Terrain ruggedness and human activities influence the distribution of Grauer's gorillas and eastern chimpanzees in the Tayna Nature Reserve, Democratic Republic of Congo

Alice Michel[1], Jackson Kabuyaya Mbeke[2], Benezeth Kambale Visando[2,3], Sonya Kahlenberg[2], Katie Fawcett[2], Damien Caillaud[1]

[1]Department of Anthropology, University of California, Davis, USA
[2]Gorilla Rehabilitation and Conservation Education Center (GRACE), Kasugho, North Kivu, DRC
[3]Tayna Nature Reserve, Kasugho, North Kivu, DRC

Corresponding author email address: aljmichel@ucdavis.edu

Corresponding author address:
Alice Michel
Department of Anthropology
1 Shields Ave
University of California, Davis,
Davis, CA 95616 USA

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Abstract

The Albertine Rift Hotspot in east-central Africa is one of the most biodiverse regions in the world. It hosts a number of conservation-priority species, including critically endangered Grauer's gorillas and endangered eastern chimpanzees. Yet, prolonged insecurity in the region has made wildlife monitoring and conservation challenging. This is particularly true of the easternmost limits of the range of Grauer's gorillas, where wide stretches of unprotected forest could harbor behaviorally and genetically-unique peripheral populations of great apes and other species. Here, we developed a rapid wildlife survey method to map population distributions and monitor the impact of various human activities in the Tayna Nature Reserve in eastern Democratic Republic of Congo. Despite a lack of surveys since the early 2000s, we find that Grauer's gorillas and eastern chimpanzees, as well as a number of smaller-bodied species, have persisted in Tayna. Gorilla and chimpanzee activity was highly heterogeneous. It was the lowest near settlements and artisanal mines, and peaked in areas with rugged terrain. Maintaining connectivity between patches of suitable great ape habitat will be critical for long-term great ape conservation in the Albertine Rift region. Our findings also demonstrate the utility of priority species monitoring driven by local communities for conservation initiatives.

1. Introduction

Habitat loss and overhunting are the predominant threats to terrestrial wildlife globally (Hogue and Breon, 2022; Maxwell et al., 2016). Yet species vary in their susceptibility to different types of human activities. For example, settlements and crop fields tend to cause behavioral avoidance of formerly preferred habitat in African forest elephants (*Loxodonta cyclotis*; Blom et al., 2005), leopards (*Panthera pardus*; Van Cleave et al., 2018), and spotted hyena (*Crocuta crocuta*; Mwampeta et al., 2021), but not in forest buffalo (Van Vliet and Nasi, 2008), leopards, or brown hyena (Van der Weyde et al., 2018). Sometimes, human activities attract wildlife. For example, crop fields present foraging opportunities for chimpanzees (*Pan troglodytes*; Bessa et al., 2015), savanna elephants (*Loxodonta africana*; Chiyo et al., 2005), and wild boar (*Sus scrofa*; Morelle & Lejeune, 2015). Similarly, some species tend to recolonize habitats with high hunting pressure (*e.g.*, cougar, *Puma concolor*; Robinson et al., 2008; African wild dog, *Lycaon pictus*; van der Meer et al., 2014), whereas others avoid them (*e.g.*, Pampas fox, *Lycalopex gymnocercus*; Santo Domingo et al., 2021; black bear, *Ursus americanus*; Stillfried et al., 2015; elk, *Cervus canadensis*; Spitz et al., 2019). Identifying how specific threats, ranging behavior, and habitat preferences interact at the population level is important to the design of conservation plans (Martin, 1998).

Habitat degradation is rapidly intensifying in tropical forests, the most biodiverse terrestrial biome (Aleman et al., 2018). The Albertine Rift in the Eastern Afromontane biodiversity hotspot includes 40% of the continent's mammalian taxa in less than one percent of its total land area (Mittermeier et al., 2004). Though 60% of the Albertine Rift hotspot is under some degree of protection, the region faces numerous conservation challenges, including armed conflicts, deforestation for charcoal production, agricultural expansion, artisanal and large-scale mining, oil extraction, and climate change (Plumptre et al., 2017). Many of these factors tend to elevate hunting pressure, as demand for bushmeat for local consumption and market export grows, centered around villages and infiltrating into forests along routes to mines and logging sites (Spira et al., 2019; Thibault and Blaney, 2003; Vliet et al., 2015; Ziegler et al., 2016).

Keystone vertebrate species from the Albertine Rift have been severely impacted by these threats, including forest elephants (*Loxodonta cyclotis*), forest buffalo (*Syncerus cafer nanus*), eastern chimpanzees (*Pan troglodytes schweinfurthii*), and gorillas (*Gorilla beringei*), with long-term consequences on the ecosystem (Mittermeier et al., 2004). In particular, the critically endangered Grauer's gorilla (*Gorilla beringei graueri*), endemic to eastern DRC, declined from ~17,000 individuals in the mid-1990s (Hall et al., 1998a) to between 4,500 to 9,500 in 2019 (Plumptre et al., 2021, 2016). In addition to overall loss of numbers, the Grauer's gorilla population has become fragmented (Plumptre et al., 2021, 2016). Sympatric endangered eastern chimpanzees have experienced a similar situation (Plumptre et al., 2021, 2016).

Only a fraction of the range of Grauer's gorillas has been surveyed in the past 20 years (Plumptre et al., 2021, 2016). In particular, there is a lack of data from the northern range of Grauer's gorillas, due to regional insecurity and logistical challenges (Hart and Hall, 1996; Plumptre et al., 2016). Recent range-wide assessments of great ape species in the region have relied on extrapolation of occupancy models across different landscapes (Plumptre et al., 2021, 2016), an approach subject to high levels of uncertainty (Elith and Leathwick, 2009). The 899 km^2 Tayna Nature Reserve (TNR; **Figure 1**) lies at the northeastern edge of the historical range of Grauer's gorillas, at the border of the Lubero and Walikale territories in eastern DRC. The only published wildlife survey of TNR gorillas covered the central and southern portion of the area in 2003 (Mehlman, 2008). Two surveys were attempted since, in 2006 and 2013, but neither was completed due to security issues (Nixon, 2013). Nevertheless, Plumptre et al. (2015) suggested a possible crash of the gorilla population in TNR by nearly 90%. If a viable population of Grauer's gorillas still persisted in TNR, it would be one of the furthest north and east populations of Grauer's gorillas left, aside from the few individuals remaining at Mount Tshiaberimu, Virunga National Park (Iyer et al., 2023). As a peripheral population, it would likely have high genetic value (Van Der Valk et al., 2018), warranting improved protection of the reserve itself and of the forest connecting TNR to Maiko National Park as a critical biological corridor.

Here, we investigate the spatial distribution, terrain covariates, and impacts of anthropogenic disturbances on Grauer's gorillas, eastern chimpanzees, guenons (*Cercopithecus spp.*), duikers (*Cephalophus spp.* and *Philantomba monticola*), and red river hogs (*Potamochoerus porcus*). We conducted a survey that covered the entire reserve with 380 km of transects and used a modified distance transect protocol that leveraged generalized additive models to examine how wildlife distribution related to terrain and human activities. We hypothesized that, if Grauer's gorillas and eastern chimpanzees were present, their density would decline in the vicinity of human settlements and other human activities in the forest, such as artisanal mining and snare-trapping. We expected the density of other wildlife species to also be impacted by human activities, but we predicted that more resilient, faster-reproducing species, such as red river hogs and duikers, would be less affected than slow-reproducing great apes and guenons. Finally, we hypothesized that habitat suitability varies across TNR due to ecological factors and long-term human activities. As such, we predicted that the distribution of wildlife populations would relate to terrain, with different patterns for different species.

2. Methods

2.1. Study area

The Tayna Nature Reserve (TNR; 0° 20' 36" S, 28° 43' 0" E; **Figure 1**) was created in 2006 at the border of the Lubero and Walikale territories, North Kivu, eastern Democratic Republic of Congo. It encompasses 899 km^2 of closed-canopy primary forest, open-canopy forest, and agricultural clearings. It lies in the transition zone between the Congo Basin and the Albertine Rift, generating a heterogeneous mix of high-altitude terrain up to 2,028m above sea level (asl) stretching along the east of the reserve, with rugged hills and valleys near the center, and lower, flatter areas to the northwest dipping to 919m asl (**Figure 2A**; **2B**). These forests of TNR extend continuously to the west to Maiko National Park. Vegetation is typical of low- to medium-altitude primary and secondary equatorial forest, though botanical surveys have not yet been undertaken. Rainfall averages 1,800-2,300mm per year, with the rainiest season from October to November and a second rainy season from March to April (CBFP, 2006). The largest human settlements in the region are to the northeast. Additional villages are found along the eastern and mid-western boundaries. There are also smaller dispersed settlements and encampments within the reserve (**Figure 2C**).

2.2. Fast-Transect Survey

Great ape surveys typically attempt to estimate animal density by relying on standing crop nest counts (Kühl et al., 2008; Morgan et al., 2006). Field teams walk along randomly placed transect lines and record the perpendicular distance between nest sites and the transect line (Buckland et al., 2015). When the nest production rate and the decay rate are known, nest density can be converted to individual density (Buckland et al., 2015). This method is accurate as long as both rates are well known. However, since nest decay rates vary significantly among habitats and seasons, density estimates based on nest decay rates calculated at another site can be unreliable (Morgan et al., 2006; Tutin et al., 1995; Walsh and White, 2005). For example, a decay rate of 106 days, which was originally recorded for central chimpanzee arboreal nests in Gabon (White, unpublished data), has been widely used in Grauer's gorilla

surveys conducted in eastern DRC (Hall et al., 1998b; Mehlman, 2008; Plumptre et al., 2021, 2016). Another challenge of the transect method is due to the difficulty to walk along a perfectly straight line in dense forests. In central Africa, field teams can often only walk 1-2km/day along line transects (Caillaud, personal communication), which limits the number of nest sites that can be detected. Lastly, the line transect method only relies on signs with known production and decay rates. Most published great ape line transect surveys are solely based on nests and ignore other signs such as feeding signs, dung piles, and prints. When the animal density is low, the sampling effort required to reach the recommended minimum of 60-80 groups of nests is considerable (Kühl et al., 2008). Taking the example of Grauer's gorillas, the exceptional 689-km, multi-year transect survey conducted by Plumptre et al (2021) only found 118 groups of nests. This means that observing 60-80 groups of nests requires 350-467 km of transects. Such a sampling effort can only rarely be attained due to prohibitive costs and lack of qualified staff.

We developed a wildlife survey method that did not attempt to provide absolute abundance estimates but allowed rapid, economical surveying of wildlife and the estimation of relative abundance estimates. The method was termed the "fast-transect method". To initiate the survey, we designated 200 linear transects in a horizontally-staggered gridded pattern across the reserve (**Figure 1**). Each transect was 2km long, oriented north to south, and spaced apart by 1.5km east to west and 750m north to south. Five survey teams walked 196 of the transects; the remaining four were inaccessible. Each team comprised four members: one team leader, one trail opener who walked ahead and cut minimally through the dense vegetation, sometimes walking around major obstacles, and two observers on either side of the leader. The team leader carried a Garmin 64 handheld GPS unit, which automatically recorded points every 50m. Waypoints for the start and end of each transect and any obstacles encountered were manually entered in the GPS. The two observers "swept" the 50m to the left and right of the leader for signs, covering an 100m wide strip over each 2km transect. Observers remained within sight of the team leader, who recorded GPS points for each observation. All signs of animal presence that could be attributed to a particular species were recorded: nest sites, prints, feeding remains, dung, burrows, and direct visual or

auditory observations. Only equivalent consecutive signs at least 50m apart were considered, to reduce bias due to the clustering of signs produced by the same animal or group of animals.

Compared to traditional distance transects (Buckland et al., 2015), fast transects do not require measurement of perpendicular distances to signs, and rely on a variety of types of signs of animal presence. This enables coverage of a larger survey area and collection of more data in the same amount of time, at the expense of being unable to compute absolute animal densities. In this regard, they are similar to reconnaissance surveys ("recce walks"), but, contrastingly, fast transects are not biased by habitat type to only follow the path of least resistance. This means that they produce more accurate relative density estimates and can be used to evaluate animal relative abundance, distribution, and influencing factors within a survey area. To summarize, for a given sampling effort (*i.e.*, number of people times days spent collecting data), the fast transect methods generates more data than the distance transect method, allowing for more precise relative density estimates, and is not biased towards certain habitat types like reconnaissance surveys. The only major drawback of the fast transect methods is that it produces relative instead of absolute animal density estimates.

We followed the method used by Plumptre et al. (2016) to assign great ape nest sites to species, based on nest height, odor, dung, hairs, and trails. In addition, we recorded signs of human activities, such as camps, paths, snares (aerial and terrestrial, traditional and wire), artisanal mines (operational and abandoned), logging, and crop fields. Five teams conducted a total of 22 two-week patrols, covering seven to twelve transects per patrol. The survey was undertaken between September 12 to December 24, 2020.

All data were collected strictly non-invasively in accordance with Congolese laws and regulations for wildlife research by survey teams coordinated by GRACE (Gorilla Rehabilitation and Conservation Education Centre). Disturbance to wildlife during field work was negligible.

2.3. Predictor Variables

We used satellite imagery and on-transect observations of human activity to identify environmental and anthropogenic predictors of wildlife distribution. The predictor variables were altitude, terrain ruggedness, proximity to human settlements, and mining density (**Figure 2**).

To measure the altitude and terrain ruggedness in the region, we downloaded the Shuttle Radar Topography Mission (SRTM) 1 Arc-Second Global 30m resolution digital elevation model (DEM) for the tile at 1˚S, 28˚E (USGS, 2015). Altitude (meters asl) was taken at the precise coordinate of each data point. The terrain ruggedness index was computed by first calculating the average difference between each 30 x 30m DEM raster cell and its eight adjacent cells (Wilson et al., 2007), then averaging this value around each data point over a radius of one kilometer, from the average daily distance travelled by Grauer's gorillas in a low-altitude site during the rainy season (van der Hoek et al., 2021a).

To evaluate the impact of human settlements, we calculated a 'proximity index'. This variable considers both the distance to settlements and their relative size, since settlements in TNR ranged from several-dwelling camps to small villages. To do this, first we drew polygons around settlements, fields, and camps visible in satellite imagery (Google Earth V7.3.3.7786, 2021) in TNR plus a five-km buffer around it using QGIS (v.3.20). We converted the multi-polygon to a raster with resolution five-meters, using the R package 'fasterize' (R Core Team, 2023; Ross, 2020). Next, we converted the raster to a spatial points object, such that the located settlement areas were covered by points every five meters, using R functions *rasterToPoints* and *SpatialPoints* from the 'raster' package (Hijmans et al., 2013) and the 'sp' package (Pebesma and Bivand, 2005), respectively. We then used kernel density estimation in the R function *kernelUD* from package 'adehabitatHR' to interpolate the relative density of settlements points across all of TNR at the same resolution as the DEM (30m), setting the smoothing parameter, *h*, to 1000 (Calenge, 2006). Finally, we rescaled the values by dividing by the maximum value so that they ranged between zero (far from settlements) to one (proximate to large settlements). Using the KDE approach captured the relative size of settlements as well as distance to them, as the larger the settlement, the higher the density of settlement points, so, at a comparable distance, the closer the resulting 'settlement proximity index' value was to one. We chose the smoothing parameter (*h*) arbitrarily, but this did not

affect downstream statistical analyses because we opted for generalized additive models, which are able to capture non-linear relationships. Since the variables were smoothed, the only requirement for the settlement function itself was that it captured some spatial variation in distance to settlements and gave more weight to larger settlements.

Artisanal mines are typically one to a few small holes in the forest with an adjacent rudimentary camp (Mbeke, personal communication) and are thus too small to be detectable on satellite images, but signs of artisanal gold mining, ranging from current to abandoned for months, were found along transects. To map mining density across TNR, we randomly added 10,000 pseudo-absence "dummy" points to the survey area (similarly for the animal models, described below) and fit a binomial generalized additive model (GAM) to these presence/absence data in 'mgcv' (Wood, 2017). The predictor variable was a bivariate smoothing term of latitude and longitude, smoothed used thin-plate regression splines. This model allowed mining density to vary over two-dimensional space. The smoothed latitude-longitude predictor variable significantly influenced the probability of mining presence ($p = 0.02$). We used the fitted GAM to predict the relative density of mines for each 30 x 30m grid cell, scaled so the mean equaled the observed mean mining density in transect strips (0.55 observed mining signs/km^2; **Figure 2D**). We utilized the same approach to model the density of snares found along transects. However, the latitude-longitude smoothing predictor variable did not significantly influence snaring ($p = 0.8$), meaning that these data did not reveal any spatial variability in snare distribution. Snare density could therefore not be incorporated into animal distribution models.

2.4. Animal population distribution models

2.4.1. Modeling framework

We chose to use generalized additive models (GAMs) to model wildlife spatial distribution and identify predictors of animal relative density in TNR because of their ability to incorporate nonlinear effects and two-dimensional (spatial) effects. Models were fit in the R package 'mgcv' with a binomial

distribution and logit link function. We used restricted maximum-likelihood (REML) to find the optimum smoothing parameters (Wood, 2018). Separate models were fit for each of the following animals: Grauer's gorilla, eastern chimpanzee, guenon monkeys, duikers, and red river hogs. We modelled animal sign presence/absence in relation to the smoothed predictor variables described above: altitude, ruggedness, settlement proximity index, and mining density. All smooths were fit by the thin-plate regression spline method with the basis (k) restricted to five to avoid overfitting.

2.4.2. Data preparation

To reflect the true sampling area over which to randomly generate absence points, the GPS track points automatically recorded every 50m along transects were interpolated to a track polyline and clipped to the start and end of each transect, using QGIS. We excluded track detours around obstacles and GPS errors (deviations over 50m from previous point). The transect polyline was buffered by 50m on each side, resulting in a 100m-wide transect multi-polygon covering the area "swept" by field teams. We retained only observations within this polygon for the models, excluding observations made off-transect, such as during travel between transects, near camps, or more than 50m from the transect line. The overall surface area delimited by the transect polygons was 41.7km^2.

To evaluate spatial heterogeneity in animal presence and absence, we created 10,000 pseudo-absence points within the surveyed transect area. We randomly placed these dummy points at a density of 240 points per square kilometer of transect strip covered, using the function *spsample* in the 'sp' R package to weight pseudo-absences equally by actual transect area surveyed (Bivand et al., 2013; Pebesma and Bivand, 2005). We chose to generate pseudo-absence points randomly and to use 10,000 because this is recommended for species distribution models using binomial generalized linear and additive models (Barbet-Massin et al., 2012). We verified that models from 100 runs of generating pseudo-absence points revealed the same conclusions.

2.4.3. Differentiating between gorilla and chimpanzee signs

Though we followed established protocol, gorilla and chimpanzee signs can be difficult to distinguish (Sanz et al., 2007). As confirmation, we compared the characteristics of nest sites by species and through space, with the hypothesis that the spatial distribution of nests with gorilla characteristics would match the gorilla population distribution model using all gorilla signs, not just nests, if the species assignments were accurate. Specifically, we compared characteristics of nest sites attributed to each species, including terrestriality (fraction of terrestrial nests per site) and nest group size, using generalized linear models and χ^2 tests. We evaluated spatial heterogeneity in great ape nest group size and terrestriality independent of species assignment using GAMs with Poisson and Gaussian error distributions, respectively, with a bivariate smoothing term of latitude and longitude as the predictor variable and the same pseudo-absence points as detailed above.

2.4.4. Testing and accounting for spatial autocorrelation

Spatial autocorrelation is important to consider in species distribution modelling (Gaspard et al., 2019). If left unaccounted for, strong spatial autocorrelation violates model assumptions of nonindependence and can give rise to spurious association with environmental covariates (Dormann et al., 2007). Animal sign data are susceptible to endogenous spatial autocorrelation, a type of spatial autocorrelation that is separate from the autocorrelation due to unmeasured environmental characteristics between spatially nearby locations. It is not directly attached to space, but rather to pairwise distance via biological processes, such as animal home range size, dispersal, social behavior, etc. (Gaspard et al., 2019). For example, in the case of great ape signs, presence or absence of signs are likely to clump in space because the same animal or group of animals may leave multiple signs. Our data collection protocol only considered successive observations that were more than 50m apart, which likely reduced the risk of spatial autocorrelation. To determine whether this was sufficient, we evaluated spatial autocorrelation among points near to one another using semi-variograms of GAM residuals. We focused on presence/absence points within 5km of one another, as 1km is the average daily travel distance of unhabituated Grauer's gorillas in lowland forests (van der Hoek et al., 2021a). At this scale, we did not

detect a signature of spatial autocorrelation in the variograms for any of the animal populations considered (**Figure A1**). Thus, we did not attempt to account for spatial autocorrelation in our models.

2.4.5. Model diagnostics

We used two strategies to assess the fit of GAMs. First, we mapped predicted relative abundance for each species using the *predict* function in the 'raster' package, taking as predictor variables a raster stack of the terrain and anthropogenic variables in our model (Hijmans et al., 2013). We converted model predictions from probability of occurrence to density (observed signs/km^2) by multiplying the model prediction at each 300 x 300m raster cell by average sign density (total number of observed signs over 41.7 km^2 of transect polygons) divided by average predicted probability of sign occurrence across TNR. We plotted observations of animal signs on top this map to visually inspect model fit.

Second, we mathematically checked the expected fit of the GAM against observations. For each data point used as the response variable in the model, there is both the observed value – presence or absence of animal sign – and the expected probability of occurrence predicted by the GAM. Because the former is binary, we pooled the data points into 25 bins of predicted value. Each bin had an equal number of points in it, meaning some bins could be wider in terms of predicted values than others, to avoid differences in variance obscuring any trends. For each bin, we computed the mean observation frequency (fraction of points with animal sign observed) and standard error and plotted it against the mean predicted probability.

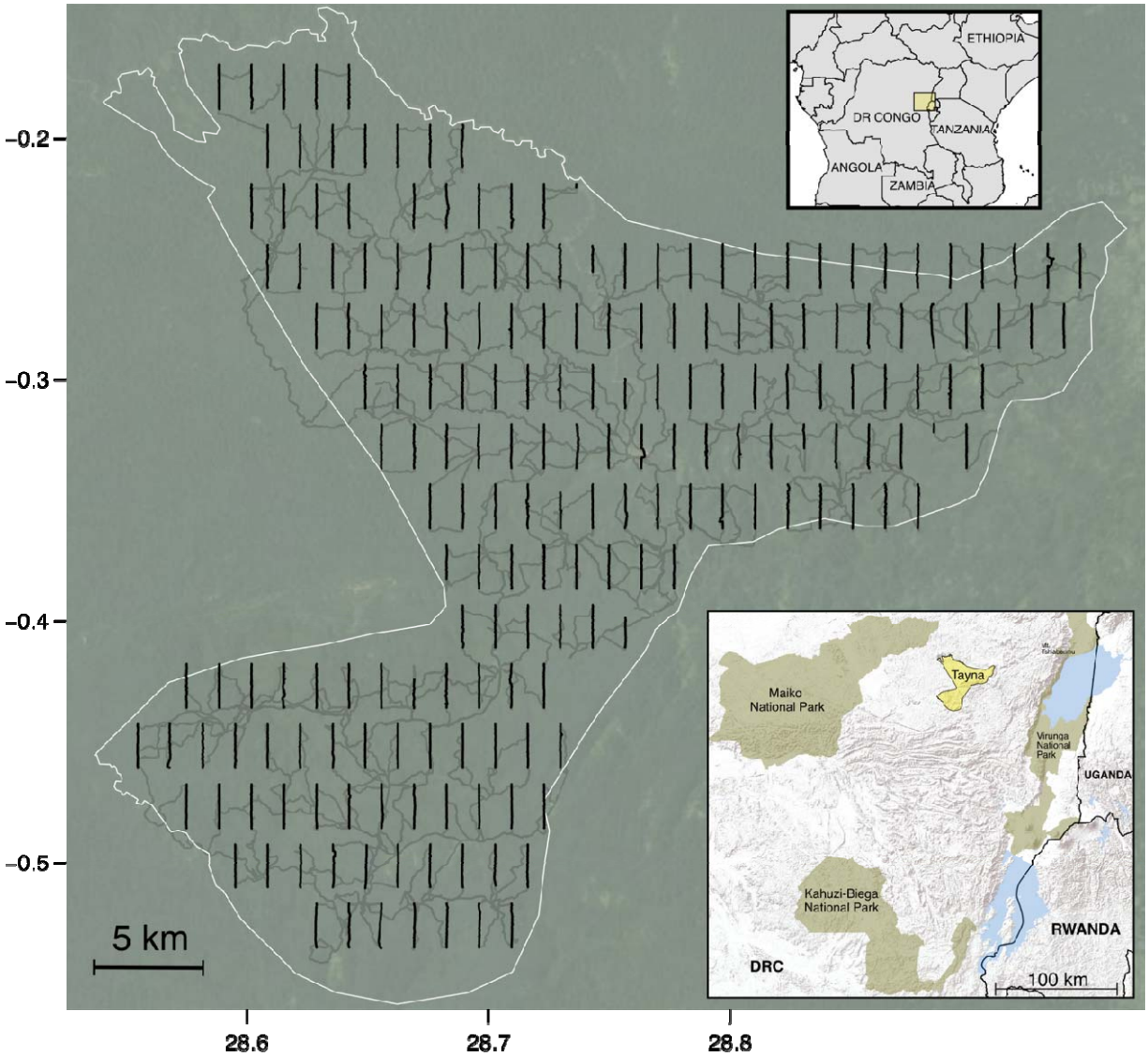

Figure 1. Situated in the eastern DRC (upper inset), Tayna Nature Reserve (yellow, lower inset) lies in an ecological transition zone between the Albertine rift mountains to the east and the Congo Basin rainforest to the west. Shown on the main map, wildlife surveys were conducted along 196 line transects, sweeping the 50m to either side of the transect (100m width) for primate and other species' tracks, dung, feeding remains, and other signs, as well as indicators of human activities. The walked tracks for transects (black lines) were extracted from GPS tracks that recorded every 50m as teams travelled to transect start points and walked line transects (grey lines). The background forest cover map is a composite satellite image from Google Earth (Maxar Technologies, Landsat/Copernicus 2020).

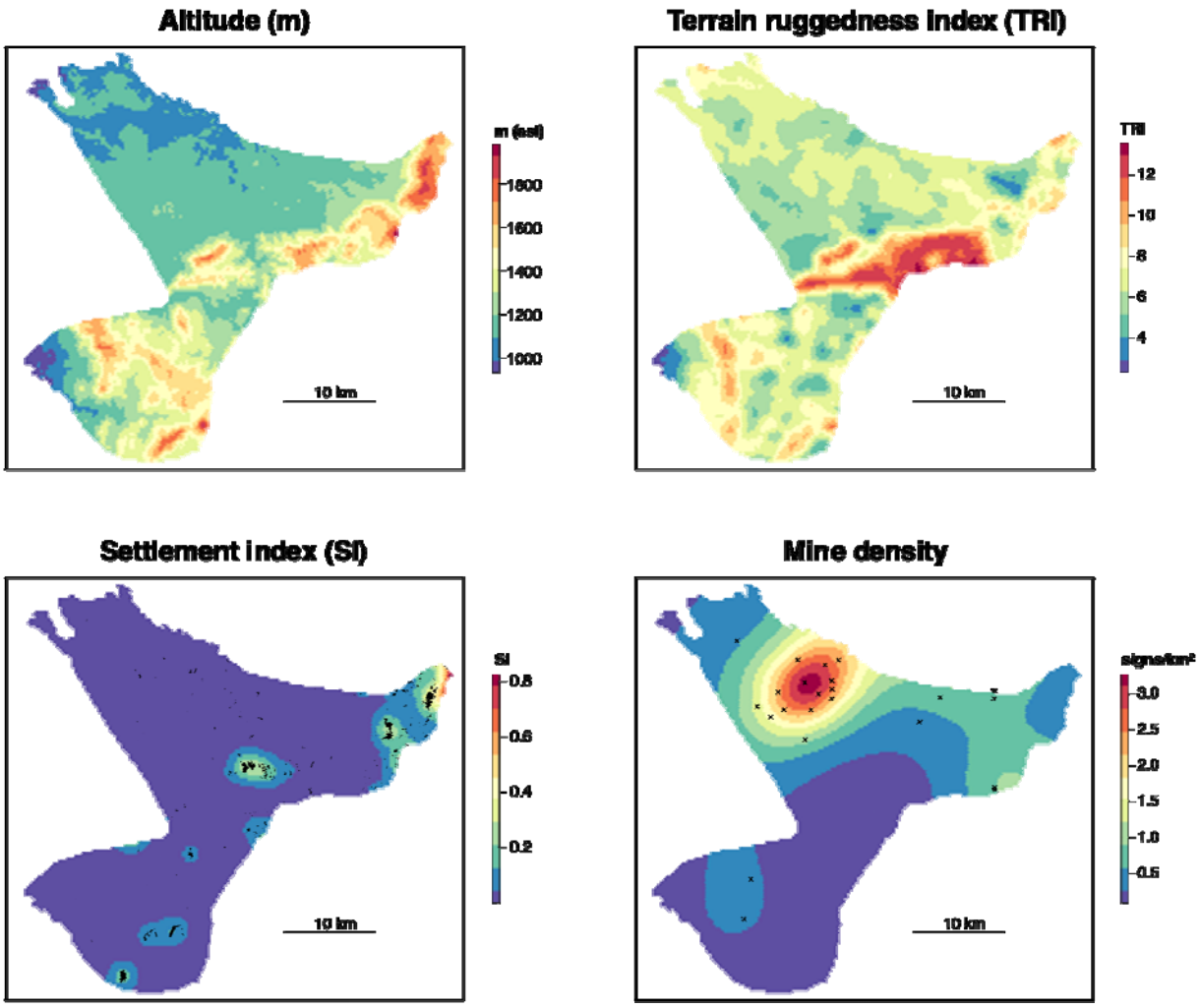

Figure 2. Maps of predictor variables for wildlife species distribution models in Tayna Nature Reserve. Altitude and TRI were calculated from a 30m resolution digital elevation model (USGS, 2015; see methods). Calculation of the Settlement Index and Mine density are described in the Methods section.

3. Results

3.1. Fast transect survey

We recorded 87 GPS waypoints for signs observed of Grauer's gorilla and 151 for eastern chimpanzees both on and off transects in Tayna Nature Reserve. Signs included nest sites, tracks, trails, feeding remains, dung, and auditory and visual (for chimpanzees) observations. Among those signs, a total of 41 gorilla signs and 119 chimpanzee signs were found along transects (**Table 1**). There were 3.86 great ape signs observed per km^2 of transect (0.99 per km^2 from gorillas and 2.87 per km^2 from chimpanzees). In addition to great apes, we recorded signs of five cercopithecine monkey species (*Cercopithecus ascanius, C. denti, C. hamlyni, C. lhoesti,* and *C. mitis*), four species of duikers (*Cephalophus dorsalis, C. nigrifrons, C. silvicultor,* and *Philantomba monticola*), three species of pangolins (*Phataginus tricuspis*, *P. tetradactyla*, and *Smutsia gigantea*), red-river hog (*Potamochoerus porcus*), brush-tailed porcupine (*Atherurus africanus*), forest buffalo (*Syncerus caffer nanus*), aardvark (*Orycteropus afer*), and leopard (*Panthera pardus*) (**Table 1**). There was no sign of forest elephant (*Loxodonta cyclotis*).

During the survey in TNR, both on and off transects, we found 109 great ape nests, of which 40 were assigned to Grauer's gorillas and 69 to eastern chimpanzees. Excluding 23 solitary nests, the average great ape group size was 6.38 nests/site, ranging from two to 25. There were 15 solitary nests assigned to chimpanzees and 8 solitary nests assigned to gorillas. Group nest sites attributed to gorillas (n=32) were larger than those attributed to chimpanzees (n = 54) (8.88 vs. 4.91; GLM estimate = -0.23, SE = 0.07, z = -3.20, p = 0.001; **Figure A2**). More small nest sites (two to three nests) were attributed to chimpanzees, but the distributions overlapped substantially (**Figure A3**). Regardless of species identity, nest group size tended to be larger in the rugged central and southwestern regions of the reserve and smaller near the eastern border (GAM edf = 6.687, χ^2 = 17.91, p = 0.01), where nests were attributed to chimpanzees (**Figure A4a**). The fraction of terrestrial nests per site was higher in same area as where sites were larger (GAM edf = 5.546, F = 3.208, p = 0.007; **Figure A4b**). Gorilla nest sites were more terrestrial (39% vs. 18%; GLM estimate = -2.09, SE = 0.83, z = -2.51, p = 0.01; **Figures A5 & A6**).

Table 1. Species identified along transects in Tayna Nature Reserve (TNR). Animal signs were recorded on 196 transects that covered 41.7 km^2 of the 899 km^2 of TNR.

Wildlife species	**Seen**	**Heard**	**Tracks, trails, dung, and food remains**	**Sleeping sites, *i.e.*, nest sites or burrows, etc**
Gorilla beringei graueri	0	1	24	16
Pan troglodytes schweinfurthii	1	18	45	55
Cercopithecus spp.	65	108	28	-
Cephalophus spp. & Philantomba monticola	11	0	380	18
Potamochoerus porcus	0	0	223	5
Atherurus africanus	1	1	196	7
Phataginus spp. & Smutsia gigantea	0	0	12	34
Syncerus caffer nanus	0	0	19	-
Panthera pardus	0	0	5	-
Orycteropus afer	0	0	1	5

3.2. Population distribution models

3.2.1. Grauer's Gorillas

The density of gorilla signs observed in TNR was associated with terrain ruggedness (GAM, χ^2 = 14.50, p = 0.003), but not altitude (χ^2 = 1.84, p = 0.2). It was negatively associated with the anthropogenic factors, settlement index (χ^2 = 9.98, p = 0.002) and mining density (χ^2 = 12.37, p = 0.0004; **Table 2**). The model's fitted values aligned visually with off-transect observations of gorilla signs (**Figure 3a**). There was a clear positive relationship between observations and model predictions, indicating that the model was able to capture population distribution (**Figure A7a**).

The model showed that gorilla sign relative density was maximized at ruggedness values above 7.5, which was above the average ruggedness of TNR (7.1, range = 3.2-12.7; **Figure 4a**). The settlement index was directly inversely correlated with gorilla sign density, with gorilla sign density declining to below average at values just above the median in TNR (0.0056, median = 0.004; **Figure 4a**). The effect of mine density had a larger confidence interval (**Figure 4a**), which could be due to correlation between mine density and terrain ruggedness: mine density peaked at a low terrain ruggedness index of 6.1 (GAM R^2 = 0.19, F = 292, p < 0.001). The settlement index also associated significantly with terrain ruggedness, peaking at minimum ruggedness, but the effect was weak (GAM R^2 = 0.017, F = 23.06, p < 0.001).

3.2.2. Eastern chimpanzees

As for gorillas, the density of chimpanzee sign was positively associated with terrain ruggedness (GAM, χ^2 = 45.33, p < 0.001) but not altitude (χ^2 = 2.89, p = 0.09), and negatively associated with the settlement index (χ^2 = 4.12, p = 0.04) and mining density (χ^2 = 5.94, p = 0.047; **Table 2**; **Figure 3b**). While observed gorilla signs peaked at intermediate terrain ruggedness and plateaued thereafter, chimpanzee sign density was predicted to peak at maximal ruggedness (TRI > 12; **Figure 4b**). This mirrors the more uniform distribution of signs attributed to chimpanzees, some of which were recorded far north in the reserve where great ape signs were never attributed to gorillas (**Figure 4b**). The fitted GAM for observed chimpanzee signs predicted well the distribution of observations (**Figure A7b**).

Table 2. Generalized additive models of great ape sign density in TNR

Gorilla beringei graueri				
Term	**Edf**	**Ref df**	χ^2	***p***
Thin-plate smoothed terms				
Altitude	1.000	1.001	1.838	0.2
Terrain ruggedness index	2.879	3.285	14.504	**0.003**
Settlement index	1.000	1.000	9.977	**0.002**
Mining density	1.000	1.000	12.373	**0.0004**
n = 10041				
Deviance explained = 19.6%				
Pan troglodytes schweinfurthii				
Term	**Edf**	**Ref df**	χ^2	***p***
Thin-plate smoothed terms				
Altitude	1.000	1.001	2.886	0.1
Terrain ruggedness index	1.918	2.371	45.327	**<0.001**
Settlement index	1.000	1.000	4.124	**0.04**
Mining density	1.883	2.298	5.936	**0.047**
n = 10119				
Deviance explained = 8.63%				

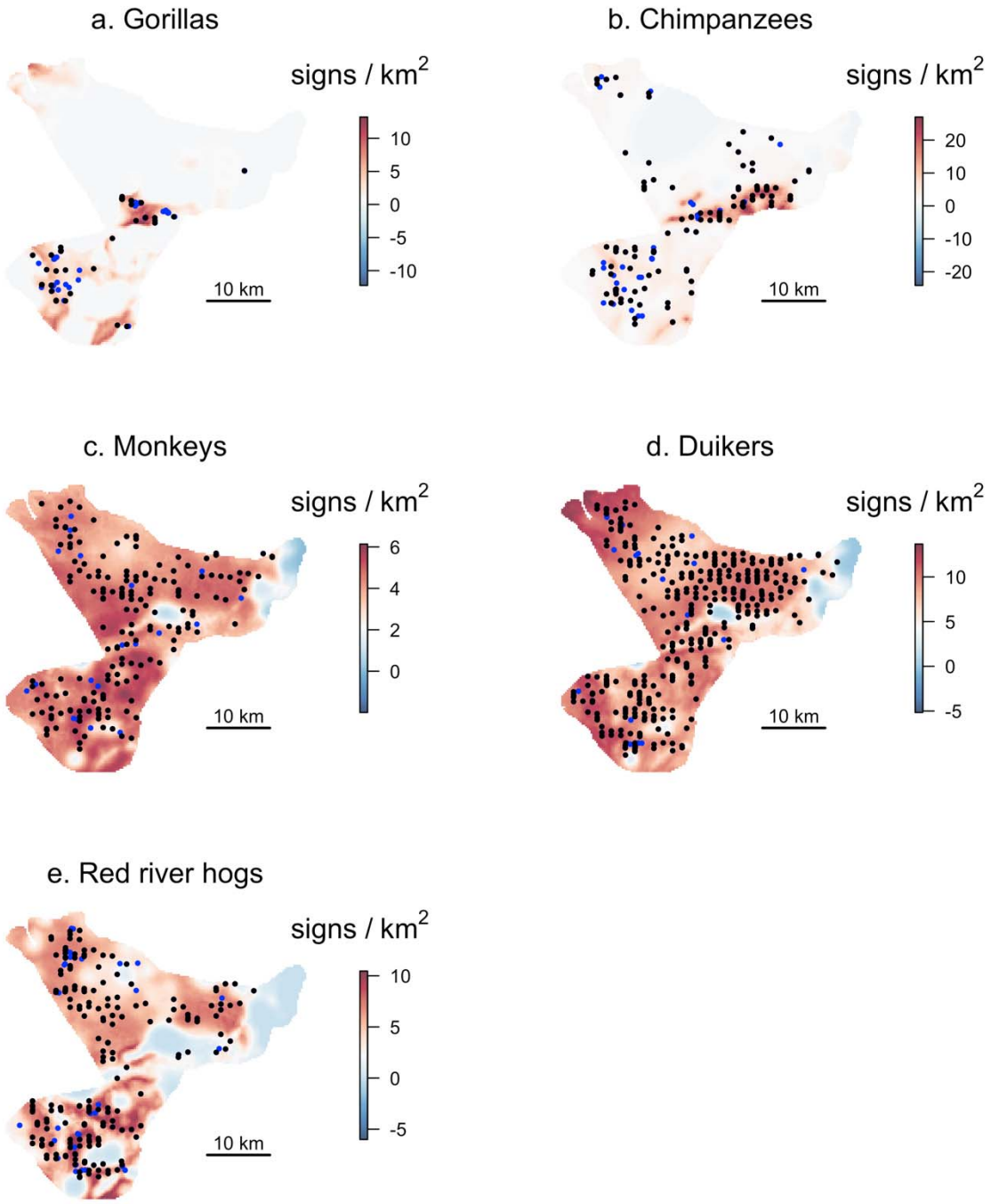

Figure 3. Predicted relative densities of animal populations in observed signs/km^2 in TNR based on GAMs. The average density of signs of gorillas, chimpanzees, monkeys, duikers, and red-river hogs on transects were 0.99, 2.87, 4.15, 8.52, and 4.46 per km^2, respectively. Animal sign observations on transects are marked in black circles, which were the presence points in the model. Off-transect sign observations are shown in blue.

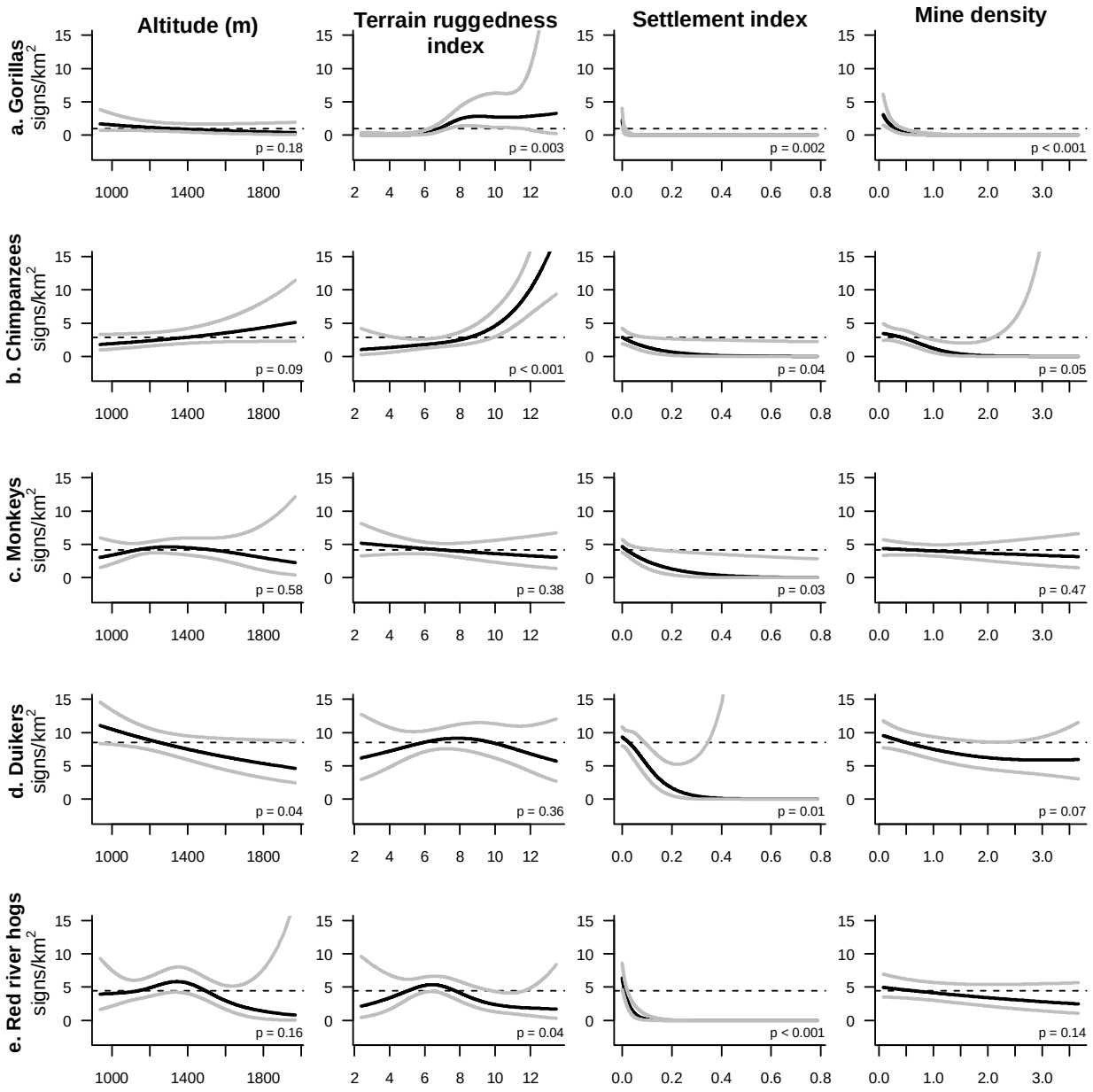

Figure 4. Partial effects of altitude, terrain ruggedness, settlement proximity, and mine density on predicted animal sign density in observed signs per km^2. The dashed line shows the mean sign density for each population. Gray lines show the upper and lower 95% confidence intervals around the main effect prediction (black line).

3.2.3. Monkeys

The survey recorded sightings, vocalizations, prints, and food remains of red-tailed monkey (*Cercopithecus ascanius*), blue monkey (*C. mitis*), owl-faced monkey (*C. hamlyni*), mountain monkey (*C. lhoesti*), and Dent's mona monkey (*C. denti*). Monkey sign observations were less spatially variable than those of great ape (**Figure 3c**) and were not statistically associated with variation in altitude (GAM χ^2 = 1.66, p = 0.6), ruggedness (χ^2 = 0.76, p = 0.4), nor mine density (χ^2 = 0.52, p = 0.5). Settlement index, however, had a significant negative effect on the relative density of monkey signs observed (*edf* = 1.003, χ^2 = 4.77, p = 0.03; **Figure 4c**). As expected from the relatively even sign distribution, the predictive capability of the GAM for monkey signs was low (**Figure A7c**).

3.2.4. Duikers

Signs and sightings of locally-called "red" duikers (duikers of similar size with similar footprints and dung: black-fronted duiker, *Cephalophus nigrifrons*, red-flanked duiker, *C. rufilatus*, and/or white-bellied duiker, *C. leucogaster*), yellow-backed duiker (*Cephalophus silvicultor*), and blue duiker (*Philantomba monticola*) were observed widely across TNR (**Figure 3d**). Duiker signs consisted of prints, trails, food remains, and dung. The significant factors influencing their distribution were settlement index (GAM *edf* = 1.77, χ^2 = 9.27, p = 0.01) and altitude (*edf* = 1.00, χ^2 = 4.28, p = 0.04), with more duiker signs recorded at low values of both. Relative density appeared to decline in low-lying areas with high mining density, but this effect was not significant (χ^2 = 4.53, p = 0.05; **Figure 4d**). There was a clear positive relationship between observations and model predictions, indicating that the model was able to capture population distribution (**Figure A7d**).

3.2.5. Red-river hogs

Red-river hogs (*Potamochoerus porcus*) left signs including trails, prints, dung, and food remains on transects. They were heard and seen once (three individuals) off-transect. Settlement index had a strong negative effect on the distribution of observed red river hog signs (GAM *edf* = 1.000, χ^2 = 20.58, p

< 0.001; **Figure 3e**; **Figure 4e**). Terrain also mattered, with sign density peaking just below the average ruggedness (*edf* = 2.64, χ^2 = 8.95, p = 0.04; **Figure 4e**). There was a clear positive relationship between observations and model predictions, indicating sufficient predictive power of the model (**Figure A7e**).

4. Discussion

We used a novel field data collection method, termed "fast transects", to survey the entirety of the Tayna Nature Reserve (TNR) in north Kivu, DRC, in 2020. Our survey identified populations of critically endangered Grauer's gorillas and endangered eastern chimpanzees. Observed signs of gorillas and chimpanzees were both positively associated with increasing terrain ruggedness, but not altitude, and negatively influenced by proximity to human settlements. Gorilla signs additionally showed a negative association with observations of recent artisanal mining activity. Signs of duikers, monkeys, and red river hogs were distributed more homogeneously throughout TNR than either of the great apes. Nevertheless, they too were all negatively impacted by proximity to human settlements. The survey also detected a number of other wildlife species, including a few signs of forest buffalo, leopard, pangolins, and aardvark.

4.1. Comparison with prior surveys

This is the first survey to cover the entirety of TNR. We found that the Grauer's gorilla population in TNR is restricted to the rugged mountains and valleys in the center and south of the reserve. Gorillas were present in this sector in the early 2000s, based on partially-completed surveys (Mehlman, 2008; Nixon, 2013; Plumptre et al., 2015). The gorilla population seems to have persisted over the past 15-20 years, at least in this central and south sector. This may indicate that poaching of gorillas has been minimal since the legal establishment of TNR in 2006, although firm conclusions cannot be drawn in the absence of data from the 2000's from the vast northern sector of the reserve (Mehlman, 2008; Nixon, 2013; Plumptre et al., 2015). Like gorillas, we found the greatest chimpanzee activity to be localized in the center and south, but chimpanzee signs were also found in the far northwest of TNR. Other species have not been formally surveyed previously, though a 2012 survey team in the center of TNR reported that no monkeys were heard or seen (Nixon, 2013).

4.2. Influence on terrain on species distribution

Gorilla and chimpanzee signs in TNR were positively correlated with ruggedness, but not altitude. In the tropics, plant diversity tends to be maximized in mountainous ridges and valleys with high slopes (Baldeck et al., 2013). Great apes have diverse diets, comprising terrestrial herbaceous vegetation, seasonal fruit, roots, and more (*e.g.*, Basabose, 2002; Michel et al., 2022; van der Hoek et al., 2021), and may select areas with diverse plant communities where they can find both fallback foods and preferred foods within short distances. Our model showed that gorilla density peaked at moderately-highly rugged areas, whereas chimpanzee density peaked at the highest ruggedness in TNR. This subtle difference may reflect ecological differences in the availability of food plants. The apparent preference for rugged terrain observed within TNR is visible at the regional scale as well, with both species of great apes concentrated in more rugged areas across the Grauer's gorilla range (Plumptre et al., 2021).

Combined, these results could reveal a habitat preference among these great apes for rugged terrain. Yet contrarily, in the Itombwe Massif, relatively flat secondary forest in abandoned mining areas and village outskirts have actually supported higher densities of Grauer's gorillas than rugged primary forest (Omari et al., 1999). Hence an alternative hypothesis is that TNR gorillas may have been extirpated from flatter areas by past hunting activity hunting or driven to rugged mountains and valleys in avoiding current and/or historical human activities. Unlike great apes, monkeys were not influenced by terrain. While they probably also select for areas with high heterogeneity in fruiting tree communities, their larger population sizes and faster reproduction rates could enable them to rebound quicker from losses due to hunting. Importantly, in our analysis we combined numerous monkey species together due to sample size, though each species has distinct habitat preferences, potentially smoothing over the variation. Duiker and red river hog signs were more common in low-altitude and below-average-rugged areas, respectively, though the former is notably also an amalgamation of different species with different habitat preferences.

4.3. Influence of human presence & activities on species distribution

Human settlements and signs of artisanal mining had a negative effect on the density of Grauer's gorillas and, to a slightly lower extent, eastern chimpanzees. Negative associations between great apes

and both small-scale mining and villages have been reported in the Grauer's gorilla range at large (Plumptre et al., 2021), as well as for closely related great apes in west central Africa (Morgan et al., 2018; Ordaz□Németh et al., 2021; Strindberg et al., 2018). Hunting is one of the greatest threats to most wild primates globally (Estrada et al., 2017). Artisanal mining in forests poses a threat to wildlife due to miners' reliance on bushmeat. Moreover, significant removal of wildlife changes forest structure and ecosystem functioning that impacts individuals and species that are not themselves hunted (Effiom et al., 2013).

Like the great apes, signs of monkeys, duikers, and red river hogs were also all concentrated away from human settlements. Duikers are the most commonly consumed bushmeat locally in the region, with red river hogs second (Batumike et al., 2021; Mbete et al., 2011; Vliet et al., 2015). However, mining did not appear to have as strong an effect on these populations. They may have rebounded from temporary elevations in hunting pressure associated with abandoned small-scale artisanal mining operations. It is also possible that our sampling design and sample size did not allow detecting the impact of mining on these species. Great ape generation times, size, and social structure, meanwhile, makes them less capable of quick recovery. Similarly, the fission-fusion social system and behavioral flexibility of chimpanzees could have helped them to persist in or move back into the more impacted north of TNR where signs of artisanal mining were centralized. For example, eastern chimpanzees living adjacent to croplands seem to shift their activity patterns and foraging and nesting ecology (McCarthy et al., 2017; McLennan et al., 2021). Nevertheless, this very behavioral plasticity that may confer endurance to human-induced change has itself been reduced due to human-induced change, again emphasizing the need for protection of independent populations where unique cultural variants may persist (Kühl et al., 2019).

Local community culture, including preferences, taboos, traditional forest products, and tactics for harvesting them, can also result in prioritized offtake of different wildlife species (Malimbo et al., 2020). Such factors vary between the many different ethnic groups in the region (Cuni-Sanchez et al., 2019; Mbete et al., 2011; Ziegler et al., 2016). While cultural transitions and the increasing demand for

bushmeat in cities is likely eroding this source of variation (Chausson et al., 2019; Mbete et al., 2011), historical patterns in hunting could drive the observed wildlife distributions.

4.4. Methodological limitations

Fast transects provide a rapid means to map the distribution of wildlife activity at the population level through the signs they leave behind. This method enables collecting more data than distance transects without having the biases of reconnaissance surveys. Compared to distance transects, the larger amount data collected along fast transects allows for narrower confidence intervals on relative density estimates and an increased sensitivity to detect the effect of environmental covariates. The main limitation of fast transects is their inability to estimate absolute population size (Buckland et al., 2015). However, even distance transects based on standing crop nest counts often fail at providing reliable absolute density estimates as well due to their reliance on published nest decay rates from other geographical areas. A variation of the distance transect method requiring marking observed nests and revisiting transects regularly reduced this bias, but this requires a substantial data collection effort often incompatible with large geographical areas (Spehar et al., 2010).

Importantly, although our survey results are not yet directly comparable to other studies, they provide a critical baseline for future surveys using the same method in TNR.

4.5. Conclusion

The persistence of gorillas and chimpanzees in TNR affirms the importance of protection of community lands in the eastern Albertine Rift biodiversity hotspot. As TNR lies as the periphery of the range of Grauer's gorillas and eastern chimpanzees, further research into the behavioral ecology and genetics of these populations has the potential to extend our understanding of great ape diversity. By emphasizing local participation and rapid, unbiased data collection, our method is well-suited to long-term conservation in TNR and broadly applicable to variety of challenging environments.

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CRediT authorship contribution statement

Alice Michel: Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Jackson Kabuyaya Mbeke:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Benezeth Kambale Visando:** Data curation, Investigation, Project administration, Resources, Supervision, Writing – review & editing. **Sonya Kahlenberg:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **Katie Fawcett:** Funding acquisition, Project administration, Supervision, Writing – review & editing. **Damien Caillaud:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

All data and code will be made available through the A.P.E.S. database (Kühl et al., 2007).

Appendix A: Supplementary Materials

Separate Word document containing supplementary figures.

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