

ORIGINAL RESEARCH

A satellite perspective on the movement decisions of African elephants in relation to nomadic pastoralists

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Abstract

The African savannah ecosystem is populated by nomadic pastoralists who herd livestock in the day and corral them at night in temporary enclosures, called bomas, to protect them. The number and distribution of bomas on the savannah is important from an ecological perspective and may have a significant impact on wildlife movement. However, no study has yet examined this relationship. Here, using very high-resolution satellite imagery from two time periods, we quantified changes in boma distribution and density across an area of 3377 km² in the Laikipia-Samburu ecosystem of northern Kenya between 2011 and 2019. To assess wildlife movement in relation to bomas, we used a GPS data set on African bush elephant *Loxodonta africana* movement from 27 collared matriarchs representing herds of 9–15, covering 112 467 hourly GPS fixes over 31 months between 2018 and 2020. Our results showed a more than 46% increase in the total number of human-built structures between 2011 and 2019, the majority of which were bomas, representing a 21.9% increase in human-modified land area. Elephants readily adjusted their foraging habits and itineraries in this habitat shared with humans, who were also nomadic in space and time. Assessing the night–day activity ratio, we found elephants move more nocturnally when in closer proximity to bomas, particularly during the dry season. This temporal separation means elephants avoid the times humans are active in and around bomas while still accessing required resources—water and forage. The temporal shift was stronger during the dry season when shared resources are scarce. Using daily travel distance as a metric, we show elephants moved further in closer proximity to bomas which was likely linked to the need to travel between forage patches. Given the rise in human settlements, understanding the consequences of animals' behavioral adjustments is critical to understand the long-term population viability of elephant populations.

Introduction

The planet has entered the geological era of the Anthropocene with an estimated 50%–70% of the Earth's land surface now modified by human activity (Barnosky et al., 2011; Marchant & Lane, 2014). Increasing human presence is having a sizeable impact on animal movement

on a global scale (Doherty et al., 2021; Tucker et al., 2018). There is a need to understand these changes as movement impacts species' fitness and their ability to perform wider ecosystem functions. Advances in tracking technology are enabling large quantities of spatiotemporal data on animal movement to be collected at increasing levels of accuracy and precision (Fraser et al., 2018).

However, to understand how human activities impact wildlife movement, accurate representations of where human impacts occur on the landscape are required at equally fine spatial and temporal scales. Satellite imagery allows changes in anthropogenic activity to be observed and tracked over large geographic areas. This is particularly useful in the context of rural environments where wildlife and human population census data are often sparse or nonexistent. Freely available satellite imagery provided by government agencies is limited in terms of spatial resolution which makes it challenging to observe fine-scale features and semi-permanent structures. However, the increased availability of commercial satellite imagery at <1 m spatial resolution presents an opportunity to monitor human, livestock, and wildlife populations at finer scales (Duporge et al., 2021; Robinson et al., 2021). This is particularly applicable in large rural ecosystems, such as Africa, where there are limited resources for monitoring.

The African continent is composed of 65% savannah and harbors the highest density and greatest diversity of ungulate herbivores in the world (Hopcraft et al., 2014; Lorenzen et al., 2012). However, this fauna is currently undergoing a severe decline in the populations of mega-herbivores—in particular, African bush elephants *Loxodonta africana* (Du Toit & Cumming, 1999; Sitters & Olde Venterink, 2018). This reflects the broader sixth mass extinction event the planet is undergoing (Cafaro, 2015; Ceballos et al., 2017; McCallum, 2015; Pimm et al., 1995). This is the first human-driven extinction event, caused by the rising global human population. Africa displays the highest population growth rate of any continent (UNICEF, 2014) with an associated rise in the population of domestic livestock (FAO, 2019). Wildlife will continue to be heavily impacted. Currently, approximately 85% of habitable land for elephants is estimated to occur outside of protected areas (Wall et al., 2021) and elephant populations are threatened by numerous human activities including habitat fragmentation, illegal hunting for ivory, and retaliatory killing for crop-raiding (Goldenberg et al., 2017; Poulsen et al., 2017). To ensure long-term population viability for the species, there is a need to be able to quantify the extent of human expansion on the continent and understand how elephants and humans coexist in shared landscapes.

Over millennia, the African savannah ecosystem has been populated by nomadic pastoralists (Marshall et al., 2018), termed as such, as they relocate seasonally, moving with their livestock to fresh pasture when land no longer provides adequate grazing (Blench, 2001). Pastoralists guard livestock during the day as they forage and corral them at night in temporary enclosures that exclude nocturnal predators. In sub-Saharan Africa these

enclosures, often called bomas (or kraals in southern Africa), range from 30 to 100 m in diameter, protected by fences built largely from acacia thorn trees *Vachellia tortilis*, formerly *Acacia tortilis* and associated shrubs (Blackmore et al., 1990; Porensky et al., 2013; Western & Dunne, 1979). Bomas can be occupied for several months or years before being abandoned when the adjacent ground is no longer suitable for grazing or the dung buildup and parasite load becomes detrimental to livestock (Muchiru et al., 2008; Reid & Ellis, 1995). The establishment and abandonment of bomas redistribute organic matter by shifting soil and foliar nutrients due to the patterns of livestock grazing and dung deposition, thus altering plant community composition (Augustine, 2003; Muchiru et al., 2008; Muchiru et al., 2009; Veblen, 2013; Young et al., 1995) and maintaining the functional heterogeneity of the savannah ecosystem (van der Waal et al., 2011; Veblen, 2012; Veblen, 2013; Veblen & Young, 2010).

The nutrient hotspots created by bomas are attractive to both domestic and wild herbivores, including elephants (Huruba et al., 2021). Elephants are the largest herbivore in the savannah and are important ecological engineers (Lennox et al., 2016). They maintain open woodland by debarking and knocking down trees, opening the landscape for grasses that attract other grazers (Ihwagi et al., 2009; Marchant et al., 2018). Where elephants share foraging areas with livestock, they reverse at least some of the negative impact of livestock grazing on soil chemistry (i.e., depletion of carbon, nitrogen, and phosphorus [CNP]) as dung deposition—among other mechanisms—replenishes the depleted C and N in the soil (Sitters et al., 2020). Dung deposits from livestock and wild herbivores support distinctive, nutrient-rich plant communities that persist as long-term hotspots of highly fertilized soil in and around boma sites (Augustine, 2003; Blackmore et al., 1990; Stelfox et al., 1986; Yusuf et al., 2015). Studies using soil sampling and dung pile counts have shown that former boma sites contain elevated foliar nitrogen, phosphorus, and potassium indices compared with reference plots (Augustine, 2003; Muchiru et al., 2009; van der Waal et al., 2011; Veblen, 2013; Verdoodt et al., 2010).

The number and distribution of bomas in the savannah are ecologically significant; however, no ground-based or remotely sensed data set exists, which shows the number, size, or duration of use of these structures at a landscape scale. Previous studies have relied on a series of aerial photographs covering <50 bomas (Muchiru et al., 2008). The use of high-resolution satellite imagery now provides the observational capabilities to monitor these fine-scale structures at large scales. The Human Footprint Index (HFI) is an index of human pressure in the landscape (Venter et al., 2016a, 2016b) which is often used to assess wildlife movement in relation to the human presence (Creel

et al., 2020; Di Marco et al., 2018; Hill et al., 2019; Main et al., 2020; Monsarrat et al., 2019; Wall et al., 2021). Bomas are not factored into this index (HFI), despite being an important feature in much of sub-Saharan Africa. While many studies examining the rising number of pastoralists in the savannah have stressed the negative effects of livestock, attributing the degradation of arid and semi-arid lands to overuse by pastoralists (Boles et al., 2019; Charney et al., 1975; Schlesinger et al., 1990), understanding long-term ecological impacts requires nuance and evidence. Without data on the density and distribution of bomas, the long-term changes taking place cannot be sufficiently studied at a landscape scale.

For elephants, boma sites represent an example of human modification in savannah landscapes and are a place of potential interaction with humans. Understanding how the presence of bomas impacts elephant movement and behavior is therefore critical to understanding how elephants respond to pastoralist presence in the landscape. When and where elephants move can impact the likelihood of encounters with humans and their livelihoods (Graham et al., 2009) with direct relevance to human–wildlife coexistence and the conservation of elephant populations. Elephant movement strategies, similar to other species, are influenced by survival risk and availability of forage, mates, water, predation risk, and competition for resources (Hopcraft et al., 2014; Polansky et al., 2013). Similar to other African ungulates, elephants exhibit antipredator behavior in response to humans (Yamashita et al., 2018). In areas where there has been heavy poaching, elephants increase their walking speed (Ihwagi et al., 2019), move more at night, and have lower tortuosity (increased path straightness) (Ihwagi et al., 2018; Ihwagi et al., 2019). Elephants can distinguish between ethnic groups recognizing which humans cause a threat and which do not and if not perceived as a threat, certain humans are not actively avoided (McComb et al., 2014). Shifts in wildlife movement in response to human presence are context- and taxon-specific, driven by the cost–benefit of sharing space and resources (Lennox et al., 2016). The mechanisms driving the movement of elephants in a landscape dominated by nomadic pastoralists remain poorly understood. To better understand this relationship, we analyze changes in pastoralist presence in relation to elephant movement using a large set of high-resolution satellite images and a rich GPS elephant-tracking data set. Three hypotheses are tested:

1. We hypothesize that there will be a significant increase in land occupied by human settlements between 2011 and 2019, in line with global human population growth trends. This hypothesis will be tested by quantifying the number and distribution of bomas over

3377 km² of land in the Laikipia-Samburu ecosystem using high-resolution satellite images.

2. We hypothesize that elephants will alter their daily movement patterns in response to boma presence to move more at night when the chance of encountering humans is lower. This will be assessed by modeling the night–day activity ratio of elephants in relation to the presence of bomas.
3. We hypothesize that elephants will travel further when in areas of high human settlement due to increased fragmentation of habitat patches. This will be assessed using the daily travel distance of elephants.

Materials and Methods

Study area

This analysis focuses on a pilot study area in the Laikipia-Samburu ecosystem delineated by the availability of two sets of four concurrently collected WorldView-2 satellite image swaths. The imagery covers 3377 km² clipped to an area where cloud cover was less than 10% in both 2011 and 2019 (Fig. 1). The Laikipia-Samburu ecosystem is adjacent to the Rift Valley in north-central Kenya; it is a semi-arid system encompassing a wide range of habitats characterized by more mesic highlands in the south to hot, dry lowlands in the north (Wall et al., 20). The landscape is a mixture of national parks, commercial ranches, and areas supporting pastoral and/or sedentary subsistence production (Ihwagi et al., 2015).

Digitizing bomas from satellite imagery and change detection

The analysis relies on two sets of four adjacent WorldView-2 image swaths from the wet season acquired in 2011 (6th April and 9th May) and 2019 (11th May and 7th June). The spatial resolution of pansharpened WorldView-2 natural color composite image (RGB: 532) varies between 48 and 54 cm per pixel, and images were captured in the early morning between 08:03 and 08:17 local time. We digitized the dimensions of the human footprint (predominantly bomas) and water points in the imagery using ArcGIS Pro over a period of 8 months. We used visibility and intactness of the fence line to differentiate between active and inactive bomas (Fig. 2). We labeled all bomas that had a partial fence line that was visible but had largely decomposed as inactive. Other categories included permanent buildings and fenced agricultural areas that often included bomas.

To understand changes in the number of bomas and distribution of other human-built structures between 2011 and 2019, we implemented a change detection

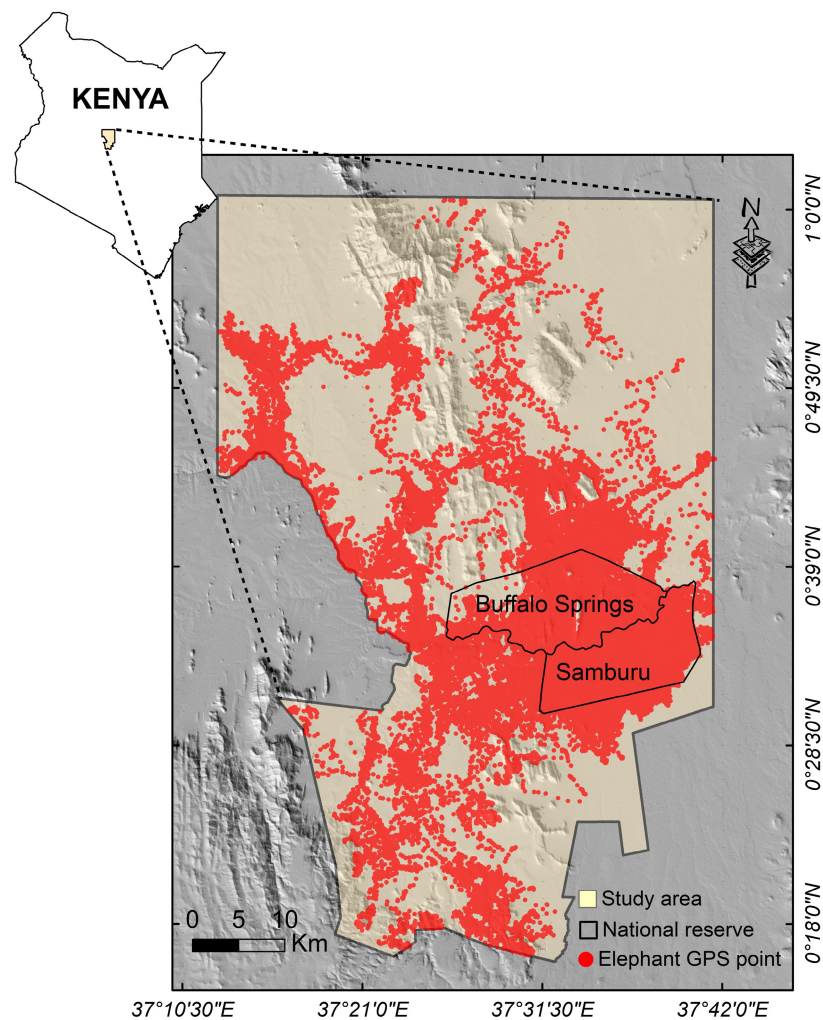


Figure 1. Study area in the Laikipia-Samburu ecosystem of northern Kenya and the spatial distribution of elephant GPS tracking data (red dots, $n = 4708$ days) representing 27 collared adult female elephants collected between 2018 and 2020. The location of two national reserves (Samburu and Buffalo Springs) in the study area are also highlighted.

analysis to compare the number and distribution of bomas. We gridded the study area using a grid size of 0.25 km^2 ($500 \times 500 \text{ m}$) and calculated the density of bomas (defined as the number of bomas and other human-built structures per grid cell) and the area covered by bomas for each year.

GPS tracking data and calculation of movement metrics of elephants

The wild elephant population in the Laikipia-Samburu ecosystem lives close to human settlements primarily on communal and private land; <2% of the ecosystem is government-protected national parks (Ihwagi et al., 2015). It is the second-largest elephant population

in Kenya (approx. 8500 elephants) and is continuous and freely intermixing, with several distinct but overlapping subpopulations (Douglas-Hamilton et al., 2005). Elephants have a matriarchal herd structure, with GPS fixes from collared adult females representing approximate locations of 9–15 individuals (Ihwagi et al., 2009). We analyzed tracking data from 27 collared female elephants within the study area between January 2018 and July 2020 (31 months), covering 1 year prior to and after the 2019 image acquisition. We did not include single bull elephants in the analysis because they disperse from the herd at maturity and have different resource requirements and movement strategies from herds. We removed GPS fixes representing biologically implausible movements using a speed filter of 9 km/h, consistent with previous

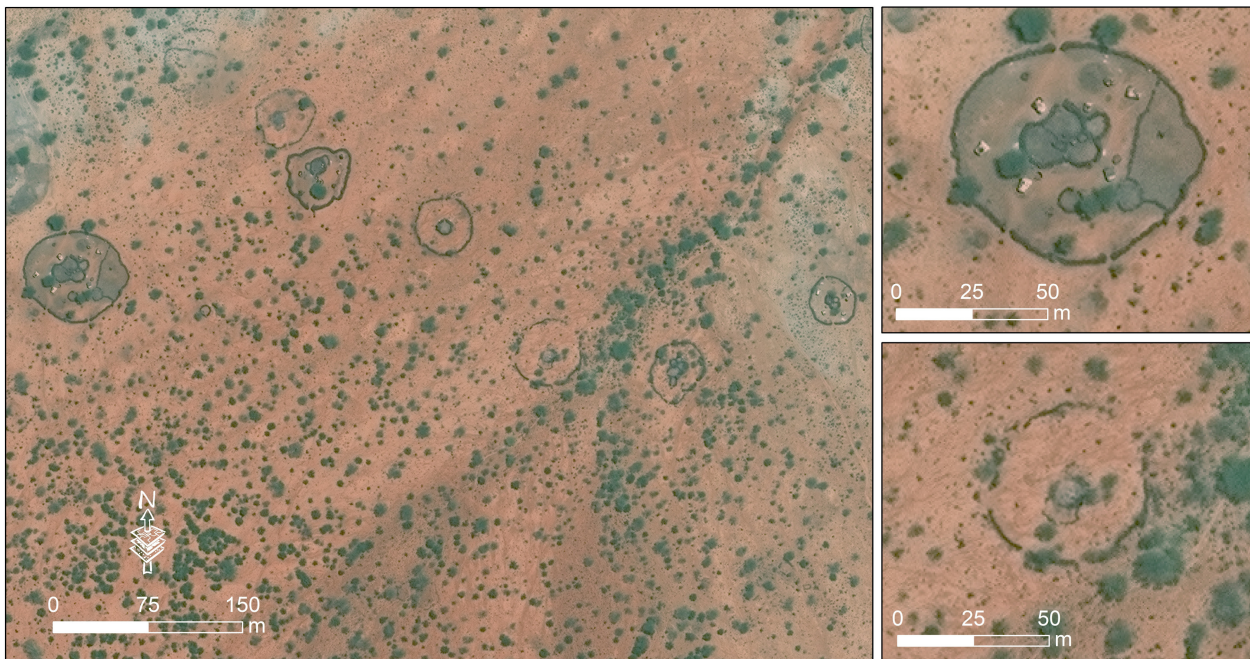


Figure 2. Example of bomas visible in pansharpened WorldView-2 natural color composite imagery. On the left, combination of active and inactive bomas; on the right, example of active boma (top image) and inactive boma (bottom image). Satellite image (c) 2020 Maxar Technologies.

approaches (Bastille-Rousseau et al., 2019; Bastille-Rousseau & Wittemyer, 2019; Wall et al., 2013).

To describe the movements of elephants in response to the presence of bomas on the landscape, we calculated two metrics: the daily travel distance and the night–day activity ratio (see below). We considered the spatial extent and resolution of data in the study area, and the biological process of interest—negotiating human-modified landscapes—to select the timescales for the movement metrics. Daily movements within the home range are reflective of short-term space and resource requirements and provide an important indicator of how animals use the environment (Carbone et al., 2005). The two metrics capture complementary aspects of elephant space use while daily travel distance maps closely to energetic budgets, and the night–day activity ratio describes temporal activity patterns. Both have strong theoretical links to accommodate human presence on the landscape.

As there is minimal variation in sunlight hours across the year at this equatorial site, we defined night and day as equal duration lasting 12 h, starting at 18:00 and 06:00 h, respectively. We defined travel distance as the sum of straight-line displacements (SLD) between sequential fixes over the course of 24 h (beginning at 06:00 h) for daily travel distance or each 12-h period in the case of the night–day activity ratio. We calculated the night–day activity ratio as the total night travel distance/total day travel distance, making this equivalent to the metric

average speed used in previous studies (Ihwagi et al., 2018). SLD represents the minimum distance required to explain the observed displacement between points and is sensitive to the sampling schedule. Therefore, we resampled periods of higher frequency data (15- and 30-min fix rates) to the most common fix rate of hourly and excluded days missing more than two fixes. Although SLD is likely to underestimate true travel distance (Isbell et al., 1999; Noonan et al., 2019), a consistent fix rate and the exclusion of days with missing locations ensure comparability between collared matriarchs to allow examination of population-level variation. We only included days where all GPS fixes fell within the study area, generating a final sample size of 4708 elephant-days from 27 GPS-collared adult females.

Environmental variables

To describe the presence of bomas across the landscape in relation to elephant movement, we used the digitized boma layer described above to calculate the distance to the nearest human-built structure for each location in the data set. In addition to proximity to bomas, we considered several important spatial covariates that influence elephant movement. These include variables that represent ecological productivity, habitat types, distribution and availability of surface water, elevation, and land surface temperature. We used land cover (Team,

C.L.C.L., 2019) and Normalized Difference Vegetation Index (NDVI) layers generated from European Space Agency Sentinel-2 satellite data, both at the 20-m resolution, to represent habitat type and ecological productivity. The NDVI layer is from 2019 and the land cover data are from 2016 based on 1 year of Sentinel-2A observations from December 2015 to December 2016 (Team, C.L.C.L., 2019). For elevation, we included a 30 m Digital Elevation Model (DEM) from the shuttle radar topography mission (SRTM) (Shuttle Radar Topography Mission, N.A.a.S., 2019). We digitized rivers and seasonal water points from the pansharpened WorldView-2 imagery (48–54 cm resolution) to describe the distribution of water across the landscape. We used precipitation data (mm/day) from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) 0.05° spatial resolution (van der Waal et al., 2011) to describe surface water availability in the 30 days preceding each fix and calculated the average daily 2 m air temperature using ERA5-Land hourly data at 0.1° resolution (Hersbach et al., 2020). To summarize variables at the daily level for use in the movement models, we extracted the values for covariates under each locational fix and averaged these across each 24-h period. For a full summary of layers, processing steps, and how we generated model variables, see Appendix S2.

Statistical analysis

To assess the relationships between bomas and elephant movement, we implemented two linear mixed effect models—one for each of our movement metrics—using the *nlme* package (Bates et al., 2015) in R version 4.0.2 (Team, R.C., R, 2018). As the data set includes multiple observations per individual, we modeled elephant ID as a random intercept to account for baseline differences in the average response. As the data are both spatially explicit and temporally structured, we tested for both spatial and temporal autocorrelation in the model residuals and accounted for this by specifying appropriate correlated residual error structures (for more detail, see Appendix S3). We performed this process prior to model selection to avoid misinterpretation of the statistical support for model parameters.

We modeled our two response variables—daily travel distance and night–day activity ratio—as a function of the spatial covariates described in Appendix S2: season (based on the availability of water from rainfall), daily averages for distance to the nearest boma (km), elevation (m), productivity (represented by NDVI), distance to nearest water (km), daily temperature (K), and proportion of daily points in wooded savannah and forest. We excluded the proportion of points in open savannah as it

was highly correlated with the proportion in wooded savannah (correlation coefficient -0.87 , see Fig. S1 in Appendix S2). We included an interaction term between the distance to boma and season, to allow for potential variation in elephant response to humans because of surface water availability in different seasons. As these variables fall on very different scales, we centered and standardized our continuous inputs by subtracting the mean and dividing by one standard deviation to facilitate more interpretable regression coefficients (Schielzeth, 2010). We assessed formal support for the inclusion of predictors using likelihood ratio tests, comparing the maximal model with nested models via single term deletions. We inspected models for evidence of collinearity using the performance package (Lüdtke et al., 2021) and checked model residuals visually to identify any major violations of model assumptions.

Results

Changes in the distribution and density of boma and other human-built structures

There was an increase in the number of human-built structures and the area of land occupied by humans in the savannah. Bomas were the most numerous structures in the landscape (Table 1) and have increased at a faster rate than other structures. The ratio of bomas to permanent buildings increased by nearly 10% from 3.2:1 to 3.5:1, whereas the ratio of area coverage of bomas to buildings increased by 16.6%, from 8.1:1 to 9.4:1. Other human-built structures included permanent buildings and fenced agricultural areas (which often contain bomas). There was a more than 46% increase in the total number of human-built structures between 2011 and 2019, the

Table 1. Number and total area of the boma and human-built structures over the study area in 2011 and 2019.

Designation	Structures 2011	Structures 2019	Area km ² 2011	Area km ² 2019
Active bomas	4521	7359	12.74	18.72
Inactive bomas	5473	7678	12.5	15.71
Total number of bomas	9994	15 037	25.11	34.01
Permanent building	3054	4202	3.1	3.6
Fenced agricultural area	940	1194	33.82	42.94
Total number of structures	13 988	20 433	62.03	75.56

Table 2. Changes in the number of active and inactive bomas between 2011 and 2019 and the number not visible in 2011 but present in 2019.

2011	2019	Number
Active bomas	Still active	1430
	Inactive	856
	No longer visible	2235
Inactive bomas	Still inactive	889
	Active	598
	No longer visible	3986
Not visible in 2011	Active	5331
	Inactive	5933

majority of which were bomas. The average size of bomas increased from 36 m in diameter in 2011 to 50 m in 2019. The area of land covered by structures increased by 13.53 km² representing a 21.8% increase in human-modified land, covering approximately an additional 0.8% of the landscape (Table 2, Fig. 3).

Between 2011 and 2019, the distribution of bomas was very different in the landscape. Few bomas remained active over the entire 8-year period. Of the 4521 active bomas in 2011, less than a third were classed as active in 2019. Although they could have been reoccupied and abandoned in the intervening years, very few active bomas in 2011 have bomas reestablished in an overlapping area

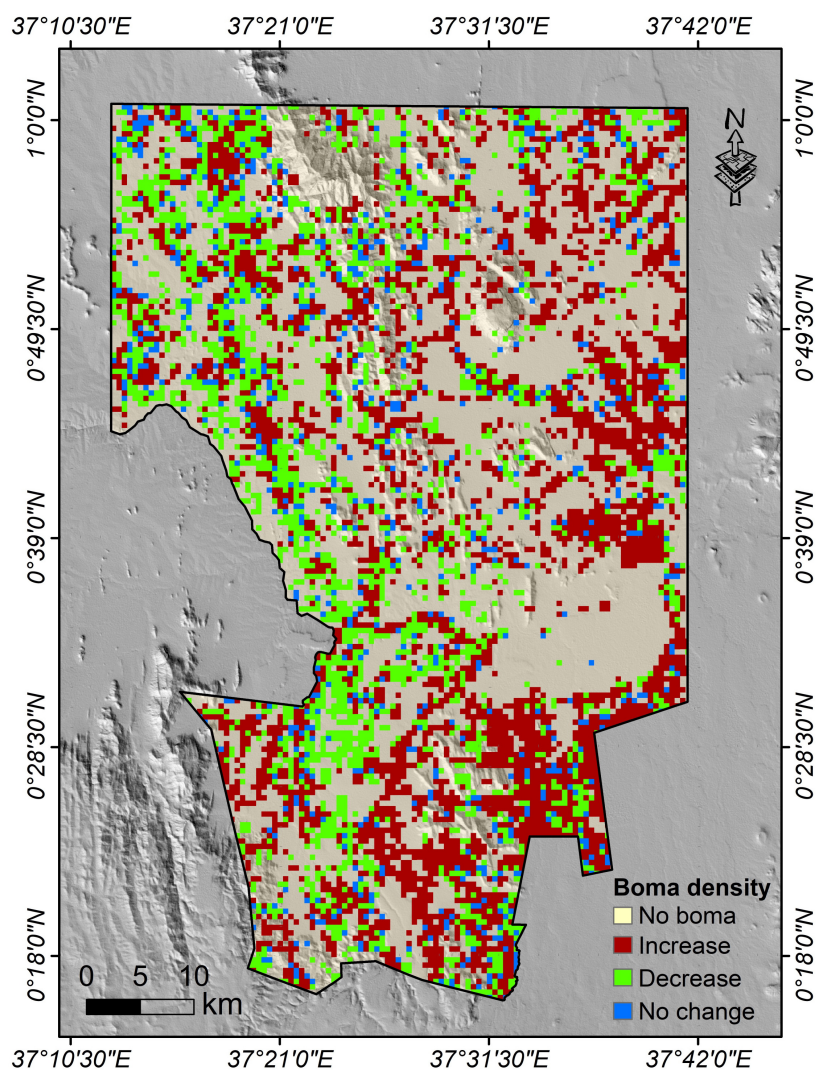


Figure 3. Map showing changes in the density of bomas and other human-built structures (the majority of which are bomas) between 2011 and 2019. Grid size is 0.25 km² (500 × 500 m).

in 2019 (598). The rate of disappearance of remotely sensed recently active bomas was high, only 24% of bomas labeled in the 2011 images were visible in 2019. Although the number of bomas reestablished on former sites in this 8-year period was small, the proximity of inactive to active bomas in 2019 was high, that is, new bomas are built near former boma sites.

Relationship between elephant movement and distance to bomas

We found statistical support (at the $p < 0.05$ level) from likelihood ratio tests (LRT) for the inclusion of elevation, average productivity, temperature, and interaction between season and distance to boma in the night–day activity ratio model (Table S2, Appendix S4). Elevation, average productivity, and temperature had a positive effect on the night–day activity ratio, that is, elephants were predicted to, on average, be more nocturnal with increasing values (Table 3). Female-led herds become more nocturnal on days when in closer proximity to bomas (χ^2 (Barnosky et al., 2011) = 29.677, $p = < 0.0001$; LRT statistic for the main effect of distance to boma in the absence of interaction term), with this effect being more pronounced in the dry season (Fig. 4A).

The rainy season (vs. dry) had a negative effect on predicted night–day activity ratio values (Table 3), that is, animals were more nocturnal in the dry season, however, this main effect was not significant at the $p < 0.05$ level (χ^2 (Barnosky et al., 2011) = 2.354, $p = 0.125$; LRT statistic for the main effect of the season in the absence of interaction term).

For the daily travel distance model, we found statistical support for the inclusion of season, elevation, average productivity, the proportion of time elephants spend in forest, and distance to boma (LRT statistics all $p < 0.05$;

Table S2, Appendix S4). Elephants moved further in the rainy season (vs. dry), and when they spent a greater proportion of time in the forest, increasing elevation and average productivity have a negative effect on the travel distance (Table 3). Elephants moved further in closer proximity to bomas, and there was no evidence that this effect varied between seasons (LRT statistic for interaction term was > 0.05 ; Table S2, Appendix S4). After standardizing input variables, there was no evidence for substantial multicollinearity in either of our final models, with all terms producing variance inflation factor (VIF) values < 2 . Point estimates and confidence intervals from the linear mixed effect models are given in Table 3, with plots for each covariate and support for the inclusion of terms from likelihood ratio tests presented in Appendix S4.

Discussion

This is the first methodological proof-of-concept to demonstrate the application of using satellite remote sensing to monitor pastoralist movement at a landscape scale. The density, distribution, and relocation of the bomas were tracked using satellite images from two periods. We found that there was a 46% increase in human-built structures, covering an additional 13.53 km² of the landscape and representing a 21.9% increase in human-modified land. These results clearly confirm our hypothesis that there will be a significant increase in land occupied by human settlements between 2011 and 2019. It reflects the global trend of an expanding human footprint and the associated rise in livestock numbers (Gilbert et al., 2018).

Quantification of active versus inactive bomas between 2011 and 2019 revealed that few bomas remained in the same location over an 8-year period. The dynamic movement of bomas means positive influences from moderate grazing on plant productivity and plant diversity are

Table 3. Output for fixed effects portion of linear mixed effect models.

Predictors	Daily travel distance		Night–day activity ratio	
	Estimates	CI (low, high)	Estimates	CI (low, high)
(Intercept) ¹	10.2414	9.2032, 11.2795	1.0437	0.9497, 1.1376
Season (rainy)	1.0058	0.7714, 1.2357	−0.0487	−0.1005, 0.0032
Elevation	−1.3745	−1.6342, −1.1147	0.0981	0.0361, 0.1601
Habitat productivity	−0.6473	−0.7952, −0.4994	0.0516	0.0211, 0.0822
Distance to nearest boma	−0.6498	−0.8220, −0.4775	−0.1411	−0.1852, −0.0971
Proportion in forest	0.1266	0.0160, 0.2372	–	–
Daily temperature	–	–	0.1031	0.0784, 0.1279
Distance to nearest boma: season (rainy)	–	–	0.0697	0.0201, 0.1193

Estimates are given to 4 d.p. and represent standardized coefficients with a unit change of one standard deviation on the original scale as a result of the centering and standardization of input variables.

¹Reference category for season is dry.

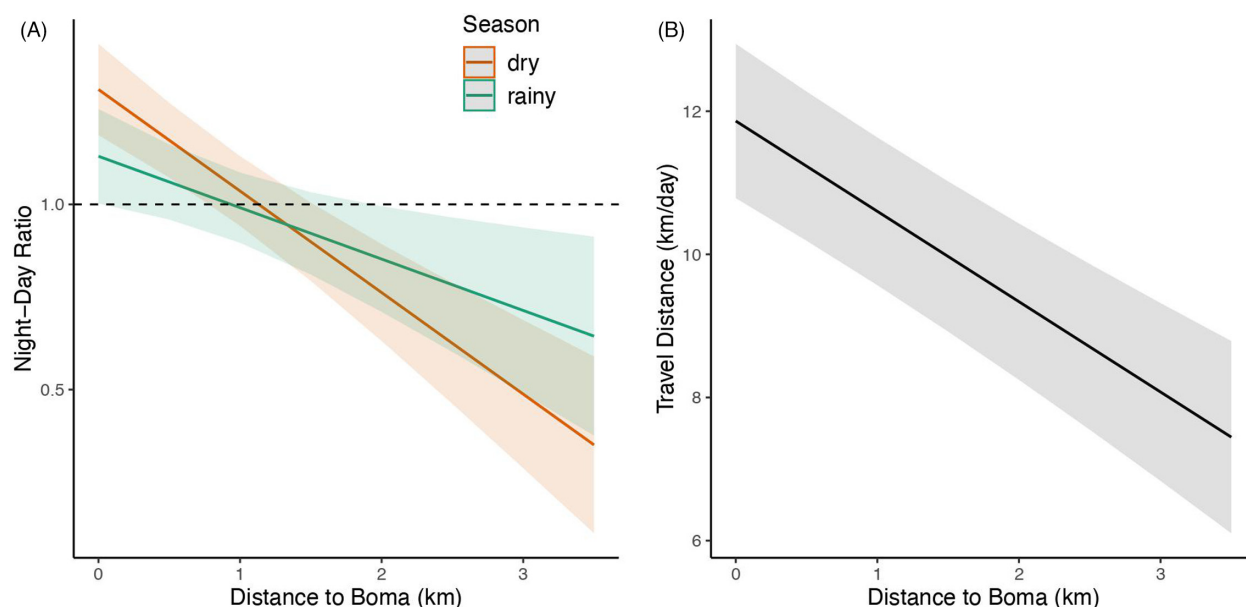


Figure 4. Predicted values from two linear mixed effect models describing female elephant movement metrics as a function of their average daily distance to bomas in the study area. (A) The ratio of nocturnal to diurnal travel distance, with increasing values representing greater distance traveled at night compared with the day; (B) the total daily travel distance. The lines and associated 95% confidence intervals were generated using the ggeffects package and represent predicted values for the response across the range of observed values for distance to boma holding the nonfocal variables constant, that is, marginal effects.

spread across the landscape (David et al., 2011). The last decade is characterized by high climate variability, reduced and erratic rainfall, and unpredictable availability of water and forage resources for pastoralists and livestock. Frequent movement can help to buffer livelihoods against these effects and mitigate the impact of increased environmental insecurity.

Most bomas digitized in 2011 were no longer visible in 2019. In contrast to permanent man-made structures, bomas are only temporarily visible, discernible by the intact or decomposing fence line which leaves a short-term footprint on the landscape. Although the ecological impacts from abandoned bomas are long term, it takes time for glades (i.e., treeless areas of improved soil texture and increased nutrient levels in former boma locations) to become visible. The previous study from aerial photographs shows that succession is slow and resettlement of sites occurs only after 20–25 years (Muchiru et al., 2009). Less than a third of the bomas visible in 2011 were visible in 2019 and in the timescale of this study, few bomas were reestablished in an overlapping area, although many are in close proximity. Pastoralists are becoming more numerous, and they shift bomas short distances to avoid manure pileup and buildup of parasite load which can lead to fungal infection in hooves.

One limitation of this study is the reliability of differentiating between active and inactive bomas. From ground

impressions, it is possible to see inactive bomas of varying ages, that is, circles of shortgrass, but these cannot be reliably identified, and it is not clear how long-ago abandonment occurred, so the focus of the study is on active and recently abandoned bomas—identified by the decomposition of the fence line (Fig. 2). The rate of visible disappearance is influenced by image quality and rainfall in the intervening years between image capture. Without significant ground-truthing, the number of bomas inaccurately identified as active or inactive is unclear, but the large sample size (15 037 bomas in 2019) enables us to be confident in the observed trend. The imagery is of sufficient resolution that there is no risk that other features have been mistakenly labeled as bomas.

In the African savannah, the dominant human-built infrastructure is often temporary structures (i.e., bomas) rather than permanent buildings, as shown in this study. Thus, the use of the Human Footprint Index (HFI) in these landscapes is limited, as small structures such as bomas are not captured in the index. The HFI is from 2009 and combines eight variables derived from remote sensing and ground survey data (including population density, electric infrastructure, built environment, cropland, pastureland, roads, railways, and navigable waterways) to provide an index of human pressure in the landscape (Venter et al., 2016a, 2016b). However, anthropogenic changes occur at smaller spatial scales, not

captured in this index, and the human population has significantly increased in many landscapes since 2009. High spatial resolution satellite imagery (<2 m) can be used to create finer scale data layers on human impact including small temporary structures, but this imagery is only available from commercial providers. Access to this imagery is currently limited by high cost and narrow spatial coverage of the Earth's surface compared with freely available imagery from state-run space programs (e.g., Landsat from NASA and the Sentinels from the European Space Agency). However, as costs fall and new constellations come online (e.g., WorldView Legion & Airbus Pleiades Neo) increased spatial and temporal satellite image resolution will be available to enable finer scale analysis. The boma layers included in this study are available for other researchers to utilize. Expanding to all of Kenya or other countries is possible if the acquisition of imagery and digitization is undertaken. This effort would enable large-scale studies to track human development and detailed analysis of wildlife movement in relation to land cover change. It should be possible in the future to automate the detection of bomas using machine learning if a large training data set is developed.

The expanding human footprint shown in this ecosystem is reflective of the broader global situation and is likely to have increased impacts in the future on wildlife movement dynamics. In this study, we demonstrate that fine-scale human structures, such as bomas, play a substantial role in elephant daily movement patterns, particularly their temporal dynamics, where the distance to boma produced the largest standardized effect size for the elephant night-day activity ratio of any of our covariates (Table 3). Animals adjust their movement patterns in various ways to account for increased human settlement, and both spatial and temporal separation is often found to occur, possibly reflecting a risk-avoidance strategy (Ihwagi et al., 2019; Oriol-Cotterill et al., 2015; Yamashita et al., 2018). We test two hypotheses about how we expected elephants to respond to the pastoralist community in this landscape.

The first hypothesis concerns temporal movement. We hypothesized that elephants would move more at night when the risk of encountering humans is lower. Previous studies have found that elephants exhibit increased nocturnal movement after increases in poaching (Ihwagi et al., 2018). We assumed that in areas of high human activity, represented by increased number and distribution of bomas, we would find the same temporal shift as a risk-avoidance strategy. Increased nocturnal activity around bomas can be interpreted as a strategy that enables coexistence in a landscape where pastoralists and elephants rely on the same resources—forage and water. This time-sharing strategy may be optimal to ensure

long-term access to required resources. A previous study shows a similar dynamic between livestock and wild elephants in the same ecosystem where water points are accessed at different times of the day (Raizman et al., 2013). We found the temporal response to bomas was stronger in the dry season (as indicated by support for an interaction term between season and distance to boma). During the dry season, there is higher competition for water thus during this time elephants increase nocturnal movement that decreasing the risk of conflict with pastoralists.

Our second hypothesis was that we would see a shift in the total travel distance elephants exhibited in response to increasing the presence of boma sites on the landscape. We found that this phenomenon does indeed occur and unlike the shift in temporal movement, the response of elephant daily travel distance as a function of distance to the nearest human structure was consistent between the seasons (as indicated by higher support for a model without an interaction term between season and distance to boma). The increased daily travel distance when closer to bomas may be due to habitat fragmentation as elephants are required to travel greater distances to move between suitable forage patches and areas of refuge away from human presence. This result is interesting as it contradicts previous results based on the HFI where movement distances for numerous species, including elephants, were reduced due to increased human presence in the landscape (Tucker et al., 2018; Wall et al., 2021). The HFI index is often used to assess wildlife movement in relation to the human presence (Creel et al., 2020; Di Marco et al., 2018; Hill et al., 2019; Main et al., 2020; Monsarrat et al., 2019; Wall et al., 2021) but it has a resolution of 1 km and is over a decade old. Many wild animals decide on foraging excursions at a smaller spatial scale than 1 km. The difference in our findings highlights the importance of examining how animals respond to different kinds of human modification on the landscape at finer spatial scales.

Results from our other spatial covariates indicate that elephants travel significantly shorter distances in areas where there is higher average biomass productivity (Appendix S4, Fig. S2C), suggesting that at a daily scale distance traveled is responsive to forage quality. Elephants and other large mammals in semi-arid environments exhibit thermoregulatory behavior linked to temperature and water availability (Fuller et al., 2014). Elephants increased their nocturnal movement in response to higher average temperature (Appendix S1, Fig. S3) presumably to minimize heat load as it is cooler during the night. They also moved, on average, shorter daily distances at higher elevations (Appendix S4, Fig. S2B) indicating energetic and thermal constraints. Elephants are highly water-

dependent for hydration and evaporative cooling, and water access is a key limiting factor for elephants in this system (Bastille-Rousseau et al., 2019). When water availability is low, there is reduced potential for evaporative cooling, and we would expect elephants to switch to a more nocturnal movement which they do to a greater degree during the dry season (Appendix S4, Fig. S3). Elephants in this ecosystem moved greater daily distances during the rainy season (Appendix S4, Fig. S2A), supporting the fact that elephants are less restricted to permanent water during the rainy season (Bastille-Rousseau et al., 2019) allowing greater daily travel distances.

Both the spatial and temporal hypotheses regarding movement were shown to be accurate in this ecosystem. The metrics show a clear response to the presence of bomas on the landscape, particularly temporally where elephants became nearly three times more nocturnal in the closest proximities to bomas. The fixed effects portion of the daily travel distance model explained more of the overall variance than the night–day activity ratio model, indicating that there are other important variables that influence elephant temporal activity. There was strong support for consistent baseline differences between individual elephants in the daily travel distance model (see Appendix S4), while the variance components showed little support for consistent individual differences for the night–day activity ratio—consistent with previous findings (Ihwagi et al., 2018). A better understanding of the factors influencing shifting temporal activity is an area of study that would benefit from further research. Our results show substantial changes in both the extent of human modification of the landscape over time and clear support that such modification affects elephant movement and behavior. As human settlement continues to grow, this could have impact on elephant fitness via foraging opportunities and energetic budgets that are closely linked to survival.

Conclusion

This study shows the human footprint in our study site has increased and elephants readily adjust their habits and itineraries in habitats shared with humans who are also nomadic in space and time. This paper is the first proof-of-concept that satellite remote sensing can be used to monitor pastoralists and elephants, showing how livestock and wildlife are coexisting. It also offers fine-scale insight into the movement strategies of elephants in a shared habitat. As the human population continues to expand, more bomas will be established. As conservation agencies work to conserve the elephant population in such landscapes, a better understanding of how elephants adjust movement to shifting human occupation can help in long-term planning.

The improved temporal and spatial resolution of satellites combined with better geolocation accuracy, coverage, and falling costs of GPS tracking devices will enable more precise observation of human–wildlife movement in rural landscapes as demonstrated in this study.

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Authors' Contributions

I.D. conceived the idea of the paper and designed the methodology with oversight from T.W. & D.W.M.; I.D. acquired, processed, and analysed the satellite data. F.I. & J.W. digitised the bomas in the image data; G.F. designed and implemented the analysis of the movement data. S.L. and E.T. contributed comments on the manuscript. I.D. led the writing of the manuscript and G.F. contributed significantly to the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The authors have no conflict of interest.

Data Availability Statement

Given the sensitive nature of the location of elephants due to ongoing illegal killing, GPS data cannot be made public. Further information and requests for information and data related to the analysis should be directed to the corresponding author: Isla Duporge (Isla.duporge@zoo.ox.ac.uk)

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Additional information on tracking data.

Appendix S2. Spatial covariates included in movement model.

Appendix S3. Testing and accounting for spatial and temporal autocorrelation in the models.

Appendix S4. Linear-mixed effects model selection and output.