



OPEN Bird mortality at wind farms in a tropical desert

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The global aspiration for clean energy needs to accommodate biodiversity concerns. While India's wind energy has grown annually by ~15% in recent past, their ecological impacts have not been assessed systematically. We studied bird mortality at wind farms in Thar Desert; a renewable energy hotspot, harboring ~300 bird species including critically endangered vultures and bustards. Our study spanned 3000 km² open natural ecosystem with ~900 turbines. We searched carcasses at 90 randomly selected turbines using seven multi-season surveys. We compared mortalities from the first survey to concurrent surveys at 28 control sites. We corrected mortality estimates for persistence and detection biases. We observed bird crossings at 16 turbines to examine relative vulnerability of species. We found 124 bird carcasses at turbines and none at control sites. Bias adjusted mortality was $1.24 \pm 0.18_{SE}$ bird turbine⁻¹ month⁻¹ which yielded annual mortality of ~4464 birds per 1000 km² area. Mortality was lower in undulating grasslands, higher at single turbines than clustered turbines, and increased with hub height. Bird biometry or overlap between flight height and turbine impact zone did not influence relative vulnerability of bird families. To minimize these impacts, the transition from fossil fuels to renewable energy should mainstream regional assessments and mitigation measures.

Keywords Carcass, Raptors, Open natural ecosystem, Renewable energy, Thar desert, India

Economic development for humanitarian needs have often neglected the natural capital that sustain ecosystem services. Industrialization and automation have increased energy demands, resulting in depletion of fossil fuels, global warming and environmental degradation. In a global drive to switch from traditional to clean energy, national policies are promoting wind, solar and other renewable sources as they are considered relatively environment friendly. In India, the renewable energy capacity has been gradually increasing with an average annual increment of 15.5% from 2006 to 2020^{1–7}. Consequently, the share of renewable energy generation comprises 29% of global energy as of 2021⁸. However, these technologies are not free from environmental hazards. Recent studies have raised concerns about the impact of wind turbines on biodiversity, especially birds and bats^{9–12}. These concerns necessitate assessing and mitigating adverse impacts of renewable energy infrastructure while commissioning them in habitats shared with wildlife.

Wind turbines can adversely impact birds and bats through collision mortality, as they collide with turbine blades or get drawn into the wind vortex^{13,14}. Such mortality risk varies with bird taxa and traits, space, season and weather conditions¹⁵. Additionally, it may depend on the wind turbine characteristic such as hub-height, blade length and operational frequency. Many raptors, which play vital ecological functions, are particularly vulnerable to collisions with turbines because of their large size, reduced maneuverability and foraging behavior^{14,16,17}. Raptors use open habitats with good visibility for foraging that are also suitable sites for wind turbines. Additionally, wind thermals expose soaring raptors to the wind turbines, resulting in collisions^{15,18}. Such mortality may have serious population-level impacts particularly for endangered species¹⁹. Declines in breeding populations of raptor and other birds have been observed post wind installations¹⁴. Wind turbine caused mortality may vary across space in response to local abundances of resident species, migratory routes, and habitat characteristics influencing the density of vulnerable species^{10,13}. Wind farms can also impact birds through habitat loss, as they perceive these structures as disturbances. They can displace local bird populations²⁰, act as barrier to their flight paths, and even alter migratory patterns^{10,12}. These studies call for careful selection of sites for wind farms that avoid areas with large congregations of birds, especially raptors, bats, and on migratory flyways²¹.

The direct impact of wind turbines has been usually measured as fatalities per unit per year. While reporting such mortalities, most studies do not correct for biases (with a few exceptions) arising from the following sources²²: (a) crippling bias, when an individual is injured by collision but dies away from the impact zone, (b) persistence/removal bias, when a carcass gets scavenged and completely disappear before the survey, (c)

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detection bias, when a carcass is not detected during survey because of vegetation cover, degradation of the carcass, or size and contrast of plumage^{21,23}. While crippling bias is very difficult to account for, persistence and detection biases can be corrected by placing and monitoring carcasses^{24,25}. Bias correction aids in accurate comparison of mortality estimates across space and time, and in examining the effectiveness of mitigation measures. Further, very few studies have examined how bird and habitat traits influence wind turbine induced mortality. Such understanding is vital for spatial planning of wind operations, and will vary across regions, thereby necessitating regional assessments of this problem.

India has an ambitious target of generating 500 GW renewable energy from current capacity of ~101 GW. Thar Desert in western India is a hotspot for wind energy because of suitable wind resources²⁶, availability of land, and large wind power potential (5050 MW). Wind projects have expanded from 16 to 2820 MW here between 2002 and 2014²⁷. The region is also important for conservation, as it supports many threatened and migratory species of the Central Asian Flyway, and is home to the single viable population of the Critically Endangered Great Indian Bustard *Ardeotis nigriceps*. Such intersection between wind farms and birdlife creates potential conflict in the alliance between renewable energy and nature conservation. Some published studies from India have assessed impacts of wind turbines on birds; none of them are from this area^{28–34}. A recent study of power line impacts in this landscape estimated high mortality of 87,367 (24785 SE) birds in 4200 km² area²⁵. However, this study was focused on power lines and it did not highlight the specific impact of wind turbine or lines directly associated with them. The scenario merits comprehensive assessment of bird mortality for ecological auditing of existing wind turbines. Such examinations are relevant and timely given the projected growth of wind energy generation that is being achieved without ecological scrutiny of its impacts.

This study presents the first comprehensive assessment of bird mortality at wind farms in this important conservation area. (1) We estimated bias adjusted bird mortality at turbine- and landscape- levels, by conducting multi-season carcass surveys at randomly selected wind turbines, that was corrected for persistence and detection biases through experiments. (2) We examined the influence of turbine and habitat characteristics on bird mortality for planning mitigation strategies. (3) Finally, we studied collision to crossing rates vis-à-vis flight patterns of bird families to identify relatively vulnerable taxa. We hope that our approach and findings will inform eco-friendly development policies, to bridge the gap between green energy and biodiversity conservation.

Results

Mortality estimates

We found 124 bird carcasses in 630 turbine-searches. Out of these, 93 carcasses belonged to 9 families and 19 species, whereas 13 carcasses were of unidentified raptors and another 18 could not be identified (Table 1). No carcass was found in the single survey of control sites (Fig. 1).

Species/taxa	Family	No. of carcasses	No. of crossings	Conservation status	Migratory status
Buzzard	Accipitridae	1	0	–	–
Egyptian Vulture	Accipitridae	2	5	Endangered	Resident
Griffon Vulture	Accipitridae	13	5	Least concern	Winter visitor
Shikra	Accipitridae	1	0	Least concern	Resident
Short-toed Snake Eagle	Accipitridae	1	1	Least concern	Winter visitor
Tawny Eagle	Accipitridae	1	2	Vulnerable	Resident
White-rumped Vulture	Accipitridae	1	1	Critically endangered	Resident
Unidentified Raptors	Accipitridae, Falconidae	15	–	–	–
Lark	Alaudidae	1	17	–	–
Cattle Egret	Ardeidae	1	4	Least concern	Resident
Eurasian Collared Dove	Columbidae	5	72	Least concern	Resident
Blue Rock Pigeon	Columbidae	51	104	Least concern	Resident
European Roller	Coraciidae	2	0	Least concern	Passage visitor
Indian Roller	Coraciidae	1	0	Least concern	Resident
House Crow	Corvidae	1	27	Least concern	Resident
Common Kestrel	Falconidae	4	0	Least concern	Winter visitor
Laggar Falcon	Falconidae	3	0	Near threatened	Resident
Variable Wheatear	Muscicapidae	1	12	Least concern	Winter visitor
Eurasian Hoopoe	Upupidae	1	0	Least concern	Resident
Other birds	Miscellaneous	18**	372*	–	–
Unidentified bat	–	8	–	–	–
Total	–	132	622	–	–

Table 1. Number of carcasses detected ($n = 630$ turbine-searches), number of crossings ($n = 16$ turbine-scans) along with conservation and migratory status of bird species found in wind turbine surveys in Thar desert during 2020–21. *Recorded in crossing observations but not in carcass surveys; **unidentified species in carcass surveys. # Source: Birds of the Indian Subcontinent.

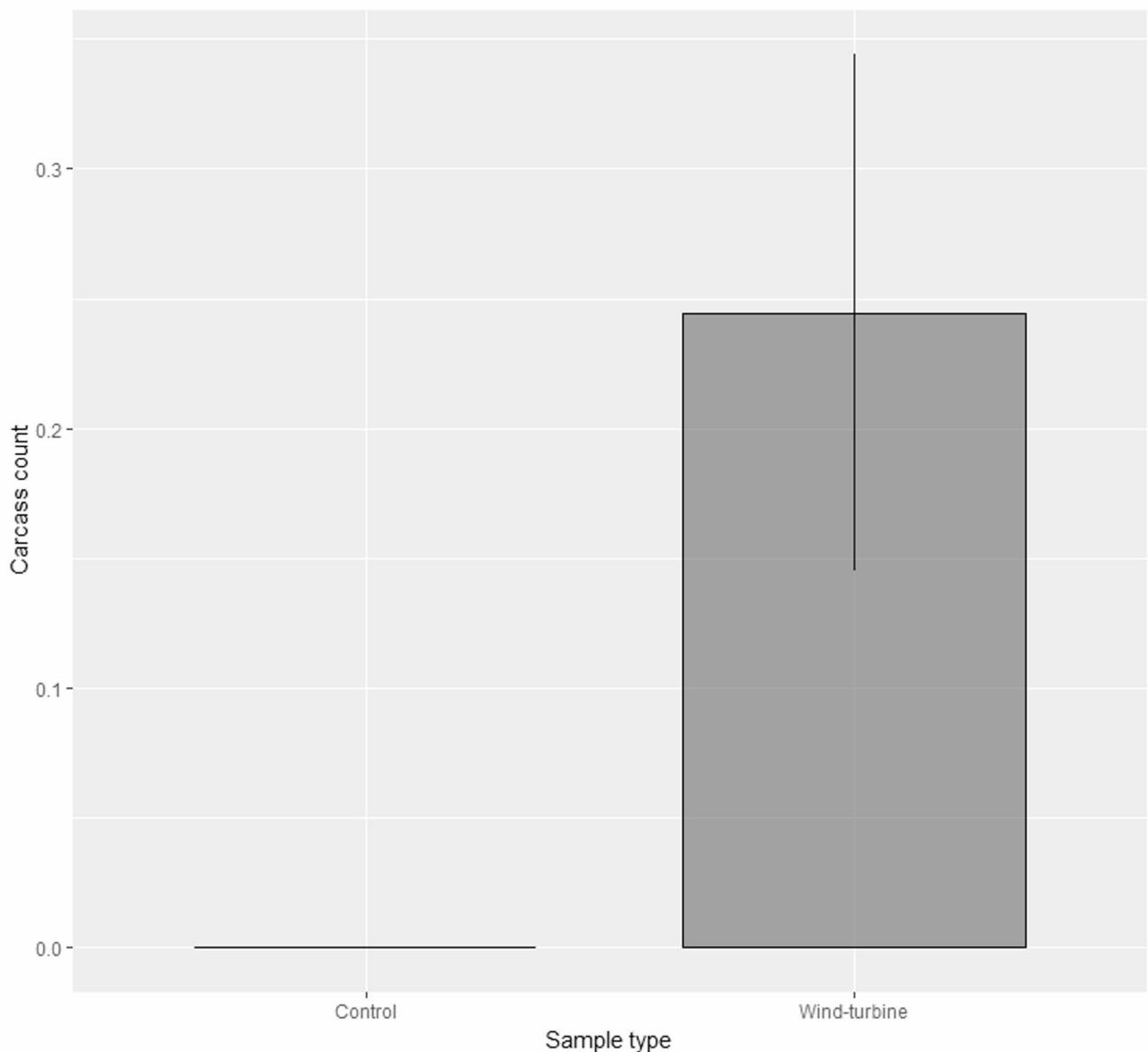


Fig. 1. Mean (SE) carcass encounter rate (bias unadjusted) between wind turbines and control sites from a single survey in February 2020 in Thar desert.

Carcass persistence probability was highest for raptors >> other large birds > medium birds > small birds (Fig. 2). Mean probability of carcass persisting if deposited on any day within a month leading up to the survey, was estimated as 0.04 (SE 0.0004) for small birds, 0.15 (0.003) for medium birds, 0.22 (0.017) for large birds, and 0.71 (0.02) for raptors. Correcting carcass encounter rate for persistence bias yielded estimate of 0.93 (SE 0.11) bird turbine⁻¹ month⁻¹. Further, carcass detection probability²⁵ was 0.53 (SE 0.12) for small birds, 0.78 (0.04) for medium size birds, and 0.96 (0.04) for large birds and raptors. Correcting for imperfect detectability, persistence and detection bias adjusted mortality rate was estimated as 1.24 (SE 0.18) bird turbine⁻¹ month⁻¹, comprising 0.23 (0.13) small birds, 0.87 (0.12) medium size birds, 0.02 (0.01) large birds, 0.09 (0.01) raptors and 0.04 (0.02) unidentified birds. This yielded annual mortality estimate of 13,359 (95% CI 11426–15293) individuals for all birds and 953 (95% CI 801–1104) raptors for the entire study area comprising ~900 wind turbines.

About 80% of carcasses were deposited within 100 m from the turbine, and the rest were beyond this distance. Whilst, mortalities due to power lines within 150 m radius of turbines were majorly found right under the lines and negligibly beyond 30 m of the line (Fig. A.2. for details).

Factors influencing mortality

Three habitat groups identified using cluster analysis were flat grassland, flat scrubland, and undulating grassland. Information theoretic approach in multi-model inference framework found support for habitat groups (summed Akaike wt $\Sigma W = 0.60$), clustering of turbines ($\Sigma W = 0.48$) and hub height ($\Sigma W = 0.40$). Wind turbine collision rates differed between habitats and was lower in undulating grassland than other habitats (Table 2a). Collision

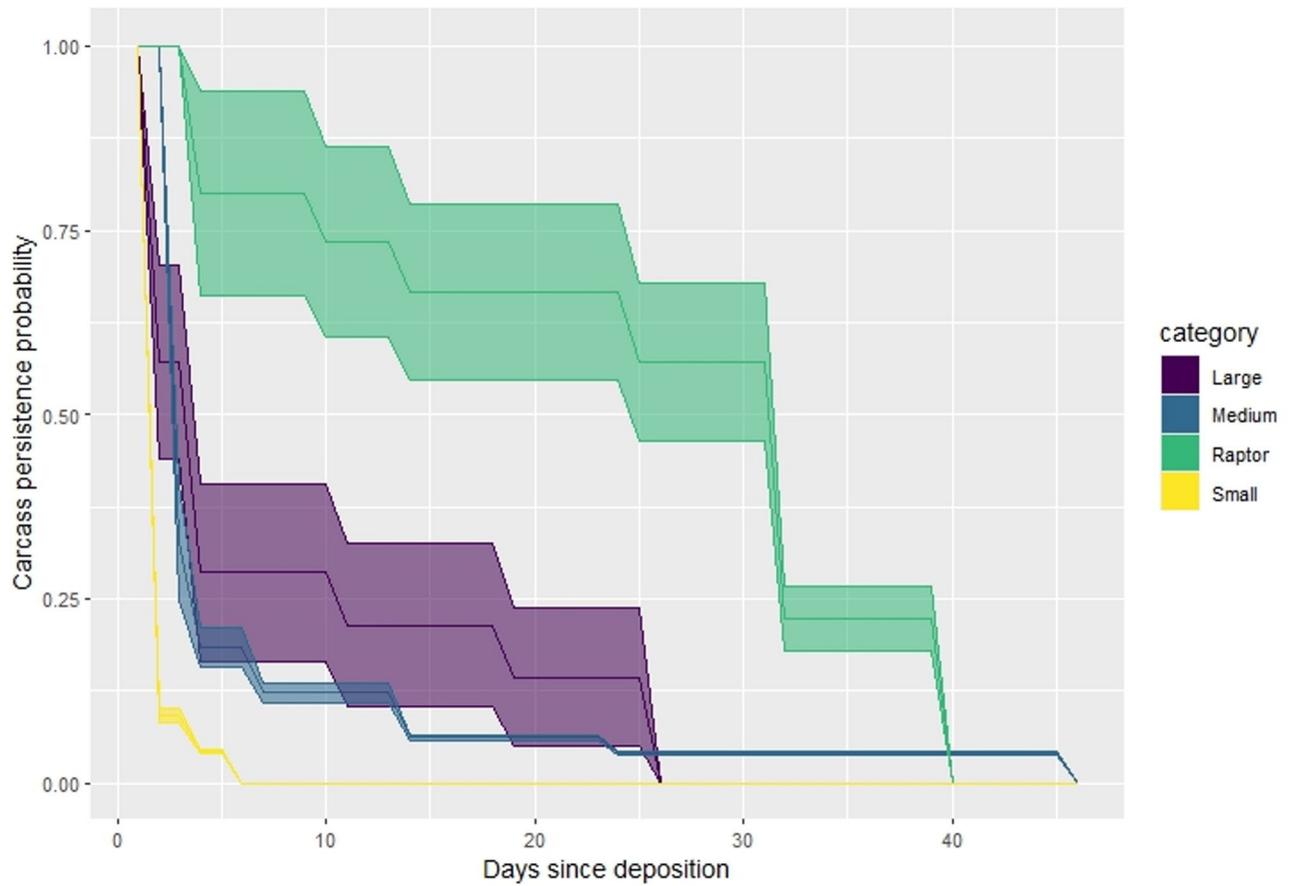


Fig. 2. Persistence probability against time since deposition of carcasses for small (< 100 g), medium (100–1000 g), large (> 1000 g) and raptorial birds in Thar desert during 2018–21.

(a) Model	Ak wt	$\Delta AICc$	AICc	K	Dev
Carcass count ~ Habitat	0.32	0.00	310.79	3	304.52
Carcass count ~ Clustering + Habitat + Hub-height	0.28	0.26	311.05	5	300.35
Carcass count ~ Clustering	0.20	0.92	311.72	2	307.58
Carcass count ~ Hub-height	0.12	1.89	312.68	2	308.54
Carcass count ~ 1	0.08	2.89	313.69	1	311.64

Table 2. Summary of models testing hypothesized effects of (a) turbine and habitat features on carcass count and that of (b) biometric trait factor and flight height overlap with turbine impact zone on vulnerability index of bird families in Thar desert during 2020–21. Models are ranked using: Akaike information criteria (AICc), Akaike weight (Ak. wt), degrees of freedom (K) and Dev (Deviance).

rates were greater in single turbines compared to clustered turbines and showed weak positive relationship with hub height ($\beta = 0.015$, $SE = 0.009$) (Fig. 3).

(b) Model	Ak wt	$\Delta AICc$	AICc	K	Dev
Vulnerability ~ 1	0.43	0.00	36.62	1	31.62
Vulnerability ~ Height overlap	0.35	0.44	37.06	2	28.88
Vulnerability ~ Biometric trait factor	0.21	1.43	38.06	2	29.88
Vulnerability ~ Biometric trait factor * Height overlap	0.01	7.34	43.96	4	27.30

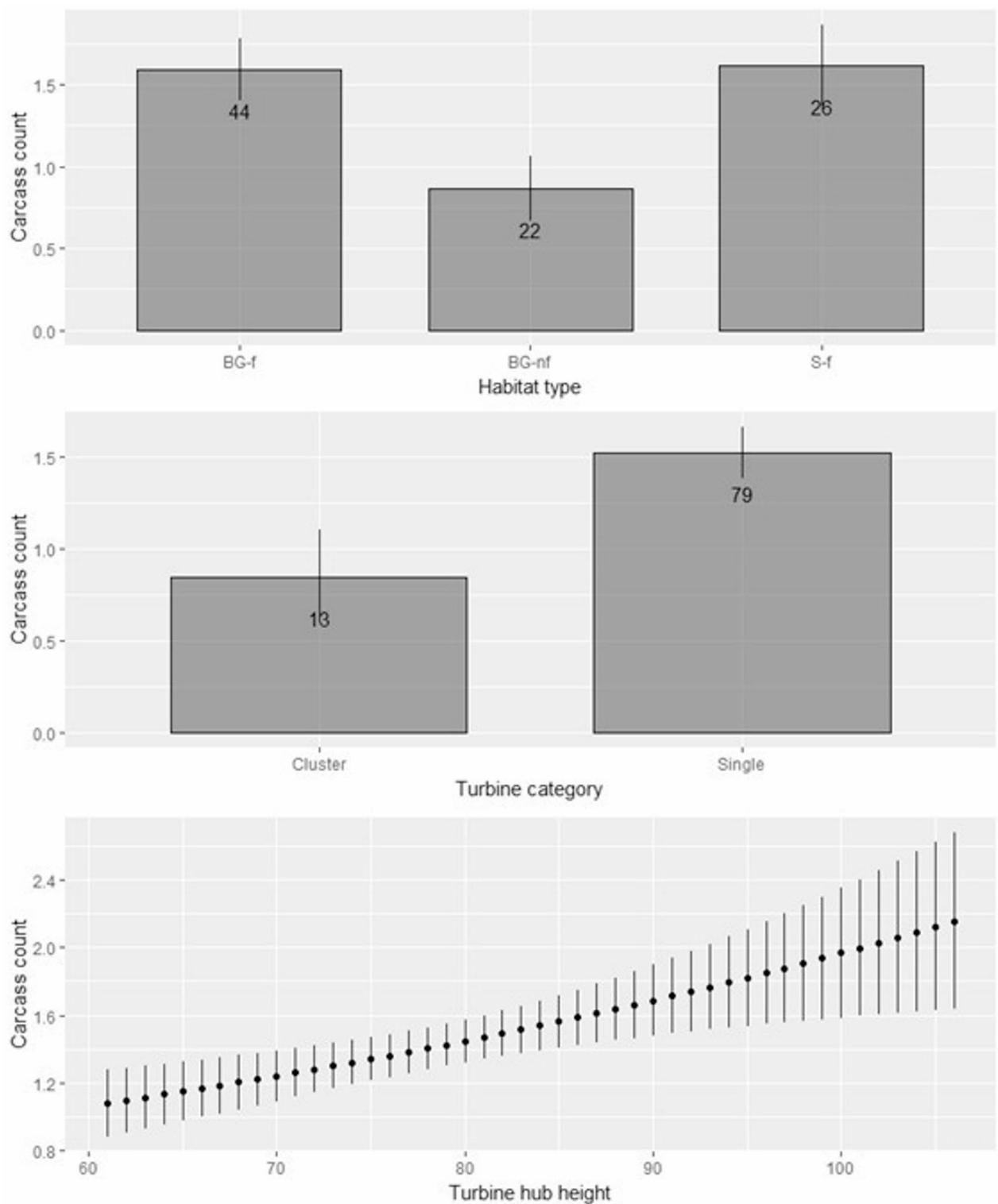


Fig. 3. Comparison of model estimated mean (SE) carcass turbine⁻¹ survey⁻¹ ('Carcass count' along Y-axis) against (a) habitats: flat grassland (BG-f), undulating grassland (BG-nf), flat scrubland (S-f), (b) single vs. clustered turbines, (c) turbine hub height (m) in Thar desert during 2020–2021.

Taxa-specific vulnerability

Carcass surveys showed highest mortality rates among Columbidae > Accipitridae > Falconidae > other families. After correcting for bird crossing rates, vulnerability was highest for Falconidae > Accipitridae > Columbidae > Ardeidae > other families (Fig. 4). Bird crossing observations showed that Falconidae, Accipitridae, Columbidae, Alaudidae, Corvidae and Pteroclididae have substantial overlap of flight

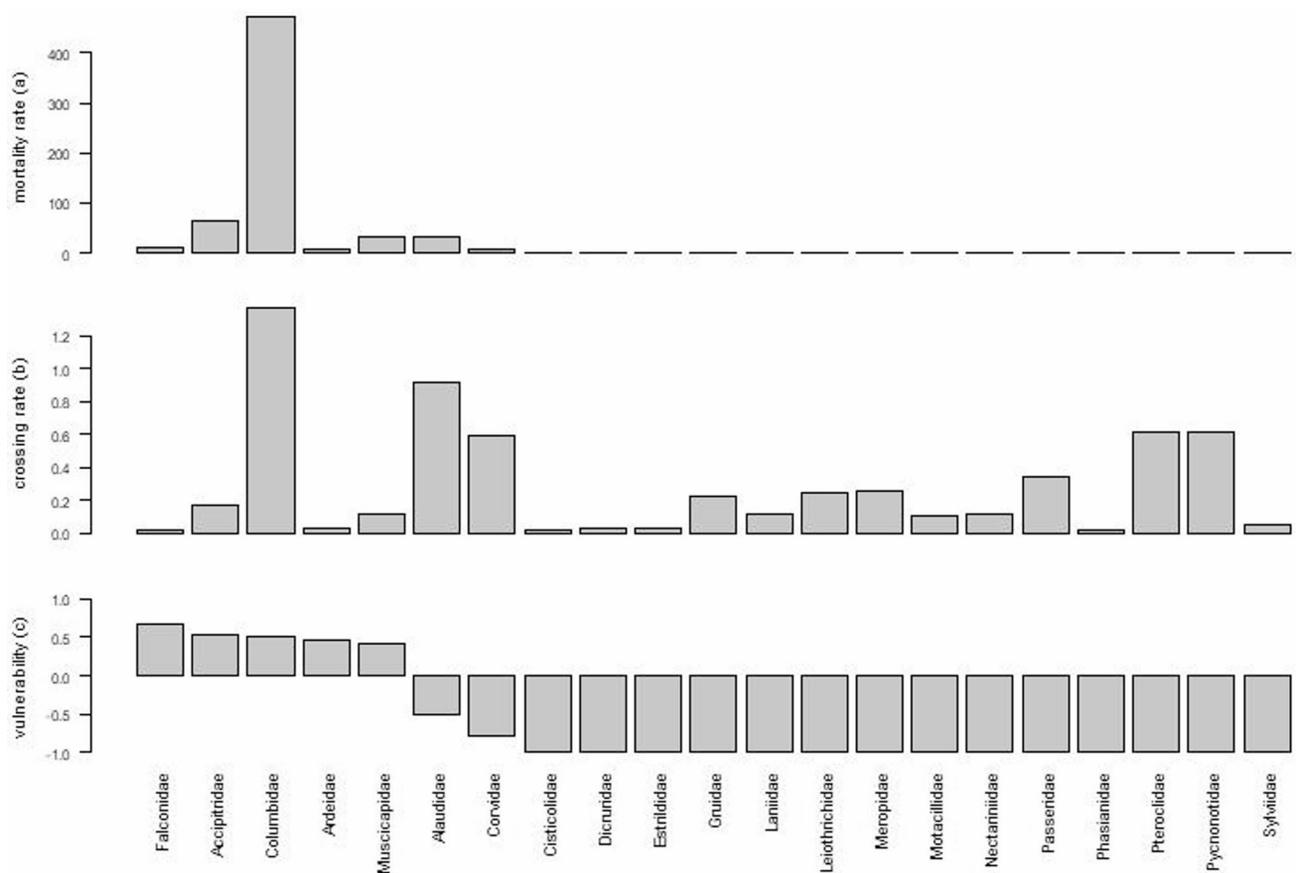


Fig. 4. (a) Bias adjusted carcass count summed over 630 wind-turbine surveys ('mortality rate'), (b) crossing per hour summed over 16 wind-turbine surveys ('crossing rate'), (c) vulnerability index computed as the ratio of proportional 'mortality rate' and proportional 'crossing rate' against bird families in Thar desert during 2020–21.

height with turbine impact zone, as indicated by greater flight frequency in these height bins (Fig. 5). However, comparison of models found no effect of overlap of flight height with turbine impact zone on vulnerability index of bird families (Table 2b). The biometric trait factor explained 62% of variance in the multi-trait data across bird species, with body mass (0.93), wingspan (0.99) and loading (0.63) being strongly and positively correlated to this trait factor. Comparison of models did not find any effect of biometric trait factor on relative vulnerability index of bird families.

Discussion

The demand for wind energy as well as the understanding of its potential impacts on birds are growing. Our study adds to this literature, by characterizing bird mortality at windfarms in an area important for both renewable energy and birds.

Mortality estimate

The estimated annual bird mortality per 1000 km² area that included ~300 turbines, was ~4470 birds when corrected for both persistence and detection biases. The single survey in control sites found no carcass. Although this is partly due to carcass removal and non-detection biases, such biases would be consistent with carcass encounter at wind turbines. Hence, compared to the prevalent natural mortality, wind turbine induced mortality was relatively higher. Carcasses found within 150 m radius around turbines could be due to collision with turbine or collision/ electrocution with power line. It was not always possible to disentangle the cause, hence our mortality estimates should be interpreted as the compounded effect of wind turbine and power line linked to it within this search radius. Our bias adjusted bird mortality estimate (~14.9 deaths turbine⁻¹ year⁻¹) was higher than majority of studies from India: 0.478 (Kutch), 0.466 (Davengere) in Gujarat³⁰ and 0.26 (including birds and bats) in Karnataka³¹. Globally, the highest reported mortality rates are 19.1–34.3 from Belgium¹⁰. Other studies which have corrected for carcass search biases reported mortality rates of 9.06–12.85 in Mexico⁹, 8.2 ± 1.4 in Canada¹², 5.25 (3.15–7.35) in contiguous United States¹¹, 1.8 in Buffalo Mountain Windfarm, USA³⁵ and <1²¹. Thus, prevalent wind turbine caused bird mortality in Indian Thar desert is near the upper limit of global estimates of its kind. This region is an Important Bird Area, supporting 65 migratory and 20 threatened bird species including Great Indian Bustard²⁵ that projects these losses to a globally relevant issue. We did not

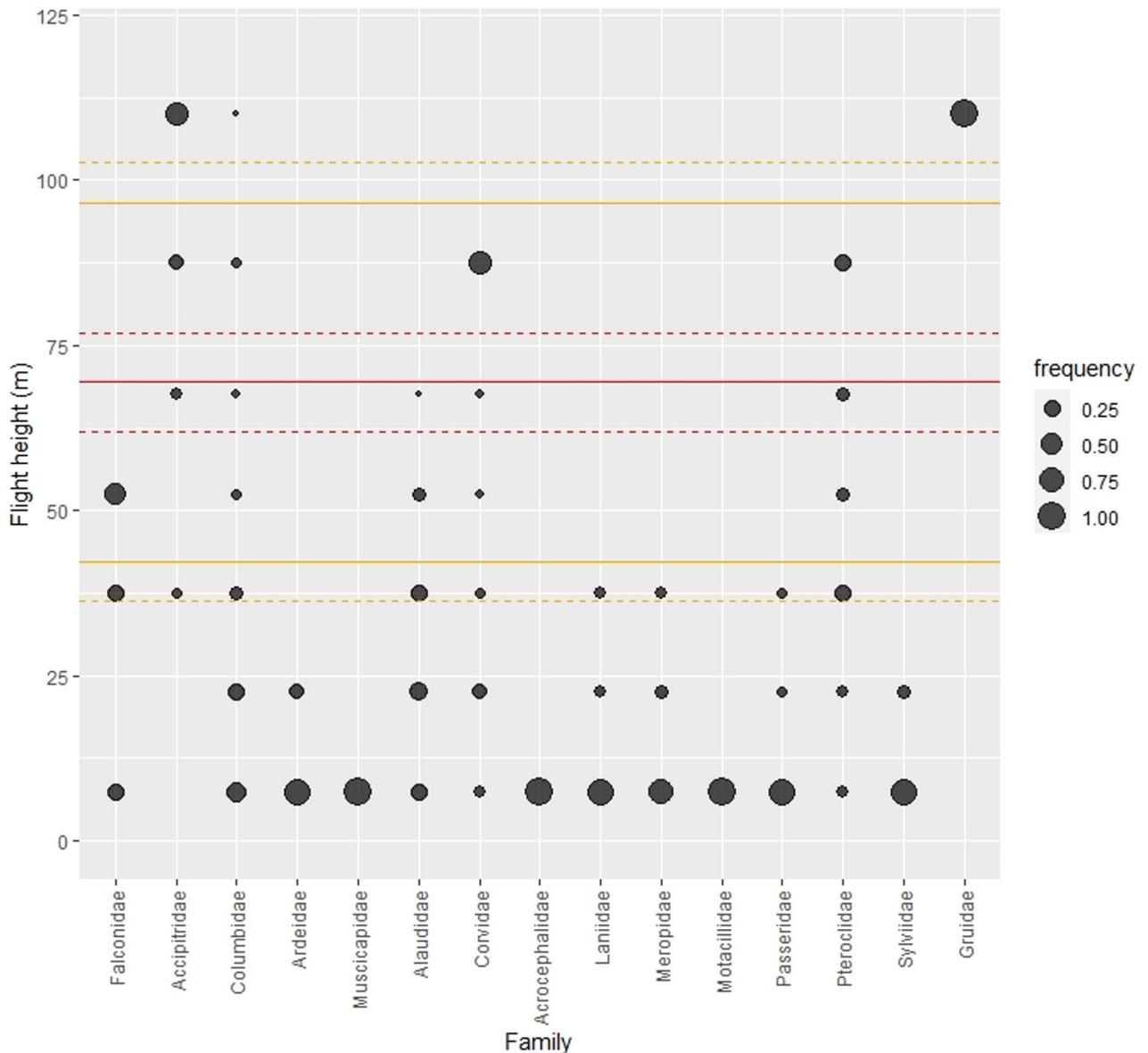


Fig. 5. Flight patterns of bird families against turbine impact zone in Thar desert, India during 2020–21. Bubbles indicate relative frequency of crossings at different flight heights, red lines indicate turbine hub height (solid: mean, dashed ± 1 SD) and yellow lines indicate blade-swept height (solid: mean, dashed ± 1 SD).

observe any collision of bustard with turbines during this study, although transmission lines evacuating power were found to be a major cause of their recent mortality²⁵.

Vulnerability across taxa

Wind turbine collision is a known conservation problem for raptors^{14,15,17,36}. Our study corroborated this view, as 39% of identified carcasses belonged to Accipitridae and Falconidae families followed by Columbidae. High mortality of Columbids especially Blue Rock Pigeon was because of their high abundance and prolific usage of turbines and associated habitats. Blue Rock Pigeon nests inside turbine monopoles that increases their encounter with wind blades and chances of collision. However, such mortality does not pose any population-level risk to this species as it is proliferating because of its synanthropic nature. On the other hand, after scaling for relative abundance and usage of bird families around turbines, Falconidae and Accipitridae were found to be most vulnerable to wind turbine deaths. Annual mortality of raptors was estimated to be about 953 individuals in the study area. Accipitrids get attracted to wind turbine induced thermals in absence of natural air thermals especially during winter and fall victim to collision¹⁵. Falconidae mortality was relatively higher in summer. These species are also at higher risk due to their preference of open habitats (for hunting); areas that have high density of turbines¹⁵. We found carcasses of White-rumped Vulture (*Gyps bengalensis*), Tawny Eagle (*Aquila rapax*) and Laggar Falcon (*Falco jugger*) at wind turbines (see Fig. A.1.). They are highly threatened and Thar

Desert is one of the few habitats which support relatively large populations of these species. Raptors are in general decline³⁷, are common victims of energy infrastructure worldwide, and many of them visit Thar Desert in large numbers for wintering. Considering these aspects, the above reported mortality can be a concerning issue and necessitates focused understanding of the population level impact of wind turbine deaths for these species.

Correlates of mortality and implications for mitigation

Habitat- and turbine- features influenced mortality rates. Collisions were higher in flat grassland and scrubland compared to undulating vegetated dunes, perhaps because of greater bird usage of former habitats. Several studies have shown that bird mortalities are site-specific and clustered in areas with favorable conditions for their movement, foraging, nesting and hunting^{38–40}. Therefore, information on birdlife should be used while planning future wind farms, to avoid areas which have higher bird usage or are more important for raptors and threatened species⁴¹, as also emphasized in the previous section. This needs prioritization exercises at country scales to develop national policy on wind energy planning as well as studies on bird usage/ movements at local scales for siting wind plants. Such exercises can benefit from recent advances in collection and analysis of citizen science data (e.g. eBird, SOIB 2023) supplemented with focused assessments of space use by sensitive species, as has been demonstrated by Hise et al.⁴² that can feed into decision support systems for siting wind plants (e.g., <http://www.avistep.birdlife.org/>).

Secondly, bird mortality rate was higher at single turbines compared to clustered turbines. Previous studies suggest that placing turbines at lower densities can reduce mortality rates⁴³. Our finding contradicted this view, perhaps because birds were avoiding dense turbine-installations. However, our data on bird observations at wind turbines were not large and seasonally replicated, to test if bird usage actually depended on turbine density. Still, such barrier effect has been reported in many studies^{10,14,20}. Reduction of bird usage post-installation can result from the loss of suitable habitat features, disturbance due to increased noise level, vibration, human presence, and impediment to flights. Such impacts may vary between species, based on their flight height and pattern, body size and flock size^{10,12,14,20,44}. A recent study from India shows that bird abundance and diversity are lower in wind turbine areas compared to control sites, and certain species have disappeared post-installation³¹. Our field observations indicate that Great Indian Bustard usage had reduced in wind turbine areas post-installation (2012–2018), but did not reduce in adjoining control areas without wind farms, likely because of the disturbances and alteration of habitat features that this species is sensitive towards.

Thirdly, we found that mortality rates increased with turbine hub height. Turbine hub heights ranged between 60 and 100 m in the study area. Collision rates nearly doubled from the lowest to the highest hub. Earlier studies have provided equivocal support for this relationship: Loss et al.¹¹ found a strong effect of hub height, associated increase in rotor diameter, and blade-swept area on bird collision rates in United States, but Barclay et al.¹³ and Smallwood⁴⁵ did not find an increase in collisions with hub height. Besides hub height, collision rate might also depend on turbine operational time and blade lengths; however, we could not quantify and test effects of these factors. After controlling for confounding factors, bird mortality rate per unit wind energy produced was found to be similar for different size and spacing of turbines⁴⁶. Similar to previous studies⁴⁷, mortality varied across seasons. Mortality rates were higher during October to February (ranging from 0.24 to 0.35) that coincides with the peak bird migration along the Central Asian Flyway into the Indian subcontinent. Mortality was relatively less during March–September (ranging from 0.07 to 0.17). Raptor mortality was also high during January–February (0.13), the migratory period, and least during April–May and September (<0.02).

Notably, a few wind turbines in this region have the tip of one blade painted orange. May et al.⁴⁸ recommended painting the top half of one turbine blade black, as a mitigation measure to minimize motion smear and increase the visibility of turbines to approaching birds. This recommended mitigation measure can be implemented in a large set of turbines in this region, to test their effectiveness.

Methodological issues

Previous studies have used carcass search radius ranging from 50 m to 130 m around turbines^{10,12,21,29,30,32,35}. Whilst Huso et al.⁴⁶ recommended search distance of 1.25 times the total turbine height. Birds may fall far from the turbine after colliding with wind blade, depending on the momentum and wind velocity, and some collisions may be missed if a smaller area is searched around the turbine. Carcass search paths also varied between these studies; zigzag, spiral and linear (in four cardinal directions) paths being the most common methods. We believe that our method of zigzag search along ~2 km length within 150 m radius of a turbine was adequately rigorous. However, we found a declining yet non-negligible proportion of carcasses (~20%) at the largest distance (100–150 m) from the turbine and there is possibility that carcasses falling farther from the turbine were missed. This might underestimate mortality to some extent.

Globally, few studies (mostly from North America) have corrected mortality rates for biases arising from removal and non-detection of carcasses^{10,15,21,30,32,35}. In our study we have corrected raw mortality rate for removal and non-detection biases.

We could not ascertain what ecological traits render some bird families more prone to collision with turbines⁴⁹. It is possible that traits other than those examined by us (bird size and flight height) are influencing vulnerability to collisions. The overlap between flight height and turbine impact zone shed some observations that need separate investigation, such as the putative reasons behind the relatively low mortality of Corvids and Pteroclidids (in contrast to Falconids and Accipitrids) despite considerable overlap with turbine impact zone, perhaps by comparing flight behaviors among these taxa.

Our study coincided with COVID 19 pandemic and the enforcement of a national lockdown impacted its overall execution. Because of restrictions on surface transportation, mobility of researchers and resource flow, our crossing rate observations was inadequate in representing the seasonal patterns of bird behavior and movements

that might affect our assessment of taxonomic vulnerability. Although carcass samples were collected, they could not be sent to remote laboratories in time for confirmation of species' identity, as postal services and lab operations were severely disrupted. Thus, a small fraction of carcasses (14%) remained 'unidentified', that could have otherwise provided more accurate understanding of taxonomic vulnerability. Further, we could not test the effect of operational time and speed of the turbines, which might influence mortality patterns that needs to be studied in future. Lastly, we could not examine the impact of wind turbines on distribution and abundance of birds, although such impacts might exist⁵⁰.

Management implications

Our study suggests that absolute mortality due to wind turbines (~ 4470 birds year⁻¹ per 1000 km² area) is lower than that due to power-lines ($\sim 20,000$ birds year⁻¹ per 1000 km² area²⁵) in the study landscape. Additionally, Uddin et al.²⁵ found > 40 bird species to be victims of power line collisions, whereas we recorded ~ 19 bird species in our study. Although wind turbines per se seem to be a lesser problem, the forecasted growth of turbines and concomitant expansion of transmission network to meet the national target of generating 140 GW wind energy by 2030 may exert a larger cumulative impact on birdlife. This impact will be disproportionately borne by remote wildlife habitats which are critical for birds, vulnerable to collisions (e.g., raptors) such as the open natural ecosystems of India⁵¹ that are considered as *wastelands* and prioritized for renewable energy. In the wake of these developments, our study urges to bring windfarms under the umbrella of environmental impact assessments. More specifically, our study highlights the need of considering the following factors in wind energy operations: (a) avoidance of critical habitats for raptors, bustards, and other threatened species while planning future installations⁵², (b) undertaking large-scale testing of mitigation measures such as painting half of one blade black⁴⁸ and other innovations (e.g., camera systems designed to detect birds and thus shut down turbines in time to avoid collision), followed by mainstreaming of effective mitigation measure(s). Proper siting and mitigation would help in ensuring that the exponential growth of wind energy is not at odds with its environment-friendly ethos.

Methodology

Study area

The study was conducted during January 2020–September 2021 in 3000 km² landscape of Indian Thar Desert in Jaisalmer, Rajasthan that included ~ 900 wind turbines (Fig. 6a). The region experiences arid bioclimate characterized by extreme diurnal and annual temperature ranges, high wind velocity, and low humidity. The temperature ranges from 0 °C in winter to 50 °C in summer. The landscape is an open natural ecosystem with sand dunes, barren areas, and short grasslands dotted with thorny shrub and sparse trees. It also includes a

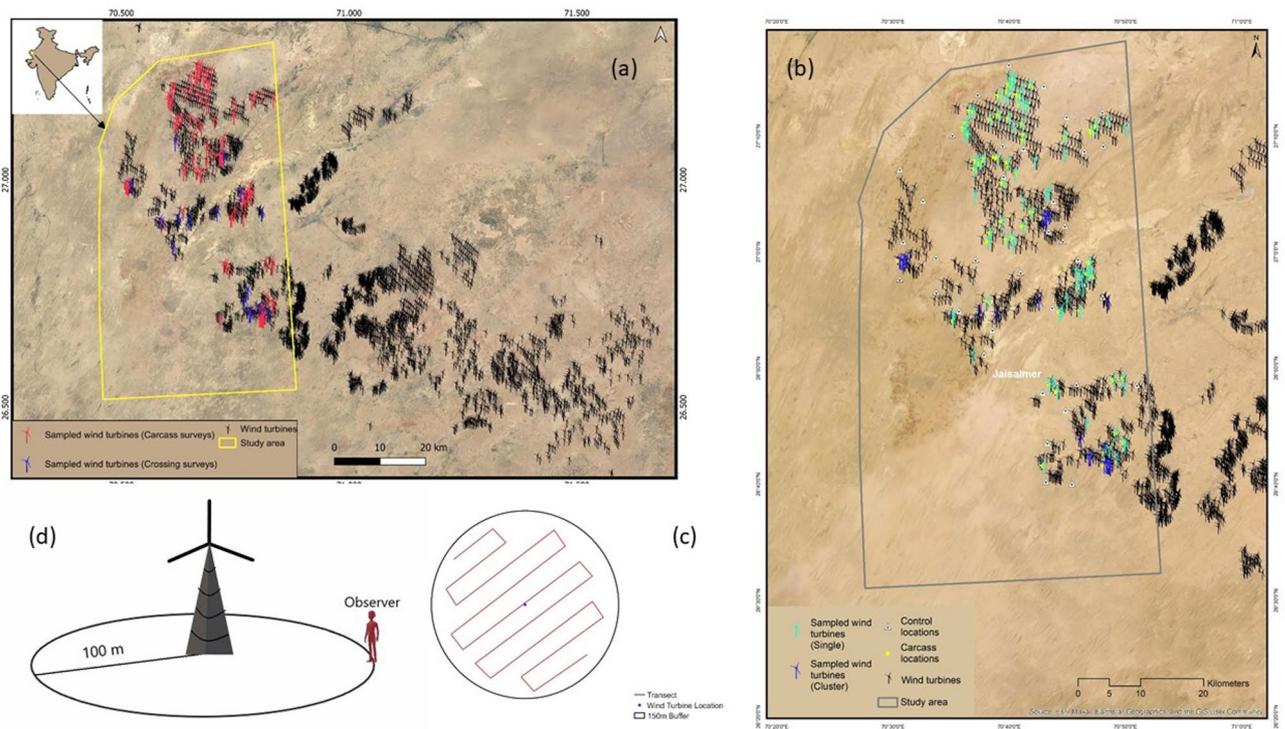


Fig. 6. Map showing (a) study area in yellow polygon, (b) wind turbines in black, sampled turbines in blue (clustered) and green (single) and control sites (triangle), (c) diagrammatic representation of bird carcass survey around sampled turbines, (d) diagrammatic representation of bird crossing survey around sampled turbines during 2020–2021.

Protected Area - the Desert National Park (Wildlife Sanctuary). Birdlife of the region includes 272 species belonging to 17 Orders and 55 Families⁵³, including 20 IUCN red-list species such as Great Indian Bustard (*Ardeotis nigriceps*), White-rumped Vulture (*Gyps bengalensis*), Red-headed Vulture (*Sarcogyps calvus*), Indian Vulture (*Gyps indicus*), Egyptian Vulture (*Neophron percnopterus*) and Steppe Eagle (*Aquila nipalensis*).

Field methods

Carcass surveys

We digitized wind turbines in the study area using high resolution Google Earth imagery. To estimate wind turbine induced bird mortality, we randomly sampled 90 out of ~900 turbines that were installed before the study (Fig. 6b). Some wind turbines were closely spaced (< 150 m distance), making it difficult to identify the unit responsible for mortality, and hence, we categorized them as 'clustered' turbines. We sampled 13 clustered turbines (in 3 clusters) and 77 solitary turbines using stratified random sampling, wherein, we selected turbines at random from the list of each stratum (single & cluster types) using MS Excel (Table 3). We searched carcasses within 150 m radius of these turbines; this search radius was based on methods and findings of similar studies, and our reconnaissance survey in the landscape. Bird carcasses within this radius was attributed to collision with the turbine or collision / electrocution with power line linked to the turbine. To maximize the detection of carcasses, we laid a zigzag trail of 2 km with 30 m spacing between the parallel lines within the search radius of each turbine (Fig. 6c). We walked slowly along the trail, searching for carcasses within 15 m on either side, which was an optimal distance to detect majority of available carcasses. We also conducted similar surveys at control sites, to account for natural mortality of birds. We sampled 28 randomly selected control points that were between 500 and 2000 m distances of any turbine, generated using program QGIS. This distance range was used for control surveys as the habitat and local bird assemblages were roughly homogenous within 2 km scale but would differ at larger scales. Control points represented areas with similar habitat as wind turbine sites, but without their influence, thereby representing natural mortality in these habitats. We conducted seven carcass surveys at wind turbines (January-February, March, April, July, September, November) to obtain seasonal variation in mortalities, and one carcass survey in control points (February). Conducting multi-season control surveys was not feasible due to logistic restrictions, hence, the bird mortality rate at control sites was compared against the first wind turbine survey done in the same month (February), assuming that the difference would remain similar between seasons (following Uddin et al. 2021)²⁵. We recorded carcasses up to species level, whenever possible, or classified them into broad taxonomic group (raptors / others).

Bias correction experiment

To account for carcass persistence bias due to scavenging and decomposition, we monitored 101 fresh carcasses periodically, representing the weight range and taxa of casualties at wind turbines (Table 4). We classified these carcasses as small (< 100 g), medium (100–1000 g), large (> 1000 g) and raptorial birds. We found raptor carcasses persisting longer than other birds of similar size, and hence considered them as a separate category. We monitored if a carcass persisted on day 2, 5, 8, 15, 30 and ~60 since deposition, and considered it to have disappeared if it was not found within the search radius or < 10 feathers remained, which could be deposited by wind actions; mimicking our search criteria (following Uddin et al., 2021)²⁵. We truncated our analysis after 60 days and considered carcasses to have persisted if they did not disappear within this period.

To correct for detection bias we used information from a previous study²⁵ conducted in the same landscape on mortality of birds due to power lines. In that study, an experiment was conducted to correct for detection bias, wherein 56 bird carcasses representing the spectrum of weight classes and decomposition conditions were placed under power lines and were surveyed by independent observers following similar survey method (zigzag walk within 30 m belt of a 2 km transect) as the wind turbine carcass survey. Given the two studies are in the

(a) Turbine features	Categories	Count	Proportion
Hub-height	40–70 m	27	0.25
	70–100 m	74	0.70
	> 100 m	5	0.05
Arrangement	Cluster	23	0.22
	Single	83	0.78
Pole type	Lattice	6	0.06
	Monopole	100	0.94
(b) Characteristics	Unit	Turbine	Control
Barren / agriculture	Frequency occurrence of land-use, terrain or substrate category	0.38	0.31
Grassland		0.38	0.30
Scrubland		0.22	0.30
Flat terrain		0.66	0.70
Rocky/gravel substrate		0.27	0.22

Table 3. (a) Features of sampled wind turbines ($n = 106$) and (b) comparison of habitat characteristics (mean frequency of occurrence) between turbines and control points ($n = 28$) in Thar desert during 2020–21.

Species	Category	Number of carcasses
Blyth's Reed Warbler	Small	1
Chicken	Small	10
Lark	Small	10
Rosy Starling	Small	1
Variable Wheatear	Small	1
Blue Rock Pigeon	Medium	4
Chicken	Medium	20
Common Teal	Medium	2
Domestic Geese	Medium	5
Eurasian Collared Dove	Medium	1
Guinea Fowl	Medium	5
Quail	Medium	10
Red-naped ibis	Medium	2
Chicken	Large	11
Indian Peafowl	Large	1
Punjab Raven	Large	2
Egyptian Vulture	Raptor	4
Eurasian Griffon Vulture	Raptor	6
Eurasian Sparrowhawk	Raptor	1
Griffon Vulture	Raptor	1
Laggar Falcon	Raptor	1
Long-legged Buzzard	Raptor	1
Spotted Eagle	Raptor	1
Grand total		101

Table 4. Bird carcasses used in persistence bias estimation in Thar desert during 2018–21.

exact same area, factors affecting carcass detection such as vegetation, terrain, target taxa, and other abiotic factors will remain the same; therefore, carcass detectability estimates will be transferable between these studies.

Bird crossing surveys

We conducted bird crossing observations at 16 wind turbines, to examine bird usage of turbine areas, flight patterns with respect to the blade-swept-area, and to identify vulnerable taxa. We observed birds once at each turbine between March and June from a mobile camouflaged hide placed at 100 m from the turbine that offered a visual detection area of 100 m radius along the centerline, without disrupting bird activity (Fig. 6d). We observed birds from sunrise through sunset with a 30 min break after every two hours to avoid fatigue bias. Species identification followed 'Birds of the Indian Subcontinent'⁵⁴. We also recorded turbine features, surrounding habitat, and single/clustered nature of these sampled turbines. Incline of hub and distance to base of the turbine were measured using range finder, from which hub height was calculated through trigonometry. Turbine blade length was measured when one of the three blades aligned with the mast. We measured bird flight heights using turbine features as reference and by counting rings present on the mast. We recorded flight heights in broad intervals of 0–20–40–60–80–100 and > 100 m.

For both carcass and crossing surveys, we collected data on wind turbines (hub height and blade length, pole type and arrangement of turbines) (Table 3), associated power lines (within 150 m of the wind turbines), surrounding habitat, date and time of surveys, location, condition of carcass (fresh, old, scavenged or decomposed) and distance of carcass from turbine during the survey. We characterized the micro-habitat within 250 m radius of each turbine and control site in terms of the land cover (barren/agriculture/grassland/scrubland/woodland), terrain (flat/undulating/sloping) and substrate (rock-gravel/sand/soil).

Data analysis

Mortality rate

We analyzed the frequency of carcasses at increasing distances from wind turbines and power lines linked to them, to examine if carcass detections became negligible at the largest distance class, which would indicate adequacy of our search radius.

We estimated the mean and 95% CI of carcass detected turbine⁻¹ month⁻¹ for each bird category (small, medium, big and raptor) and survey. We tested the difference in carcass encounter rates between the first survey of wind turbines and concurrent surveys at control sites, using ANOVA. We assumed that the difference in mortality between wind turbines and control sites, if any, will remain constant across seasons, as there was no plausible reason to believe otherwise.

Then, we estimated carcass removal bias from persistence data of experimental carcasses (Table 4) using Kaplan Meier analyses⁵⁵ implemented through R package-“*survival*”. The cumulative probability of carcass persistence on any day leading to the survey, was estimated as:

$$s_t = \frac{\text{Number of carcasses available at the start} - \text{Number of carcasses removed}}{\text{Number of carcasses available at the start}}$$

We modeled the carcass persistence probability against days to estimate the daily persistence probability of each category (small, medium, large raptors). We computed bias correction factors for each survey as the sum product of uniform deposition probability of carcass and its persistence probability on any day since the preceding survey leading to the current survey. We estimated 95% CI around mean bias correction factors by randomly sampling from a normal distribution determined by the mean and standard deviation of KM persistence probability over 1000 bootstrap iterations (following Uddin et al., 2021)²⁵. Thereafter, we adjusted carcass count by persistence bias²³, and estimated the mean and 95% CI bias adjusted mortality turbine⁻¹ month⁻¹ across spatial and temporal replicates, for each category of bird. Further, we used size-specific carcass detection probability estimates published in Uddin et al.²⁵, to adjust the above persistence bias corrected mortality rate for imperfect detection. Using the persistence- and detection- adjusted mortality rate per turbine and the number of turbines in the sampling frame, we extrapolated the overall annual mortality in the study area.

Factors influencing mortality

We examined if mortality depended on turbine- and site- features. We reduced data dimensionality by removing habitat variables that were rare (woodland, shrubland and agriculture) or had low variability (substrate). Using the remaining variables (barren, grassland or scrubland land-cover and flat or undulating terrain), we classified turbine habitats into three groups through *k*-means cluster analysis⁵⁶. Since carcass count at turbines was Poisson distributed, we used generalized linear model of Poisson family, to examine the effects of habitat groups, clustering of turbines, and hub height¹¹ on carcass count (response). We built candidate models with alternative combinations of these potential predictors against a null model of no effect. We compared these models using Akaike Information Criterion in multi-model inference framework⁵⁷, to explain turbine/ site correlates of bird mortality.

Bird crossing rates and taxonomic vulnerability

We estimated mean and SE crossing rates of bird families (individual turbine⁻¹ day⁻¹) from spatial replicates of bird crossing observations. We computed vulnerability index for each bird family as the ratio of its proportional mortality, measured as persistence bias adjusted carcass counts summed over 630 wind-turbine surveys, to proportional crossings, measured as crossings per hour summed over 16 wind-turbine surveys (Table 1). We plotted the frequency of flights at different vertical strata vis-à-vis turbine-impact height (hub height ± blade-swept area), to identify taxa that fly largely within the turbine impact zone and are thereby more prone to collisions. We examined if the vulnerability index was related to birds' biometric traits⁵⁸ and/or their tendency to fly in the turbine impact zone⁴¹. For this, we derived a composite factor from four biometric measures: body weight, wing- span, loading and aspect using factor analysis²⁵. Additionally, we classified bird families as 'high-risk' if greater frequency of flights overlapped with turbine impact zone, otherwise 'low-risk'. Thereafter, we modeled the vulnerability index on the trait factor and risk category using gaussian generalized linear model against a null model of no effect, and compared these models using Akaike Information Criteria. All statistical analysis was done in program R (see S1 for details).

Data availability

Data is provided as supplementary information file.

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References

1. Government of India. Annual Report 2016–17. Ministry of New and Renewable Energy. India. (2017).
2. Government of India. Annual Report 2017–18. Ministry of New and Renewable Energy. India. (2018).
3. Government of India. Annual Report 2018–19. Ministry of New and Renewable Energy. India. (2019).
4. Government of India. Annual Report 2019–20. Ministry of New and Renewable Energy. India. (2020).
5. Government of India. Annual Report 2020–21. Ministry of New and Renewable Energy. India. (2021).
6. Government of India. Annual Report 2021–22. Ministry of New and Renewable Energy. India. (2022).
7. Government of India. Annual Report 2023–22. Ministry of New and Renewable Energy. India. (2023).
8. Global, E. R. (2021).
9. Cabrera-Cruz, S. A. et al. Estimates of aerial vertebrate mortality at wind farms in a bird migration corridor and Bat diversity hotspot. *Glob. Ecol. Conserv.* **22**, e00966. <https://doi.org/10.1016/j.GECCO.2020.E00966> (2020).
10. Everaert, J. & Stienen, E. W. M. Impact of wind turbines on birds in Zeebrugge (Belgium): significant effect on breeding Tern colony due to collisions. *Biodivers. Conserv.* **16**, 3345–3359. <https://doi.org/10.1007/s10531-006-9082-1> (2007).
11. Loss, S. R., Will, T. & Marra, P. P. Estimates of bird collision mortality at wind facilities in the contiguous United States. *Biol. Conserv.* **168**, 201–209. <https://doi.org/10.1016/j.biocon.2013.10.007> (2013).
12. Zimmerling, R. R., Pomeroy, A. C., d'Entremont, M. V. & Francis, C. M. Canadian estimate of bird mortality due to collisions and direct habitat loss associated with wind turbine developments. *Avian Conserv. Ecol.* **8** (2). <https://doi.org/10.5751/ACE-00609-080210> (2013).
13. Barclay, R. M. R., Baerwald, E. F. & Gruver, J. C. Variation in Bat and bird fatalities at wind energy facilities: assessing the effects of rotor size and tower height. *Can. J. Zool.* **85** (3), 381–387. <https://doi.org/10.1139/Z07-011> (2007).

14. Hötter, H., Thomsen, K. M. & Köster, H. *Impacts on Biodiversity of Exploitation of Renewable Energy Sources: The Example of Birds and Bats. Facts, Gaps in Knowledge, Demands for Further Research, and Ornithological Guidelines for the Development of Renewable Energy Exploitation*, 1–65 (Nature and Biodiversity Conservation Union (NABU), 2006).
15. Barrios, L. & Rodríguez, A. Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. *J. Appl. Ecol.* **41**, 72–81 (2004).
16. Noguera, J. C., Pérez Ibarra, I. & Mínguez, E. Impact of terrestrial wind farms on diurnal raptors: developing a Spatial vulnerability index and potential vulnerability maps. *Ardeola* **57**, 41–53 (2010). <https://www.researchgate.net/publication/44270541>
17. B Thaxter, C. et al. Bird and Bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. *Proc. R. Soc. B Biol. Sci.* **284** (1862). <https://doi.org/10.1098/rspb.2017.0829> (2017).
18. Carrete, M. et al. Mortality at wind-farms is positively related to large-scale distribution and aggregation in griffon vultures. *Biol. Conserv.* **145**, 102–108. <https://doi.org/10.1016/j.biocon.2011.10.017> (2012).
19. Carrete, M., Sánchez-Zapata, J. A., Benítez, J. R., Lobón, M. & Donazar, J. A. Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. *Biol. Conserv.* **142**, 2954–2961. <https://doi.org/10.1016/j.biocon.2009.07.027> (2009).
20. Drewitt, A. L. & Langston, R. H. Assessing the impacts of wind farms on birds. *Ibis* **148**, 29–42 (2006).
21. Osborn, R. G. et al. Bird mortality associated with wind turbines at the Buffalo ridge wind resource area, Minnesota. *Am. Midl. Naturalist.* **143**, 41–52 (2000).
22. Smallwood, K. S. Estimating wind Turbine–Caused bird mortality. *J. Wildl. Manag.* **71** (8), 2781–2791. <https://doi.org/10.2193/2007-006> (2007).
23. Ponce, C., Alonso, J. C., Argandoña, G., García Fernández, A. & Carrasco, M. Carcass removal by scavengers and search accuracy affect bird mortality estimates at power lines. *Anim. Conserv.* **13** (6), 603–612. <https://doi.org/10.1111/j.1469-1795.2010.00387.x> (2010).
24. Barrientos, R. et al. Wire marking results in a small but significant reduction in avian mortality at power lines: A BACI designed study. *PLoS One.* **7** (3), e32569. <https://doi.org/10.1371/JOURNAL.PONE.0032569> (2012).
25. Uddin, M. et al. High bird mortality due to power lines invokes urgent environmental mitigation in a tropical desert. *Biol. Conserv.* **261**. <https://doi.org/10.1016/j.biocon.2021.109262> (2021).
26. Chatterji, P. C. & Kar, A. Integrated natural and human resources appraisal of Jaisalmer district. (1992).
27. Sangroya, D. & Nayak, J. K. Development of wind energy in India. *Int. J. Renew. Energy Res.* **5**, 1–13 (2015).
28. Deb, H., Sanyal, T., Kaviraj, A. & Saha, S. Hazards of wind turbines on avifauna—A preliminary appraisal within the Indian context. *J. Threat Taxa.* **12**, 15414–15425. <https://doi.org/10.11609/JOTT.5165.12.4.15414-15425> (2020).
29. Ali, H. M. S., Kumar, A. R. A. P., Samsoor Ali, S., Arun, P. & A. M., & Impact of wind turbines on birds: a case study from Gujarat, India. *Sci. J. Environ. Sci.* **1**, 9–20 (2012). <https://www.researchgate.net/publication/259390231>
30. Kumar, S. R., Anoop, V., Arun, P. R., Mohamed, A. & Ali, S. Avian mortalities from two wind farms at Kutch, Gujarat and Davangere, Karnataka, India. *Curr. Sci.* **116** (9) (2019).
31. Kumara, H. N. et al. Responses of birds and mammals to long-established wind farms in India. *Sci. Rep.* **12** (1). <https://doi.org/10.1038/s41598-022-05159-1> (2022).
32. Kumara, S. R., Ali, A. M. S. & Arun, P. R. Bat mortality due to collision with wind turbines in Kutch district, Gujarat, India. *J. Threat Taxa.* **5** (13), 4822–4824. <https://doi.org/10.11609/jott.o3503.4822-4> (2013).
33. Pande, S. et al. Avian collision threat assessment at 'bhambarwadi wind farm plateau' in Northern Western Ghats, India. *J. Threat Taxa.* **5** (1), 3504–3515. <https://doi.org/10.11609/jott.o3096.210> (2013).
34. Suthar, A. R. et al. Impact of windmills and power lines on birds: A case study at Porbandar taluka, Gujarat-India. *Inte J. Fauna Biol. Stud.* **4** (3), 93–99 (2017).
35. Fiedler, J. K., Henry, T. H., Tankersley, R. D. & Nicholson, C. P. Results of bat and bird mortality monitoring at the expanded Buffalo Mountain windfarm. *Tennessee Valley Authority*, 42 (2007).
36. Farfán, M. A., Vargas, J. M., Duarte, J. & Real, R. What is the impact of wind farms on birds? A case study in Southern Spain. *Biodivers. Conserv.* **18** (14), 3743–3758. <https://doi.org/10.1007/s10531-009-9677-4> (2009).
37. SoIB. State of India's birds, 2023: range, trends, and conservation status. *SoIB Partnersh* **119**. (2023).
38. Allison, T. D. et al. Impacts to wildlife of wind energy siting and operation in the united States. *Issues Ecol.* **21**, 2–18 (2019). www.esa.org.
39. Larsen, J. K. & Guillemette, M. Effects of wind turbines on flight behaviour of wintering common Eiders: implications for habitat use and collision risk. *J. Appl. Ecol.* **44**, 516–522. <https://doi.org/10.1111/j.1365-2664.2007.1303.x> (2007).
40. Smallwood, K. S. & Thelander, C. Bird mortality in the Altamont pass wind resource area, California. *J. Wildl. Manag.* **72**, 215–223. <https://doi.org/10.2193/2007-032> (2008).
41. Hüppop, O., Dierschke, J., Exo, K. M., Fredrich, E. & Hill, R. Bird migration studies and potential collision risk with offshore wind turbines. *Ibis.* **148**, 90–109. <https://doi.org/10.1111/j.1474-919X.2006.00536.x> (2006).
42. Hise, C., Obermeyer, B., Ahlering, M., Wilkinson, J. & Fargione, J. Site wind right: identifying low-impact wind development areas in the central United States. *Land.* **11** (4), 462 (2022).
43. Smallwood, K. S. & Karas, B. Avian and Bat fatality rates at old-generation and repowered wind turbines in California. *J. Wildl. Manag.* **73**, 1062–1071 (2009).
44. Percival, S. & Powell, D. Birds and windfarms: what are the real issues? *Br. Birds.* **99**, 45 (2005). www.bwea.com.
45. Smallwood, K. S. Comparing bird and Bat fatality-rate estimates among North American wind-energy projects†. *Wildl. Soc. Bull.* **37**, 19–33. <https://doi.org/10.1002/wsb.260> (2013).
46. Huso, M. et al. Relative energy production determines effect of repowering on wildlife mortality at wind energy facilities. *J. Appl. Ecol.* **58** (6), 1284–1290 (2021).
47. Marques, A. T. et al. Understanding bird collisions at wind farms: an updated review on the causes and possible mitigation strategies. *Biol. Conserv.* **179**, 40–52 (2014).
48. May, R. et al. Paint it black: efficacy of increased wind turbine rotor blade visibility to reduce avian fatalities. *Ecol. Evol.* **10** (16), 8927–8935. <https://doi.org/10.1002/ECE3.6592> (2020).
49. Herrera-Alsina, L., Villegas-Patracá, R., Eguiarte, L. E. & Arita, H. T. Bird communities and wind farms: A phylogenetic and morphological approach. *Biodivers. Conserv.* **22** (12), 2821–2836. <https://doi.org/10.1007/s10531-013-0557-6> (2013).
50. Thaker, M., Zambre, A. & Bhosale, H. Wind farms have cascading impacts on ecosystems across trophic levels. *Nat. Ecol. Evol.* **2** (12), 1854–1858. <https://doi.org/10.1038/s41559-018-0707-z> (2018).
51. Madhusudan, M. D. & Vanak, A. T. Mapping the distribution and extent of India's semi-arid open natural ecosystems. *J. Biogeogr.* <https://doi.org/10.1111/jbi.14471> (2022).
52. Balotari-Chiebao, F., Santangeli, A., Piirainen, S. & Byholm, P. Wind energy expansion and birds: identifying priority areas for impact avoidance at a National level. *Biol. Conserv.* **277**, 109851. <https://doi.org/10.1016/j.BIOCON.2022.109851> (2023).
53. Sivaperuman, C., Dookia, S., Kankane, P. L. & Baqri, Q. H. Structure of an arid tropical bird community, Rajasthan. *Faunal Ecol. Conserv. Great Indian Desert*, 85–98 (2009).
54. Grimmett, R., Inskipp, C. & Inskipp, T. *Birds of the Indian Subcontinent: India, Pakistan, Sri Lanka, Nepal, Bhutan, Bangladesh and the Maldives* (Bloomsbury Publishing, 2011).
55. Bispo, R., Bernardino, J., Marques, T. A. & Pestana, D. Modeling carcass removal time for avian mortality assessment in wind farms using survival analysis. *Environ. Ecol. Stat.* **20**, 147–165. <https://doi.org/10.1007/s10651-012-0212-5> (2013).

56. Wu, J. Cluster analysis and K-means clustering: an introduction. In *Advances in K-means Clustering* 1–16. https://doi.org/10.1007/978-3-642-29807-3_1 (2012).
57. Burnham, K. P. & Anderson, D. R. Multimodel inference: Understanding AIC and BIC in model selection. *Sociol. Method Res.* **33**, 261–304. <https://doi.org/10.1177/0049124104268644> (2004).
58. Rayner, J. M. Form and function in avian flight. *Curr. Ornithol.* 1–66 (1988).

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Author contributions

Y.V.J. and S.D. arranged resources for the study. S.D. conceptualized the study and designed it with inputs from M.U. A.R. and S.B. collected data. S.D. analyzed the data with inputs from A.R., M.U. and S.B. A.R. wrote the main manuscript text with inputs from S.D. and S.B. S.D., M.U. and Y.V.J. edited the manuscript. All authors contributed critically to the drafts and gave approval for publication.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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