserv. Biol. 28, 745-755 (2014).
- 23. Drewitt, A. L. & Langston, R. Ibis 148, 29-42 (2006).
- De Lucas, M., Janss, G. F. E., Whitfield, D. P. & Ferrer, M. J. Appl. Ecol. 45, 1695–1703 (2008).
- 25. Leddy, K. L., Higgins, K. F. & Naugle, D. E. Wilson Bull. 111, 100-104 (1999).
- 26. Pande, S. et al. J. Threat. Taxa 5, 3504-3515 (2013).
- Rich, E. L. & Romero, L. M. Am. J. Physiol. Regul. Integr. Comp. Physiol. 288, R1628–R1636 (2005).
- 28. Agnew, R. C. N., Smith, V. J. & Fowkes, R. C. J. Wildl. Dis. 52, 459-467 (2016).
- Thaker, M., Vanak, A. T., Lima, S. L. & Hews, D. K. Am. Nat. 175, 50–60 (2010).
- 30. Thaker, M., Lima, S. L. & Hews, D. K. Horm. Behav. 56, 51-57 (2009).
- Ripple, W. J., Rooney, T. P. & Beschta, R. L. in *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature* (eds Terborgh, J. & Estes, J.) 141–161 (Island Press, Washington DC, 2010).
- Fraser, D. F., Gilliam, J. F., Akkara, J. T., Albanese, B. W. & Snider, S. B. Ecology 85, 312–319 (2004).
- Jenkins, T. M., Diehl, S., Kratz, K. W. & Cooper, S. D. Ecology 80, 941–956 (1999).
- 34. Zambre, A. M. & Thaker, M. Anim. Behav. 127, 197-203 (2017).
- 35. Hill, G. E. Nature 350, 337-339 (1991).
- 36. Ruell, E. W. et al. Proc. R. Soc. B 280, 20122019 (2013).
- 37. Dale, J., Dey, C. J., Delhey, K., Kempenaers, B. & Valcu, M. Nature **527**, 367–370 (2015).
- 38. Lutmerding, J. A., Rogosky, M., Peterjohn, B., McNicoll, J. & Bystrak, D. *J. Rapt. Res.* **46**, 17–26 (2012).
- Darimont, C. T., Fox, C. H., Bryan, H. M. & Reimchen, T. E. Science 349, 858–860 (2015).
- 40. Bosch, J., Staffell, I. & Hawkes, A. D. Energy 131, 207-217 (2017).
- Decision Adopted by the Conference of the Parties to the Convention on Biological Diversity at its Tenth Meeting. X/2. The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets (SCBD, 2010); https://www.cbd.int/doc/decisions/cop-10/cop-10-dec-02-en.pdf

- 42. R Development Core Team R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, 2017).
- 43. Grimmett, R., Inskipp, C. & Inskipp, T. Birds of the Indian Subcontinent: India, Pakistan, Sri Lanka, Nepal, Bhutan, Bangladesh and the Maldives (Bloomsbury, London, 2013).
- Rasmussen, P. C. & Anderton, J. C. Birds of South Asia: The Ripley Guide (Smithsonian National Museum of Natural History and Lynx Edicions, Washington DC, 2005).
- Dodd, C. K. Reptile Ecology and Conservation (Oxford Univ. Press, Oxford, 2016).
- Nopper, J., Lauströer, B., Rödel, M. O. & Ganzhorn, J. U. J. Appl. Ecol. 54, 480–488 (2017).
- De Infante Anton, J. R., Rotger, A., Igual, J. M. & Tavecchia, G. Wildl. Res. 40, 552–560 (2014).
- Wingfield, J. C., Vleck, C. M. & Moore, M. C. J. Exp. Zool. 264, 419–428 (1992).
- Wada, H., Hahn, T. P. & Breuner, C. W. Gen. Comp. Endocrinol. 150, 405–413 (2007).
- 50. Blumstein, D. T. & Daniel, J. C. Proc. R. Soc. B 272, 1663-1668 (2005).
- Samia, D. S. M., Blumstein, D. T., Stankowich, T. & Cooper, W. E. Biol. Rev. 91, 349–366 (2016).
- 52. Ydenberg, R. C. & Dill, L. M. Adv. Study Behav. 16, 229-249 (1986).
- 53. Peig, J. & Green, A. J. Oikos 118, 1883-1891 (2009).
- Stevens, M., Parraga, C. A. & Cuthill, I. C. Biol. J. Linn. Soc. 90, 211–237 (2007).
- 55. Endler, J. A. Biol. J. Linn. Soc. 41, 315-352 (1990).
- 56. Grill, C. P. & Rush, V. N. Biol. J. Linn. Soc. 69, 121-138 (2000).
- 57. Bergman, T. J. & Beehner, J. C. Biol. J. Linn. Soc. 94, 231-240 (2008).
- 58. Kemp, D. J. et al. Am. Nat. 185, 705-724 (2015).

Acknowledgements

We thank the Maharashtra Forest Department for permits and Suzlon for allowing us to work on their property. We appreciate the logistical support provided by the Bhosale family in Satara, D. Gholap, and the Primary Health Centre in Thoseghar. We also thank N. Dandekar, G. Gowande, D. Joshi and R. Kashid for help in the field, A.K. Nageshkumar for remote sensing analysis, J. Endler for MatLab script, A. Ghatage for help with colour analyses and V. Giri for continued support. The Environmental Science Department of Fergusson College, Pune, provided partial support to H.B. during some of the bird surveys. Funding was provided by the MOEF-CC, DST-FIST and DBT-IISC partnership programme. Finally, we thank S.L. Lima, A.T. Vanak, K. Shanker and A. Batabyal for valuable comments on an earlier version of this manuscript.

Author contributions

M.T. and A.Z. conceived and designed the study, analysed the data and wrote the paper. H.B. conceived and designed the bird data collection. A.Z. and H.B. collected the data. M.T. contributed materials.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-018-0707-z.

 $\textbf{Reprints and permissions information} \ is \ available \ at \ www.nature.com/reprints.$

 $\textbf{Correspondence and requests for materials} \ should \ be \ addressed \ to \ M.T.$

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

 $\ensuremath{\texttt{©}}$ The Author(s), under exclusive licence to Springer Nature Limited 2018



Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see <u>Authors & Referees</u> and the <u>Editorial Policy Checklist</u>.

St	ati	sti	cali	nai	rar	ne	ters
-	u cı	901	CGI	\sim	u		

	en statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main , or Methods section).
n/a	Confirmed
	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
	The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.
	A description of all covariates tested
	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
	A full description of the statistics including <u>central tendency</u> (e.g. means) or other basic estimates (e.g. regression coefficient) AND <u>variation</u> (e.g. standard deviation) or associated <u>estimates of uncertainty</u> (e.g. confidence intervals)
	For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted <i>Give P values as exact values whenever suitable.</i>
\times	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
\times	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
	Clearly defined error bars State explicitly what error bars represent (e.g. SD, SE, CI)
	Our web collection on <u>statistics for biologists</u> may be useful.

Software and code

Policy information about $\underline{\text{availability of computer code}}$

Data collection

All data were collected in the field by the authors

All data were analysis

All data were analysed in R, and we wrote a custom code in C++ to extract color values from digital images of animals.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The data that support the findings of this study are available from the corresponding author upon request.

				· C•			
Field-specific reporti	ng	portii	ren	ITIC	l-speci	эIС	He

Please select the best fit fo	r your research. If you are not sure, read the appropriate sections before making your selection.
Life sciences	Behavioural & social sciences
For a reference copy of the docum	ent with all sections, see <u>nature.com/authors/policies/ReportingSummary-flat.pdf</u>
Ecological, e	volutionary & environmental sciences study design
All studies must disclose or	these points even when the disclosure is negative.
Study description	We conducted a field experiment where we compared multiple parameters in areas with (n=3 WT study areas) and without windturbines (n = 3 NWT study areas). Each study area was approximately 0.5 km2. We controlled for geography by selecting replicate sites on the same plateau where windturbines (main treatment effect) have been in the same locations for at least 16-20 years. All data were collected over two years, in the peak activity season for lizards (March to June). For land-cover measures, we analysed remote sensed data for the entire plateau. For substrate type analysis, we analysed 10 sampling plots (1x1m) in each of the 6 study areas (N=60 plots total). For avian predator abundance, we walked 4 (3 hour long) transects a month for 8 months, where half the transects were in the morning and the other half were in the evening. For raptor predation events, we conducted 32 vantage point counts (3 hour observation periods each) over 8 months. For lizard density measures, we walked 30 belt transects in WT areas and 39 in NWT areas and recorded all lizards seen. Parallel belt transect was 100 m x 20 m each, separated by 100 m. For hormonal stress reactivity, we measured 81 male lizards from WT areas, and 63 male lizards from NWT areas. Two blood samples were taken from each animal (baseline and stress-induced). Antipredator behaviours were measured by approaching 106 lizards in WT areas and 73 lizards in NWT areas and recording escape responses. Gross morphology was measured on 89 male lizards from NWT areas.
Research sample	Habitat and substrate measures of the study area were taken from remote sensing and on-ground measurements to demonstrate no significant differences between the structure of windturbine and non windturbine areas. Behavioral assays of predation risk was measured by (1) counting the number of avian predators seen, and (2) counting the number of times a raptor (typically Buteo sp., Butastur sp., or Elanus sp.) was seen dive bombing the ground. The rest of the samples were measures of behaviour, morphology and physiology of the superb fan-throated lizard, Sarada superba that live in areas with and without windturbines.
Sampling strategy	For the landscape-level measurement of landcover, we measured the entire study area. Sample size for substrates on the ground were decided based on overall low variability seen on the plateau. Sampling plots were evenly dispersed across each study area (see Supplementary figure 1). Sample sizes for lizards varied based on the measurements. For blood sampling, only lizards caught within 3 min of sighting were included to ensure a baseline measure of corticosterone. Capture of lizards also had to be spread out in space to ensure that capture of one individual did not elevate the stress hormones of neighbouring lizards. A similar spacing protocol was used for the measure of antipredator behaviour so that the "attack" of one individual would not affect the response of nearby individuals. Sample sizes for morphology and dewlap colour were based on the number of lizards that we were permitted to catch based on our research permit and ethics clearance. Lizards used for morphological measurements were also a different subset from the lizards that were sampled for the antirpredator and hormone measures to ensure than prior disturbance by us would not adversely influence the morphology and colour.
Data collection	All data were collected in the field by AZ and HB during the peak activity period of the lizard species. Data was collected continuously and the different measures were taken throughout the sampling season.
Timing and spatial scale	Everyday from March to June on 2013 and 2014
Data exclusions	No collected data were excluded from the analysis.
Reproducibility	These data were generated from field measures and thus could not be examined for experimental reproducibility. Analysis of data from replicate sites within treatments (windturbine vs no-windturbine) show low variance and thus support the fact that within treatment variation is lower than between treatment variation. We include cohen's d for all the statistical analyses.
Randomization	Visit to sampling sites were randomized across days and sampling type (behaviour, morphology, physiology). Care was taken to spread sampling out across space to ensure as much coverage of the environment as possible.
Blinding	Field data on wild caught animals (density, behaviour, morphology) could not be collected blind. Analyses of blood samples and dewlap colour from digital images were conducted blind, with relabeled codes.
Did the study involve field	d work? Yes No

Field work, collection and transport

Field conditions

Rocky lateritic plateau with little vegetation cover. Average temperature during the study season = 34degC (range = 21degC - 45degC). Average precipitation during the study season = 122mm (range =6mm - 152mm). Annual temperature = 26degC and annual precipitation = 91mm

Location

Chalkewadi plateau in the Western Ghats, Mahahastra, India. 17deg36'40"N; 73deg47'27"E

Access and import/export

We have Animal ethics permits from the Indian Institute of Science Animal Ethics Committee and collection/research permits from the state forest department. No import/export permits were required.

Disturbance

Disturbance of the environment was minimal, as most measurements were observational data. And all animals caught were returned to site of capture.

Reporting for specific materials, systems and methods

Materials & experimental system	s Methods		
n/a Involved in the study	n/a Involved in the study		
Unique biological materials	ChIP-seq		
Antibodies	Flow cytometry		
Eukaryotic cell lines	MRI-based neuroimaging		
Palaeontology			
Animals and other organisms			
Human research participants			
'			
Animals and other organ	nisms		
Policy information about studies invol	ving animals; ARRIVE guidelines recommended for reporting animal research		
Laboratory animals none			
antipr releas for up were I	al raptor species: only obervational data. Superb fan-throated lizard, Sarada superba. For density estimation and edator behaviours, adults were not captured. For morphology, males were captured by hand, measured immediately, and ed at site of capture within 30 min. For physiology, males were capture by hand, and were placed in individual cotton bags to 30 min before a second blood sample was taken (stress-induced corticosterone measure). While in cloth bags, lizards kept in the shade. All lizards captured for physiological measurements were released at their exact location of capture 45 min.		
Field-collected samples Blood	samples were stored in microcentrifuge vials in ETOH and kept cool until analysis in the lab.		