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ORIGINAL RESEARCH

Assessing ungulate response to conservation-oriented village relocations and their associated management practices in a tiger reserve in central India

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Abstract

Conservation-oriented village relocations are used as tools for wildlife conservation in developing nations like India, despite the potential sociocultural and economic costs associated with displacement. In tiger reserves in central India, abandoned village sites are developed as grasslands to improve tiger prey numbers. However, little is known about how village relocations and their associated management interventions influence ungulate habitat use. The aim of the study was to understand the impact of village relocations on ungulates by assessing how the intensity of habitat use by five ungulate species (sambar, chital, gaur, nilgai, wild pig), quantified using dung accumulation rates, changed with respect to time since relocation and distance from the edge of a site (relocated/active village) in the Satpura Tiger Reserve, central India. The intensity of use of relocated village sites by sambar, chital, gaur, and nilgai increased with time since relocation, while for wild pigs, it decreased. The intensity of habitat use by all five species of ungulates was negatively correlated with distance from the edge of the site. Our results suggest that village relocations coupled with grassland management activities lead to increased intensity of habitat use by some species and, over time, this may lead to increased populations of these large herbivores, aiding the recovery of large mammalian predators. While this study focused on the ecological implications of relocations, there is also a critical need to view relocations as coupled social-ecological systems to better understand their viability as conservation interventions.

Keywords Village relocations · Ungulate ecology · Habitat-use · Protected area management · Conservation interventions

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Introduction

One of the biggest challenges currently facing developing nations like India is the management of natural resources to meet social, economic, and ecological objectives for multiple stakeholders (Watson et al. 2014). The Protected Area (PA) network of India covers only ~5% of the nation's geographical area (Mathur and Sinha 2008) but nearly five million people live within these PAs and another 147 million are dependent on them to varying degrees for their livelihoods (Lasgorceix and Kothari 2009). At the same time, this miniscule proportion of land plays a disproportionately large role in providing refuge to the country's wildlife. This shared dependency on natural resources puts communities and wildlife in close proximity to each other, bringing in a variety of interactions that affect both (Rangarajan and Shahabuddin 2008). Human livelihood activities like agriculture, livestock grazing, fishing, hunting, and collection of fuelwood, fodder, timber and non-timber forest products (NTFPs) can have negative implications for wildlife and their habitat (Karanth et al. 2006). At the same time, the increased interface between wild animals and forest-dependent communities makes these communities susceptible to negative wildlife interactions in the form of livestock depredation by large carnivores or crop damage by ungulates (Madhusudan 2003), among others. From a biodiversity conservation perspective, these negative interactions have direct detrimental effects on wild populations and indirect effects in the form of reduced community support for conservation (Chan et al. 2007).

Conservation-oriented village relocations were envisioned as a tool for wildlife conservation that could benefit both wildlife and forest-dependent communities. Wildlife would benefit from a reduced human footprint, while people would benefit from improved livelihood opportunities, better infrastructural facilities and reduced instances of wildlife damage (Ghate and Beazley 2007).

In India, the inception of Project Tiger in 1973 gave way to the declaration of several tiger reserves (TRs) in the country, triggering a wave of village relocations from core areas of tiger reserves since the core area is conserved as an inviolate space, free from anthropogenic pressures (Mountfort 1983). This led to the displacement of forest-dependent communities at an unprecedented scale and this process of eviction and displacement opened up indigenous communities to severe sociocultural and economic costs (Rangarajan and Shahabuddin 2008; Shahabuddin and Bhamidipati 2014; Fanari 2019). At the same time, we know very little about what happens to forests and wildlife once villages have been relocated from PAs like tiger reserves.

This study attempts to address this gap by assessing the implications of village relocations and post-relocation grassland management interventions in the Satpura Tiger Reserve (STR) in the state of Madhya Pradesh, India, through an ecological lens. At STR, village sites have been managed as grasslands following relocation to augment ungulate numbers in the reserve to allow for the recovery of populations of large predators such as the tiger. Grassland management interventions in STR include planting of palatable grasses, removal of weeds and woody growth, and controlled burning. In this study, we assessed how ungulates in STR respond to the relocation of villages and the associated grassland management interventions that follow relocation. At present, it is not possible to distinguish between the effects of relocation and grassland management activities per se since grassland management interventions are integrally associated with relocations in this landscape. Henceforth, whenever we talk about the effect of relocations, we mean the effect of relocation and the subsequent grassland management activities that follow.

Previous research suggests that the reduction of anthropogenic pressures can result in the recovery of ungulate populations (Harihar et al. 2009) and our goal was to understand how village relocations and post-relocation management interventions affect different species of ungulates in STR. Specifically, we asked: (i) how does the intensity of habitat use by ungulates vary with time since relocation? and (ii) how does the intensity of habitat use by ungulates vary with distance from a site (relocated/active village)? The second question was included to help better understand if there was a difference between how intensely the species were using the grasslands created as a result of relocation (or an active village settlement) compared to the surrounding forests. We included currently occupied villages as control sites.

Our study included five species of ungulates: sambar (*Rusa unicolor*), chital (*Axis axis*), gaur (*Bos gaurus*), nilgai (*Boselaphus tragocamelus*), and wild pig (*Sus scrofa*). We expected sambar, chital, and gaur to show higher intensities of habitat use post-relocation as these species are known to be negatively affected by the presence of humans (Madhusudan 2004; Harihar et al. 2009; Lahkar et al. 2020). Grazers and mixed feeders like gaur and chital are particularly sensitive to the presence of livestock (Johnsingh and Sankar 1991), while browsers like sambar are less sensitive to livestock presence but are vulnerable to biomass extraction (Madhusudan 2004). Nilgai and wild pigs are generalists that often indulge in crop depredation (Chauhan et al. 2009; Chopra and Rai 2009), so the removal of villages may adversely affect habitat use by these species by depriving them of human subsidies.

The intensity of habitat use by the five ungulates could also depend on ecological covariates such as terrain ruggedness, availability of water, and canopy cover. In terms of canopy cover, we expected chital and nilgai to use relocated villages now maintained as grasslands more intensely because these species prefer open meadows or forest openings over closed forests (Schaller 1967). Gaur and sambar prefer dense forests over open fields but gaur move to grasslands during the dry season (Schaller 1967; Harihar et al. 2009; Kumar et al. 2021), so we expected gaur and sambar to have higher intensities of habitat use in grasslands and the surrounding forests, respectively. Since sambar and gaur prefer steep and hilly terrain (Kumar et al. 2021), we expected these species to have higher intensities of habitat use in areas with higher terrain ruggedness. Chital and nilgai, on the other hand, prefer flatter terrain (Schaller 1967) and, so we expected these species to have higher intensities of habitat use in areas with lower terrain ruggedness. Wild pigs are generalists with regard to terrain (Garza et al. 2018) so we did not have an a priori expectation for this species. All five species of ungulates need to drink water regularly, so we expected their intensity of habitat use to be inversely related to distance from the nearest perennial stream (Schaller 1967; Chopra and Rai 2009; Kumar et al. 2021) (Table 1).

Methods

Study site

The study was conducted from February to April 2022 within the Satpura Tiger Reserve (STR) located in Narmadapuram district of the Indian state of Madhya Pradesh. The reserve

Table 1 Predictions for how the covariates of interest would affect intensity of habitat use by the five species of ungulates

Response	Age (time since relocation)	Distance from edge*	TRI	Distance from stream	Canopy Cover
Intensity of habitat use					
Sambar	+	+	+	−	+
Chital	+	−	−	−	−
Gaur	+	−	+	−	−
Nilgai	+/−	−	−	−	−
Wild Pig	−	+/−	+/−	−	+

*Distance was measured as positive from the village–forest edge into the forest, and negative from the edge into the village/grassland

lies between 22°15′ −22°45′ N and 77°50′ E − 78°30′ E, and is composed of Satpura National Park (524.37 km^2), Bori Wildlife Sanctuary (485.78 km^2), and Pachmarhi Wildlife Sanctuary (417.78 km^2). STR has a core area of 1,339 km^2 and a buffer area of 794 km^2 (Gurjar et al. 2013). The reserve is a prime example of the Central Indian Highland Ecosystem (Jayapal et al. 2005). Terrain in the landscape is undulating, and the altitude ranges from 320 m to 1352 m above mean sea level. Vegetation in the reserve consists of southern tropical moist deciduous forests, southern tropical dry deciduous forests, tropical riparian fringing forests, southern tropical thorn forests, central Indian hill forests, dry and moist grasslands. Temperatures for the region range between 11 °C and 42 °C, while the average annual rainfall range is 1,300–1,700 mm (Jayson 1990). Dominant tree species include teak (*Tectona grandis*), sal (*Shorea robusta*), saja (*Terminalia tomentosa*) and mahua (*Madhuca indica*), along with many species of shrubs, herbs and grasses. STR supports 52 species of mammals, 31 species of reptiles and 300 species of birds (Pejaver et al. 2013). The primary carnivore species of management interest in the reserve include tigers (*Panthera tigris*), leopards (*Panthera pardus*), and dholes (*Cuon alpinus*). Potential prey for these predators include wild pig (*Sus scrofa*), chowsingha (*Tetracerus quadricornis*), chital (*Axis axis*), Indian muntjac (*Muntiacus vaginalis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), gaur (*Bos gaurus*), common langur (*Semnopithecus entellus*), black-naped hare (*Lepus nigricollis*) and Indian porcupine (*Hystrix indica*). Please refer to Edgaonkar (2008) for more details.

Villages in STR were relocated at different points in time. The first village was relocated in 2006, and by 2021, 47 villages had been relocated from STR. However, at the time of this study there were still villages occupied within the reserve. The relocation sites (here, defined as sites which are remnants of previously settled villages) are currently being managed as grasslands by the Madhya Pradesh Forest Department through interventions such as planting of palatable grasses, removal of woody growth, weeding, and controlled fires.

Study design

We used space-for-time substitution (Pickett 1989) to assess how the intensity of habitat use by ungulates changes with time since village relocation. We measured faecal accumulation rates of ungulates as a proxy for the intensity of habitat use by these species in relocation sites/active villages and in adjacent forests, along a gradient of time since relocation. The treatment was the relocation of the villages from the PA coupled with the grassland management interventions undertaken by the forest department. Controls were in the form of villages currently occupied within the reserve. We sampled a total of 12 sites, of which

Table 2 Relocated/occupied villages sampled

S. no.	Name of site	Time since relocation
1	Ghoghari	Active
2	Suplai	Active
3	Khamda	Active
4	Chapatadhana	3 years
5	Sankai	5 years
6	Raikheda	6 years
7	Bargondi	7 years
8	Dhargaon	7 years
9	Badkachhar	8 years
10	Jhela	9 years
11	Sakot	11 years
12	Dhain	17 years

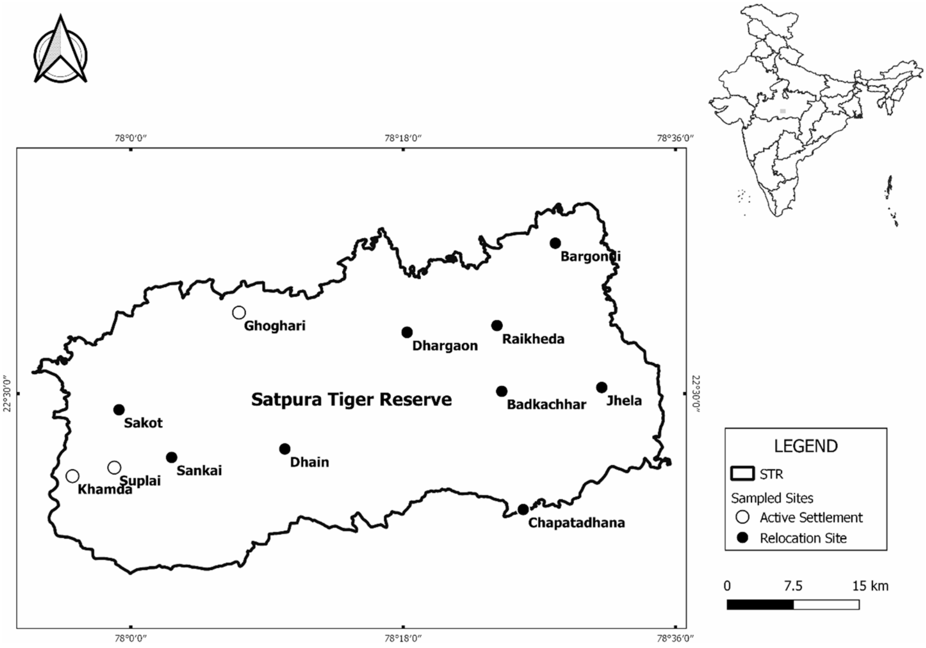

Fig. 1 Map of Satpura Tiger Reserve along with the sites sampled in the reserve; inset map shows the location of the main map within India

three were villages that were still active at the time of the study. While selecting sampling sites, we focused on selecting villages which were relocated from the reserve at different points in time (ranging from active villages to villages relocated 17 years prior; Table 2). A secondary emphasis was on selecting sites in a way that ensured maximum spatial coverage across STR (Fig. 1).

Data collection

Data collection took place in 2022 over the course of three months (February to April). We expected ungulate habitat use to change with time since relocation as well as the distance from the forest-village edge (relocation site/active village) along with other ecological covariates. To account for distance from the edge of the site, we used a piosphere-effect model (Thrash and Derry 1999; Washington-Allen et al. 2004) which indicates how the impact of an animal or anthropogenic activity radiates from a concentrator to its surroundings (in our case, the concentrator was a relocation site or a village settlement). Therefore, we sampled plots radiating out of the site (relocation site or village settlement) at varying distances from the edge of the site.

For each site, we had three transects each of 1.2 km length radiating out of the site. Along each transect, we sampled four plots (50 × 2 m) laid perpendicular to the transect at fixed distances 400 m apart (Fig. 2). One plot was laid at the edge of the site (0 m), one within the site at a distance of 400 m from the edge (−400 m), and another two plots in the surrounding forests at distances of 400 m and 800 m from the edge. During analyses, distance was

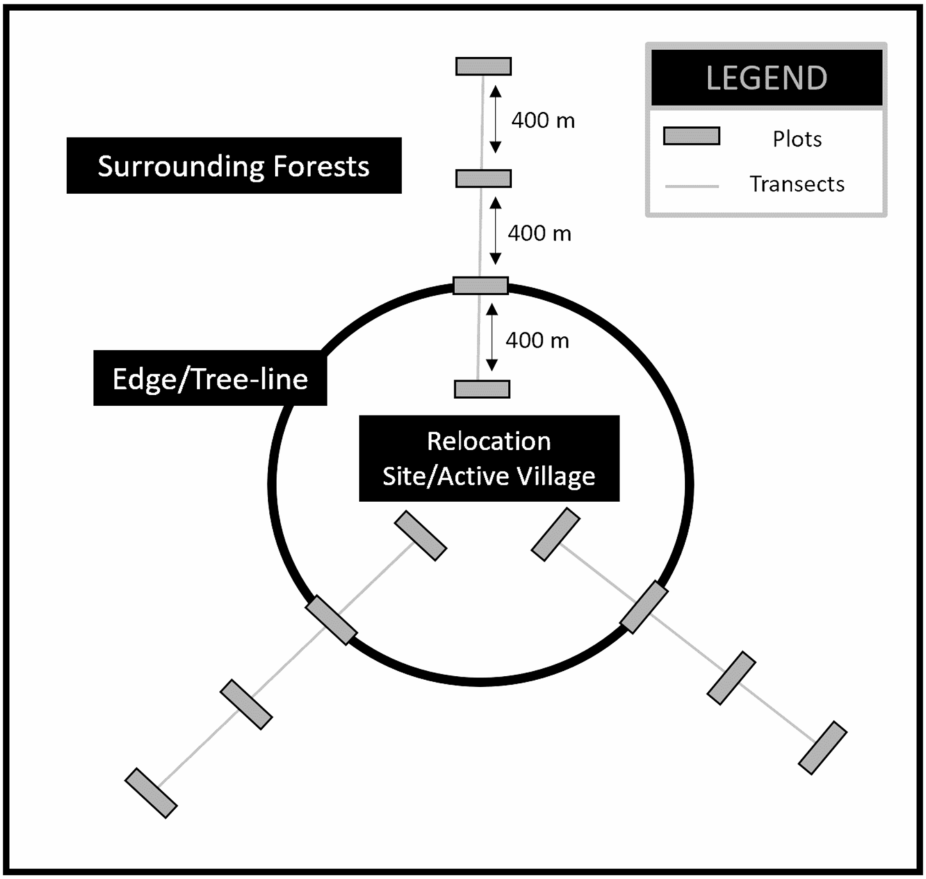

Fig. 2 Schematic for data collection design; for a given site, 12 plots were sampled across three transects at fixed distances of 400 m along each transect

measured as positive from the village-forest edge into the forest, and negative from the edge into the village/grassland.

Some plots had to be dropped owing to geographical barriers like rivers or hillocks. In some cases, plots had to be omitted because the size of the site was too small to accommodate a plot 400 m within the site. A total of 122 plots were sampled across the 12 sites. The vertices of each plot were marked to ensure that they could be resampled.

Pellet-group counts

We used the faecal accumulation rate (FAR) technique (Campbell et al. 2004; Ferretti et al. 2016; ENETWILD consortium et al. 2020) to quantify the intensity of habitat use by ungulates. We established 122 faecal accumulation plots and at the time of plot establishment, all pellet-groups (defined as pellets in case of chital, sambar, and nilgai, dung piles in case of gaur or droppings in case of wild pigs) were cleared from the plots. We resampled plots 45 days later and faecal accumulation was measured as pellet-groups/100 m^2/45 days. The duration of 45 days was chosen as a trade-off between allowing for adequate dung deposition while ensuring that no pile completely decays/disappears. We selected the 45-day duration conservatively based on Ahrestani et al. (2018). To avoid over-counting, only pellet-groups with five or more pellets (in the case of sambar, chital, and nilgai), or individual pats (in the case of gaur), or individual droppings (in the case of wild pig) were counted as a single pellet-group. In case a pellet-group was at the edge of the plot, we only included pellet-groups whose centroid fell within the plot. We chose to measure FAR over faecal standing crop as the latter is very sensitive to spatial and temporal variation in dung decay rates (Jathanna et al. 2015; Ahrestani et al. 2018).

Analysis

Model set-up

We used a Generalized Linear Mixed Model (GLMM) framework to assess how ungulate faecal accumulation rates varied as a function of time since relocation, distance from the edge of a relocation site/village settlement, TRI (terrain ruggedness index), distance from nearest perennial stream, and average canopy cover. Terrain ruggedness was calculated based on the Space Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM) of spatial resolution 30 m. The Terrain Ruggedness Index (TRI) was the difference between the mean elevation at a point (a pixel of 30 m resolution), and its 8 surrounding pixels, while distance from the nearest stream was calculated as the aerial distance between a point and the nearest perennial stream (Source– India Water Resources Information System). Average canopy cover was the average of four canopy cover readings taken in a plot using a mobile application.

Transects nested within sites were used as random effects in the model to account for pseudo-replication in our sampling strategy as our sampling units or plots were not spatially independent (McCulloch 2000; Zuur et al. 2009; Bolker 2015). All analyses were carried out using the *glmer* function within the *lme4* package (Bates et al. 2022, p. 4) in R.

Confidence Intervals (95%) for beta coefficient estimates were calculated using the *confint* function in base R.

Model selection

For each response variable, we developed a set of candidate models using different combinations of predictors, based on reviewing the available literature. We used AICc (Burnham et al. 2011) to assess support for each model. Where multiple models received support from the data, we did not derive model-averaged estimates of beta-coefficients but reported estimates from all the supported models (Cade 2015). AICc, ΔAICc, and AICc weights were calculated using the *AICtable* function in the *wiqid* package (Meredith et al. 2022) in R.

Model diagnostics

To assess the goodness-of-fit (GOF) of a model, we calculated the marginal (proportion of variance explained by fixed effects only) and conditional (proportion of variance explained by fixed and random effects) pseudo-R^2 values (Jaeger et al. 2017) using the *r.squared. GLMM* function within the package *MuMIn* (Bartoń 2022). To check for zero inflation and dispersion in the model, the functions *testZeroInflation* and *testDispersion* respectively were used. These functions are part of the package *DHARMa* (Hartig and Lohse 2022) and were used in conjunction with the *plotQQunif* function to assess model fit.

Prediction curves based on GLMMs for sambar, gaur, and wild pig

We used the fitted models to predict how intensity of habitat use by these species would change over the period of time since relocation included in our study (0–17 years), separately for a location 400 m inside the relocation site/village settlement and 400 m outside (models for chital and nilgai were not used due to unreliable estimates as the CIs for time since relocation and distance from the edge were overlapping 0). The other three predictors (TRI, distance from nearest stream, and average canopy cover) were kept constant at their mean values. All analyses were carried out using the statistical software environment R (Version 4.2.1).

Results

Intensity of habitat use by sambar, chital, gaur, and nilgai increased with time since relocation, while for wild pigs, it decreased (Table 3). The increase in use was highest for sambar (0.37 pellet groups/100 m^2/year ±0.12 SE), followed by gaur (0.27 ±0.07) and chital (0.26 ±0.18; CI overlaps 0) (Table 3). While the effect was positive for nilgai, it was not a very strong effect (0.07 ±0.08; CI overlaps 0) (Table 3). The intensity of habitat use by wild pig decreased with time since relocation at a rate of −0.14± 0.07 pellet groups/100 m^2/year (CI overlaps 0) (Table 3).

The intensity of habitat use was higher in the grassland patches within the site (negative distance from edge) than in the surrounding forests (positive distance from edge), and was also negatively correlated with distance from the edge, for all five species. The decrease in use with increasing distance was highest for gaur (−2.18 pellet groups/km ± 0.28 SE), followed by wild pig (−1.39 ± 0.28), chital (−0.53 ± 0.18; CI overlaps 0), nilgai (−0.50 ± 0.25; CI overlaps 0), and sambar (−0.30 ± 0.13; CI overlaps 0) (Table 3).

Estimated intensity of habitat use increased with TRI for sambar and wild pig, and decreased for chital and nilgai. TRI was not a predictor of intensity of habitat use by gaur in any of the supported models (Table 3). Estimated intensity of habitat use increased with distance from the nearest perennial stream for nilgai and wild pig, and decreased for sambar and chital. Distance from the nearest perennial stream was not a predictor of intensity of habitat use by gaur in any of the supported models (Table 3). Estimated intensity of habitat use increased with average canopy cover for sambar, and decreased in the case of all other species but the effect size was very small for all the five species (Table 3).

Our data suggest that the intensity of habitat use by sambar will increase with time since relocation, both within and outside the relocated village site (both show similar increases), although this exponential increase is an artefact of using the log link function to model the relationship between our response and the linear predictor (Fig. 3a) and may not be supported beyond the range of predictor values we observed. Similarly, intensity of habitat use by gaur is predicted to increase with time since relocation, but far more so within the relocated village site than in the surrounding forest (Fig. 3b). The intensity of habitat use by wild pig is predicted to decrease with time since relocation, especially within the relocated sites (Fig. 3c).

Discussion

Results from this study indicate that village relocations coupled with post-relocation grassland management interventions can lead to an increase in the intensity of habitat use by species such as sambar, gaur, and chital. In accordance with our predictions, the intensity of habitat use by sambar, chital, and gaur increased with time since relocation. This suggests that populations of these species may recover as time passes after villages are relocated (Madhusudan 2004; Lahkar et al. 2020). Intensity of habitat use by nilgai also appears to increase with time since relocation, but this effect is weak, while habitat use by wild pigs decreases with time since relocation. This may be attributed to both species being able to modify their behaviour to thrive in human-dominated spaces (Bayani and Watve 2016; Johann et al. 2020; Kumar et al. 2021). When villages are resettled, these species lose out on the benefits associated with direct and indirect subsidies provided by human settlements. In the long-run however, this may still be beneficial for these species as continued crop depredation by wild pigs or nilgai often leads to human-wildlife conflict (Koehler et al. 1990; Madhusudan 2003) and persecution of these animals by local communities.

The intensity of habitat use by all five species was higher within the relocated village sites than in the surrounding forests. Our results are in line with what previous studies have suggested for chital, gaur and nilgai (Schaller 1967; Chopra and Rai 2009; Mohanarangan 2011). The response of sambar was contrary to our expectations as sambar are known to spend more time in dense forests (Varman and Sukumar 1993) but some research suggests that sambar utilize open lowlands owing to the quality of grasses and greater visibility for predator detection (Simcharoen et al. 2014). Given that wild pigs are habitat generalists, we did not have an a priori expectation as to how actively wild pigs would use the grass-

Table 3 Estimates for models with ΔAICc < 2 for all five ungulates

Species	Model	ΔAICc	AICc weight	Time since relocation (age)	Distance from edge (dist)	TRI (TRI)	Distance from stream (dist_stream)	Canopy cover (canopy_avg)
Sambar	FAR ~ age + dist + TRI + dist_stream + canopy_avg + (1|site/transect)	0.00	0.61	0.37 (0.12) CI: 0.18–0.62	−0.30 (0.13) CI: −0.54– −0.08	0.14 (0.06) CI: 0.04–0.22	−0.64 (0.23) CI: −1.06– −0.26	0.01 (0.01) CI: 0.00–0.02
	FAR ~ age + dist + TRI + dist_stream + (1|site/transect)	1.43	0.30	0.37 (0.12) CI: 0.15–0.60	−0.16 (0.11) CI: −0.35– −0.04	0.16 (0.06) CI: 0.05–0.23	−0.64 (0.23) CI: −1.05– −0.25	-
Chital	FAR ~ age + dist + TRI + dist_stream + (1|site/transect)	0.00	0.29	*0.26 (0.18) CI: −0.09–0.62*	*−0.53 (0.18) CI: −1.08–0.05*	*−0.28 (0.14) CI: −0.68–0.02*	*−0.69 (0.40) CI: −1.66–0.19*	-
	FAR ~ age + dist + TRI + (1|site/transect)	0.59	0.21	*0.26 (0.18) CI: −0.07–0.64*	−0.55 (0.18) CI: −1.12– −0.06	*−0.24 (0.14) CI: −0.63–0.02*	-	-
	FAR ~ age + dist + TRI + dist_stream + canopy_avg + (1|site/transect)	1.64	0.13	*0.26 (0.18) CI: −0.07–0.59*	*−0.40 (0.23) CI: −1.02–0.34*	−0.30 (0.15) CI: −0.76–−0.02	*−0.67 (0.41) CI: −1.64–0.16*	*−0.01 (0.01) CI: −0.04–0.02*
	FAR ~ age + dist + (1|site/transect)	1.71	0.12	*0.27 (0.19) CI: −0.12–0.73*	−0.48 (0.17) CI: −0.97– −0.05	-	-	-
Gaur	FAR ~ age + dist + (1|site/transect)	0.00	0.40	0.27 (0.07) CI: 0.14–0.41	−2.18 (0.28) CI: −2.81– −1.65	-	-	-
	FAR ~ age + dist + canopy_avg + (1|site/transect)	1.65	0.17	0.27 (0.07) CI: 0.15–0.42	−2.03 (0.34) CI: −2.94– −1.41	-	-	*−0.01 (0.01) CI: −0.03–0.02*

Table 3 (continued)

Species	Model	ΔAICc	AICc weight	Time since relocation (age)	Distance from edge (dist)	TRI (TRI)	Distance from stream (dist_stream)	Canopy cover (canopy_avg)
Nilgai	FAR ~ age + dist + (1|site/transect)	0.00	0.29	*0.07 (0.08) CI: −0.11–0.22*	*−0.47 (0.25) CI: −1.02–0.06*	-	-	-
	FAR ~ age + dist + TRI + (1|site/transect)	0.65	0.21	*0.07 (0.08) CI: −0.09–0.20*	−0.50 (0.25) CI: −1.09– −0.02	*−0.22 (0.18) CI: −0.58–0.05*	-	-
	FAR ~ age + dist + dist_stream + (1|site/transect)	1.30	0.15	*0.07 (0.07) CI: −0.09–0.20*	*−0.49 (0.26) CI: −1.12–0.05*	-	*0.35 (0.35) CI: −0.41–1.03*	-
	FAR ~ age + dist + canopy_avg + (1|site/transect)	1.79	0.12	*0.07 (0.08) CI: −0.12–0.22*	*−0.37 (0.30) CI: −1.03–0.27*	-	-	*−0.01 (0.01) CI: −0.04–0.02*
Wild Pig	FAR ~ age + dist + TRI + dist_stream + (1|site/transect)	0.00	0.45	−0.14 (0.07) CI: −0.32– −0.01	−1.39 (0.28) CI: −1.93– −0.84	*0.26 (0.13) CI: −0.01–0.48*	0.85 (0.34) CI: 0.12–1.66	-
	FAR ~ age + dist + dist_stream + (1|site/transect)	1.38	0.23	*−0.13 (0.08) CI: −0.31–0.02*	−1.31 (0.27) CI: −1.95– −0.84	-	0.90 (0.34) CI: 0.19–1.63	-
	FAR ~ age + dist + TRI + dist_stream + canopy_avg + (1|site/transect)	1.94	0.17	−0.14 (0.07) CI: −0.34– −0.01	−1.28 (0.33) CI: −1.96– −0.67	*0.27 (0.13) CI: −0.03–0.54*	0.87 (0.34) CI: 0.07–1.57	*−0.01 (0.02) CI: −0.04–0.02*

Slope estimates for each predictor are tabulated and presented along with the standard error (SE), 95% confidence intervals (LCI and UCI); italicized values indicate confidence intervals overlapping 0. FAR is the response, age (time since relocation)/dist (distance from edge)/TRI (terrain ruggedness index)/dist_stream (distance to stream)/canopy_avg (mean canopy cover) are fixed effects and (1|site/transect) refers to the random effects of transects nested within sites

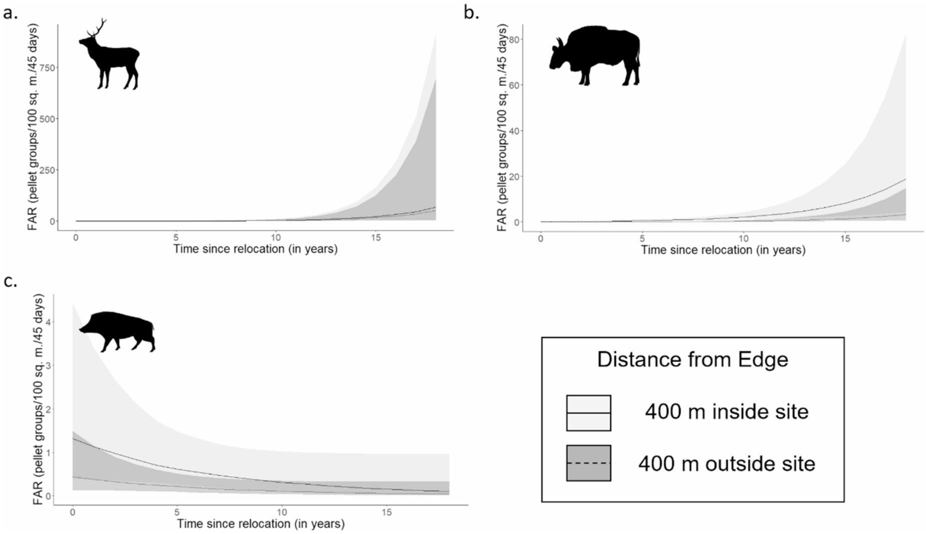

Fig. 3 Predicted mean faecal accumulation rate for (**a**) sambar (**b**) gaur and (**c**) wild pig as a function of time since relocation, 400 m inside and 400 m outside relocation site/village. Shaded regions denote the confidence intervals. Please note that the ordinate is scaled differently in each case

land patches/village settlement area as compared to the surrounding forests but our results indicate that wild pigs have a higher intensity of habitat use in the grassland patches/village settlement area.

Since the villages were traditionally located in valleys, close to perennial streams, relocation followed by the development of artificial grasslands provided the ungulates with spaces that met most of their ecological needs including the availability of fodder, water, and flat terrain. Consequently, large herbivores can be observed aggregating in these meadows, especially during the dry season when resources are scarce and immediately after the monsoons arrive when sufficient forage is available. The planting of palatable grasses in these meadows provides the ungulates with a rich source of nutrition helping them meet their dietary needs (Khan and Khan 1994; Sankar and Acharya 2004). With respect to water availability, we expected perennial streams in the vicinity of these grasslands to cater to the daily water requirements of all the five species (Ahrestani et al. 2018; Kumar et al. 2021) but found that the intensities of habitat use by nilgai and wild pig increased with distance from the nearest perennial stream. However, this may be due to the availability of other rain-fed waterholes in the area that we did not account for as part of the study. Since the terrain in this landscape is naturally undulating, the flat terrain of these managed grasslands favours species like chital and nilgai (Sharma and Chalise 2014; Pandey 2022). Sambar and wild pigs, however, had higher intensities of habitat use where the terrain was more rugged.

Village relocation as a strategy for conservation is neither new nor localized. For decades, wildlife conservation through PAs has been associated with the resettlement of indigenous communities. There is a long-standing history of conservation-oriented resettlement in Africa, South and South East Asia, and North America (Brockington and Igoe 2006). But it is important to note that resettlement in developing nations is often intertwined with issues of social equity as needs for conservation are met with the livelihoods of indigenous communities in the balance.

While village relocations may accrue some ecological benefits for wild fauna, their sociocultural and economic implications for forest-dependent communities (which were not investigated as part of this study) should not be ignored. Since village relocations were employed as a tool for wildlife conservation with a vision to improve the lives of people and wildlife both, we must ensure that all future relocations imbibe this vision into the actual implementation. Relocations should be planned and executed in a way that is fair, transparent, and equitable for all the stakeholders involved.

Conclusions

Our study suggests that village relocations and their associated grassland management interventions can lead to an increase in the intensity of habitat use by some ungulates. Grasslands developed after relocation result in a localised complex of forage, water, and visibility against predators, which helps them meet many of their ecological requirements. Species like sambar, chital, and gaur that are sensitive to anthropogenic disturbance have a higher intensity of habitat use as time passes after relocation. Nilgai also have a higher intensity of habitat use after relocation but the effect is minimal and for wild pigs, the intensity of habitat use decreases after relocation. Increased intensity of habitat use by large ungulates is an indicator of prey recovery and is expected to lead to an increase in the population of large carnivores. Since the recovery of large predators is linked to the functioning of the ecosystem, village relocations may have wider implications for reserve management.

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Author contributions RYR carried out the research including the data collection. RYR also prepared the manuscript. MS, DJ, and AA served as guides throughout the research. They also helped RYR prepare the manuscript and refine it to completion. All authors reviewed the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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