Forest Elephant Movements and Habitat Use in a Tropical Forest-Savanna Mosaic in Gabon

by

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Executive Summary

Poaching of forest elephants for their ivory has decimated their populations in Central Africa, with a decline of over 62% since 2002. The densely forested country of Gabon in the Congo Basin provides critical habitat for approximately half of the world's remaining forest elephants. With forest elephants under intense poaching pressure in most of their range, there is a need for information on their habitat use, movements, and ecology to understand how they modify their environment and to maximize the effectiveness of conservation efforts.

Movement ecology can provide insights into forest elephant resource requirements and temporal, seasonal, or spatial patterns regarding when or where an animal is at greatest risk. In 2015, the Gabon Parks Agency (ANPN) in collaboration with Duke University initiated a forest elephant monitoring program using global positioning system (GPS) collars to 1) investigate the spatial distribution and environmental drivers of elephant movements and 2) inform proactive law enforcement strategies by predicting where elephants will be found.

The Wonga Wongué Presidential Reserve (WW), on the western coast of Gabon, consists of a forest-savanna matrix, providing an opportunity to evaluate how elephants use different habitat types. In 2015 and 2016, the Gabon Parks Agency collared 17 forest elephants in the reserve. Here I used the location data from these elephants to ask:

1. Do forest elephant movements and home ranges differ temporally, seasonally, or by elephant sex?
2. Do forest elephants differentially use forest and savanna habitats?
3. What environmental variables (ecological and anthropogenic) most strongly determine habiat use by elephants?

I characterized elephant movements and measured home ranges, employing three different methods of quantifying and visualizing home range areas. I assembled environmental variables of interest (e.g. land cover type, vegetation, and Euclidean distance to streams, villages, and secondary roads) at each elephant location, and analyzed ecological patterns of habitat use across elephant sex, season, and time of day. I developed a prediction surface for the likelihood of elephant occupancy by modelling elephant habitat use during the dry and wet seasons using mixed effects logistic regression.

Forest elephants travelled up to 3000 km annually and exhibited average home range areas of 713 km^2, with males having significantly larger home ranges than females. Both female

and male elephants remained largely in and around the central savanna of WW, with a few males travelling outside the park borders and travelling up to 110 km to return to the central savanna. Forest elephants demonstrated both temporal and seasonal movement patterns. Temporally, they moved between forest and savanna at dawn and dusk, spending more time in forests during the day when temperatures are highest and entering the savanna as the sun goes down. During the short wet season when grass recruits, forest elephants spent proportionally more time in the savanna. Elephants also travelled at greater speeds during the short wet season when, in addition to greater grass availability, the abundance and diversity of fruiting tree species is greatest, suggesting that availability of fruit influences movements.

The most significant determinant of elephant movements was vegetation; elephants use areas with higher vegetation density, which afford cover and browse. When villages were nearby, elephants tended to spend time nearer to them, perhaps for access to agricultural crops. During the wet season, elephant presence was more likely at greater distances from perennial water sources, indicating decreased water limitation during this season.

The interaction between forest elephants and the large central savanna highlights the important role of the savanna for food provision and social gatherings. Park management should continue to manage the savannas of WW to maintain openness and grass regeneration. Unlike other sites, the interior of WW is well protected, and ecological factors including food and water availability more strongly affect elephant movements than anthropogenic features such as roads and villages. Even so, there is a high likelihood of human-elephant conflict along the border of the reserve where villages are located. To conserve elephants, stakeholder engagement and law enforcement should focus on these areas of potential conflict. Future GPS-tracking efforts should focus on the park boundaries and multiple-use areas between protected areas to assess the anthropogenic impacts on forest elephant movements and the capacity of the protected area network in Gabon to protect and maintain forest elephant populations.

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Table of Contents

Introduction

Poaching of forest elephants, *Loxondonta africana cyclotis*, for ivory is decimating their populations (Blake et al. 2009). Between 2002 and 2011, forest elephant populations in Central Africa decreased by approximately 62% and lost 30% of their geographical range due to poaching fueled by an increased global demand for ivory (Maisels et al. 2013; Wasser et al. 2015). The densely forested country of Gabon is one of the last strongholds of forest elephants, housing about half of the world's surviving forest elephants (IUCN, 2013; Maisels et al. 2013). But poaching is also taking a toll on Gabon's forest elephant populations – nearly 25,000 elephants, or 80% of the population, was lost from the Minkébé National Park, Gabon (Poulsen et al. 2017).

With forest elephants under intense poaching pressure in most places, there is a need for information on their habitat use, movements, and ecology to maximize the effectiveness of conservation and protection efforts. Movement ecology can provide insights into species' resource requirements, including food, water, and space, and elucidate temporal, seasonal, or spatial patterns regarding when or where an animal is at greatest risk. Animal movement studies using global positioning systems (GPS) technology have informed and facilitated conservation efforts for a variety of terrestrial species (Hebblewhite & Haydon, 2010). GPS telemetry has been employed to identify critical habitat for endangered species (Environment Canada, 2009; Sawyer et al. 2006), and understand resource-driven migrations of ungulates, such as gazelles (Leimgruber et al. 2001) and wildebeest (Boone et al. 2006). Tracking of animals can also elucidate behavioral changes in human-dominated landscapes disturbed by urban development, extractive land use, and recreation, with implications for managing these activities (Dyer et al. 2001; Sawyer et al. 2006; Hebblewhite & Merrill, 2008). Movement data from wide-ranging animals, such as wolves and elephants, have provided the empirical basis for identifying and securing movement corridors, particularly between large, protected wilderness areas (Chester, 2006; Graham et al. 2009; Roever et al. 2013).

Most current knowledge of the movement ecology of elephants comes from studies of savanna elephants, *Loxidonta africana africana,* in Southern (Cook et al. 2015; Loarie et al. 2009; Vanak et al. 2010; Chammaille-Jammes et al. 2013) and Eastern Africa (Douglas-Hamilton et al. 2005; Roever et al. 2013; Ngene et al. 2010). Vegetation (tree cover and food resources) and water limitation during the dry seasons are the main drivers of savanna elephant movements (Cook et al. 2015; Loarie et al. 2009; Chammaille-Jammes et al. 2013; Roever et al. 2013; Ngene et al. 2010). Savanna elephants are most active at night when temperatures decrease (Loarie et al. 2009), and they avoid high human density areas (Roever et al. 2013). In areas of low human density, elephants tend to avoid settlements during the daytime, with males more likely to approach villages than females (Cook et al. 2015).

By contrast, studies of forest elephant movement are rare because of the difficulty of collaring elephants in dense forests, and until recently, the challenge of reliably transmitting GPS signals through the canopy. Only four studies to date have used GPS collars to monitor forest elephant movements: a preliminary study successfully tracked one female elephant (Blake et al. 2001) and two additional studies derived descriptive metrics of home ranges and activity patterns (Kolowski et al. 2010, Schuttler et al 2012). The largest study, examining data from 28 GPS-collared forest elephants in the Congo Basin, is the only study to model determinants of elephant movements, finding that unprotected roads acted as major barriers to forest elephants (Blake et al. 2008). These limited studies demonstrate that elephant movements are constrained by human disturbance, except in the rare areas where elephants are safe from poaching (Kolowski et al. 2010), and that home ranges vary greatly across both protected and human-use zones. Much remains to be learned regarding the relative effects of ecological and anthropogenic drivers of forest elephant movements and how they change across seasons, sites, or levels of protection.

Here, I examine forest elephant movements and habitat use in the Wonga Wongué Presidential Reserve (WW), on the western coast of Gabon. The reserve consists of a forest-savanna matrix, providing an opportunity to evaluate how elephants use different habitat types. In 2015 and 2016, the Gabon Parks Agency (ANPN) collared 17 forest elephants in WW to monitor their movements in relation to environmental and anthropogenic variables. Based on previous studies of savanna and forest elephants, I use hourly GPS locations to quantify the movements and home ranges of forest elephants and to test the following hypotheses:

1. Compared to females, male forest elephants will travel greater distances and have larger home ranges, with relatively high overlap with other forest elephants;
2. Forest elephants will spend more time in forest than savanna during the dry season and daytime to avoid exposure to sunlight, high temperatures, and poaching;
3. Forest elephants will avoid roads and villages because of poaching threats, with females demonstrating greater avoidance than males;

4. During the dry season when water is limiting, forest elephants will tend to stay relatively close to permanent water sources, particularly streams and lakes.

I also map the spatial distribution and model the drivers of forest elephant movements to provide specific management recommendations for the conservation of forest elephants in WW and throughout Gabon.

Methods

Elephant Data

In October 2015, ANPN fitted 12 forest elephants with GPS collars in Wonga Wongué Presidential Reserve (WW), and collared five additional elephants in April 2016 (Table S1). Dr. Pete Morkel led the collaring efforts, accompanied by ANPN field teams. The team collared seven female and ten male elephants (Table S1). The GPS collars transmit location data at an approximately hourly rate. In this study, I use the location data for the 17 elephants from November 4, 2015 to March 4, 2017, consisting of 158,755 GPS locations. Approximately 90% of total potential hourly GPS pings were successfully transmitted.

Study Area

The WW is located on the western coast of Gabon, and has a land area of approximately 425,000 ha (Figure 1). Habitats within the reserve vary from white sand beaches and mangrove wetlands on the Atlantic coast to a mosaic of open savannas and secondary tropical forest. WW contains large areas of savanna that cover 15% of the park, and the central savanna (64,000 ha) creates a tropical forest-savanna mosaic habitat for forest elephants. The iron-rich laterite tropical soils in the reserve are composed of red and white clay and sand, with sand varying with proximity to the coast (Thibault et al. 2004). The reserve is generally flat with low elevation except for the presence of cirques, amphitheater-like valleys formed by erosion in the central savanna (Figure 1). Human population density inside WW is low at 0.2 people km^{-2}, but additional villages are located within 10 km of the southwest and southeast peripheries of the reserve (Figure 1). Elephants are free-roaming in this area and the reserve is well protected – no elephants are known to have been poached within WW since 2014 (pers. comm. David Fine).

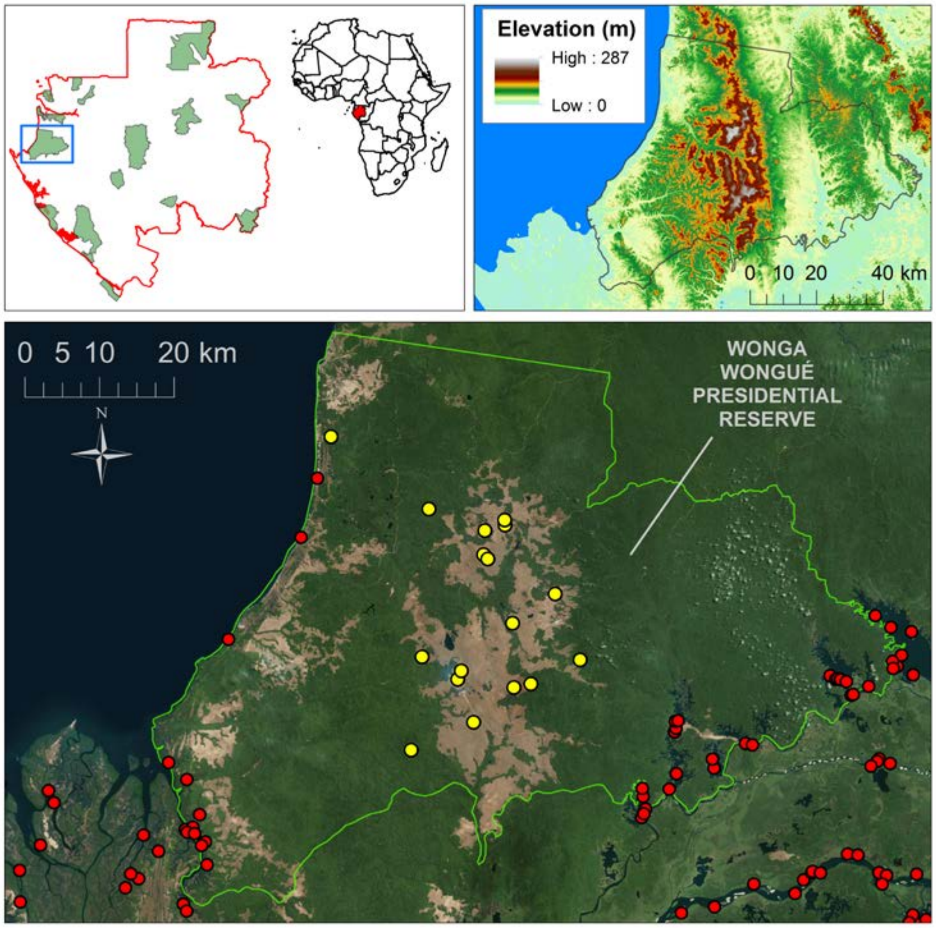

Figure 1. The location of collaring sites (yellow symbols) for 17 forest elephants in Wonga Wongué Presidential Reserve. Satellite imagery demonstrates land cover types with green indicating forest, brown indicating savanna, and small white dots indicating clouds. Human presence is low in the reserve (villages denoted in red symbols), and elevation (inset) is low except for the raised central savanna.

Land Cover Classification

To create a land cover map and examine landscape characteristics such as vegetation and wetness, I obtained Landsat 8 OLI/TIRS at the L1-T processing level from USGS Earth Explorer. The Landsat 8 satellite carries the Operation Land Imager (OLI) sensor, which includes standard Landsat bands plus three new bands: deep blue for coastal/aerosol, shortwave infrared for cirrus cloud detection, and a quality assessment band (Landsat 8, 2016). The satellite is also equipped with the Thermal Infrared Sensor (TIRS), which has two thermal bands, and the temporal resolution of Landsat 8 is full coverage every 16 days (Landsat 8, 2016). I used a total of four images: one pair of images from June 28, 2015 during the long dry season (overlapping with the time of ground truth data collection), and a second pair of images from March 10, 2016 during the long wet season (Table S2). Two tiles were sufficient to cover the study area, each with a swath width of 185 km. Bands of interest (Bands 1-7) had spatial resolution of 30 m (Table S3). At the L1-T level, all tiles were radiometrically, geometrically, and terrain-corrected.

All remote sensing analyses were performed in ENVI version 5.3 (Exelis Visual Information Solutions; Boulder, Colorado), unless otherwise specified. I calibrated the digital numbers of the original image files to top-of-atmosphere reflectance, and then conducted atmospheric corrections on all tiles for Bands 1-4 via a dark object subtraction method, as recommended by Song et al. (2001). I chose the subtracted value for each band based on histograms and the first threshold value that summed to at least 100 pixels, which in this case was the same as the band minimum.

To ground truth the remote sensing data, I collected habitat and vegetation data in WW from May-July 2016, characterizing 220 sites on attributes including land cover type, canopy cover, understory density, tree height, and the most abundant tree species (Figure S1, Table S4). Sampling of groundtruth points was stratified across elephant sex, geographical area, and general land cover (e.g., savanna vs. beach, vs. forest). The distribution of ground truth points was somewhat limited because I focused on areas with the most recent locations of collared forest elephants.

I created a thematic land cover map for the study area using the pair of images taken during the dry season, since this temporally matched the ground-truthed data. To do so, I masked out background pixels and created a spatial subset to: 1) overlap elephant locations of interest, 2) minimize cloud cover, and 3) exclude the urban area of Port-Gentil. I performed a supervised classification to distinguish land cover categories, using regions of interest (ROIs) that I created from the collected ground truth points as a training sample. The four main cover types of interest were Forest, Savanna, Water, and Sand/Chalk/Other. I excluded ground truth points in swamps and mangroves because collared elephants rarely ventured into these land cover types and they were not easily distinguishable from forest. For the water class and the Sand/Chalk/Other class, which had the fewest ground truth points, I manually created ROIs for validation using the imagery and knowledge of the study area. For the savanna class, there were large gaps in classification due to spectral differences in burned vs. unburned savannas, so I manually created additional training ROIs for savanna (see Table S5 for final set of ROIs).

I examined ROI separability before performing land classification to ensure that ROIs captured unique spectral characteristics and to minimize overlap between classes. I used Jeffries-Matusita separability, a unitless measure ranging from 0 to 2, to evaluate separation of ROI pairs. The training ROIs all had Jeffries-Matusita pair separation of at least 1.93 for the Northern tile (lowest was between Sand/Chalk/Other and Savanna) and separation of at least 1.99 for the Southern tile (lowest was between Sand/Chalk/Other and Water). I performed a supervised classification on each of the dry season tiles separately using maximum likelihood, which generally provides high accuracy for normally distributed data, incorporates multiple variables, and takes into account within-class variability (Richards, 1999). Maximum likelihood classification has been successfully used to produce thematic land cover maps in multiple recent environmental contexts, including in Ethiopia, Tanzania, and Cameroon (Wondie et al. 2016; Wichama et al. 2015, Westra et al. 2010). I used multiple value thresholds to reflect the scarcity of the sand/chalk category and to minimize unclassified pixels: 0.0001 for Sand/Other, 0.001 for Water, Savanna, and Forest. I then used the post-classification processing steps of sieving (pixel connectivity 8, minimum size 4) to remove isolated pixels and clumping (3 x 3 arrays) to group adjacent similarly classified areas of pixels. I combined the two classifications together to produce the final thematic land cover map in ArcMap version 10.4.1 (ESRI, ArcGIS Desktop). I performed an accuracy assessment on the final classification using randomly generated ground truth points and Google Earth to evaluate the performance of the supervised classification technique, excluding Unclassified and Sand/ Chalk/ Other pixels because they were rare across the landscape and I was most interested in correctly classifying forest vs. savanna types.

For all tiles, I created spectral enhancement bands for enhanced vegetation index (EVI), using coefficients adopted in the MODIS-EVI algorithm (Landsat 8, 2016), and Tasseled Cap Transformation (TCT) bands for Brightness, Greenness, and Wetness, using coefficients derived by Baig et al. (2014). In addition to the final thematic land cover map, I generated these rasters for later use as habitat covariates in habitat modeling (See *Drivers of Elephant Movements* methods).

Elephant Movements and Home Ranges

To characterize elephant movements, I mapped and analyzed elephant track distances—total and between consecutive points—across elephant sex, time of day, and season. I used

Mann-Whitney nonparametric tests to evaluate whether elephant sex, time of day, or season significantly affected elephant movement rates, movement distances, and distances to water, secondary roads, and villages. To examine the spatial extent of individual forest elephant movements across time and visualize high-use habitat areas, I generated home range polygons (see below) and used Mann-Whitney nonparametric test to analyze differences across sex and season.

I used three different methods to estimate and visualize home ranges: the minimum convex polygon (MCP), kernel utilization (KUD), and time local convex hull (TLCH) methods (Roever et al. 2013; Wall et al. 2013). Each of the home range methods prioritizes specific aspects of habitat use by forest elephants. For the MCP method, a minimum bounding polygon is drawn around a predetermined proportion of the elephant locations after outliers are removed, usually 95% of the points to estimate 95% home ranges (Burt, 1943). The MCP method is widely used, but tends to overestimate home range area by including areas containing little to no points. By contrast, the KUD method provides a more fitted distribution to location data by placing a bivariate kernel function over each location. A smoothing parameter, *h*, controls the width of these utilization distributions and thus, the area in consideration around each point. Here, I used the reference bandwidth for *h*, which is calculated for each individual based on number of points and standard deviations of x and y coordinates, (see Calenge, 2006 for equations). The final kernel density surface is the sum of all point density functions across the movement extent. For area calculations, I used isopleths representing a 95% likelihood of point occurrence (Worton, 1989). I used both the *adehabitat* package in R version 3.3.1 (R Core Team, 2016) and the minimum bounding geometry and kernel density tools in ArcMap to calculate MCP and KUD home ranges respectively, using a variety of outlier removal methods. The TLCH method calculates the ‘distance’ between points as time-scaled distance. The parameter, *s*, accounts for the time aspect of location data, and was set to 24 hours to investigate daily movement patterns. I calculated a set number of nearest neighbors for all points using the *a* or adaptive method, an alternative to the traditional *k* method, which simply adds neighbors until a set number *k* is reached. While the *k* method may include far-away neighbors in areas with sparse location points, the *a* method sums cumulative distances from the parent point and stops adding nearest neighbors when a cumulative distance *a* is reached. Therefore, many neighbors are generated in dense areas and few neighbors are generated in sparse, outlying areas. Next, I constructed minimum convex polygons, or hulls, around each point's set of nearest neighbors. I examined revisitation rate and duration of visit in the hulls and plotted these to generate the legend for the time density maps, which enable visualization of core home range areas but do not provide area calculations. TLCHM home range visualizations were generated using the *tlocoh* package in R (Lyons et al. 2016).

Elephant Habitat Use

To examine patterns of forest elephant habitat use, I assembled environmental variables of interest (land cover type and Euclidean distance (km) to streams, villages, and roads), as well as temporal variables (time of day and season) at each elephant location point. I used the final thematic land cover map produced above to extract the land cover type at each point. Time of day was split into four equal categories, using breaks at the approximate sunrise and sunset times of 06:00 and 18:00, respectively: 0:00-5:59, 6:00-11:59, 12:00-17:59, and 18:00-23:59. I defined seasons using precipitation data from the Tropical Rainfall Measuring Mission (TRMM) from November 2015 to November 2016, with dry seasons characterized by < 60mm total rainfall as defined by the Koppen climate classification. The long dry season (May 7 – Oct. 2) had no single rain event > 10 mm, and the short dry season (Dec. 7 – Jan. 13) had no single rain event > 20 mm, and the remaining two periods were designated as the long (Jan. 14 – May 6) or short (Oct. 3 – Dec. 6) wet seasons based on their duration (Figure 2). I used one-way ANOVA with Bonferroni *post-hoc* pairwise comparisons to analyze differences in land cover types at elephant locations across seasons and times of day.

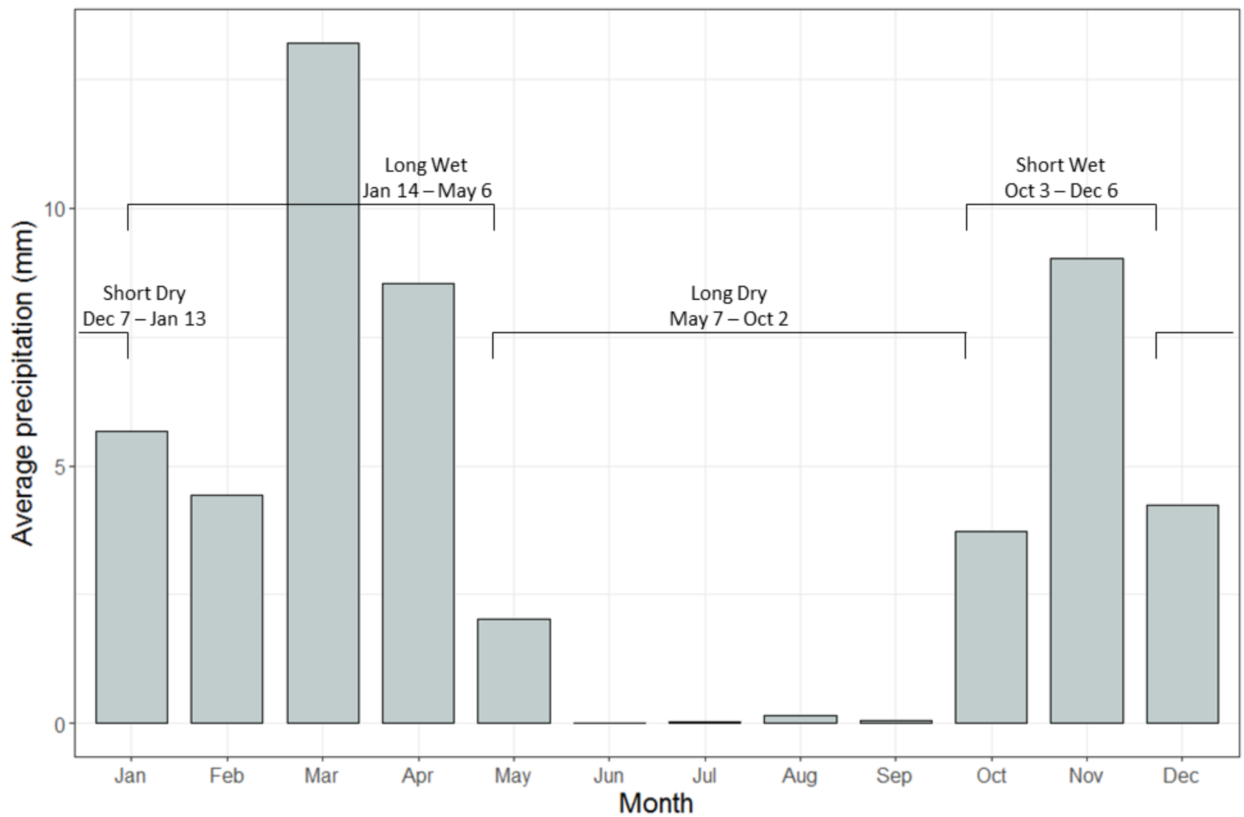

Figure 2. Average precipitation in mm by month. From these data, I defined the following seasons: short wet season: Oct. 3 – Dec. 6, short dry season (Dec. 7 – Jan. 13), long wet season (Jan. 14 – May 6), and long dry season (May 7 – Oct. 2). Note that depicting rainfall by month fails to show the daily variation in precipitation that actually determines the seasons.

Drivers of Elephant Movements

To determine the main drivers of forest elephant movements in WW, I developed a habitat model using a generalized linear mixed model with a presence/pseudoabsence design (Manly et al. 2002). Presence points were actual locations of elephants and pseudoabsence points were randomly selected points within the MCP home range of each elephant. I generated pseudoabsence points as a representative sample of available habitat within individual home ranges that was not used by elephants. Pseudoabsence points could fall within the same pixel (900 m^2), but a 50 m buffer was maintained around presence points to prevent contamination of presence and pseudoabsence points. I thinned presence and pseudoabsence points to one point per day to minimize temporal interdependence of consecutive points (Thomas & Taylor, 2006) and then generated habitat models for wet and dry seasons separately to account for seasonal differences in resources such as grass, fruiting trees, and precipitation.

The seasonal models incorporated raster data for environmental variables of interest (see *Land Cover Classification*, Table S6). I generated distance and slope rasters using ArcMap and original spatial data provided by ANPN. I also created a focal forest raster as an additional measure of openness, which represented the proportion of pixels within a 90 m circular neighborhood with land cover classification of forest.

I used mixed-effects logistic regression to model elephant presence for dry and wet seasons, with environmental variables treated as fixed effects and elephant identity treated as a random effect to account for lack of independence of points and unequal sample sizes among individuals (Roever et al. 2013). I standardized the distance to village, distance to stream, distance to road, and slope rasters as z-scores to better match the scales of spectral enhancement bands. To avoid multicollinearity, I evaluated correlations between all variables, removing one of the variables from any highly correlated pair ($r > 0.7$). I used a backwards stepwise approach from the full model and Akaike information criteria (AIC) for model selection (Boyce et al. 2002; Manly et al. 2002; Roever et al. 2013). For each seasonal model, I used k-fold cross validation with a testing ratio of 20% to evaluate model performance (Boyce et al. 2002). I used the *lme4* package in R for fitting of generalized linear mixed models (GLMMs) (Bates et al. 2015). I used the final seasonal models and a geographic information system (GIS) to create continuous prediction surfaces representing the likelihood of elephant habitat use across the study area during dry and wet seasons. For mapping purposes, only fixed effects of the models were included.

Results

Land Cover Classification

The land cover map accurately classified the three most common land cover categories with a 98.4% accuracy and a Kappa of 0.977 (Table S7; Figure 3). Forest and savanna were easily distinguishable, but mangroves and swamps were difficult to distinguish from forest given the small number of ground truth points and their relatively restricted representation across the landscape. Mangroves and swamps were likely captured within the “Other” category: for example, the southwest estuaries most likely represent seasonally inundated wetlands, but were classified as Sand/Chalk/Other.

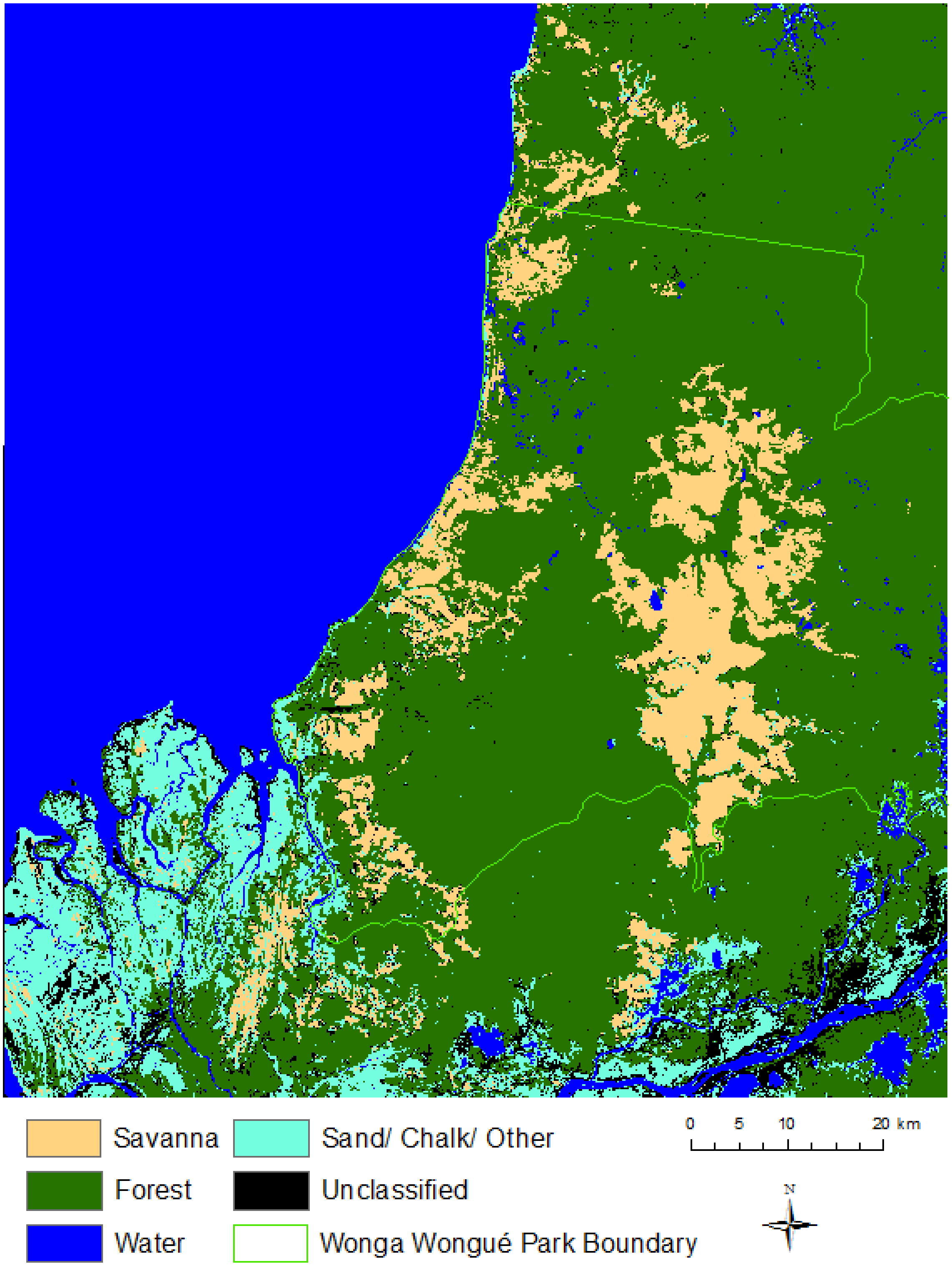

Figure 3. Thematic land cover map for the study area.

Elephant Movements and Home Ranges

From November 4, 2015 to March 4, 2017, the 17 GPS-collared elephants in WW traveled on average 3,444 km (Figure 4, Table 1). The 12 elephants with at least one full year of location data travelled on average 2,840 km annually. There was not a significant difference in total distance moved by males (mean = 3,498 km, median = 3,793 km) and females (mean = 3,367 km, median = 3,198 km; Mann-Whitney: $W = 34.0$, $p = 0.962$), or the average distance traveled per day ($W = 32.0$, $p = 0.813$), or average distance traveled per hour ($W = 32.0$, $p = 0.813$) (Table S8).

Elephants tended to move greater distances between consecutive hourly GPS locations near dawn, 6:00-8:00, and dusk, 17:00-20:00 (Figure S2, Table S9). Hourly distances moved were longest in the short wet season (October-November: mean = 448 m, range = 0-7.3 km; Figure S3, Table S10). Elephants had the second longest hourly movements during the short dry season of December-January (mean = 429 m, range: 0-8.0 km), followed by the long wet season of February-April (mean = 350 m, range = 0-16.8 km), and the long dry season (mean = 313 m, range = 0-8.1 km).

Forest elephants moved significantly greater average distances per day during the wet seasons (mean = 8.5 km, median = 8.5 km) than during the dry seasons (mean = 7.7 km, median = 7.5 km; Mann-Whitney: $W = 81.0$, $p = 0.029$). Similarly, elephants moved significantly greater average distances per hour during the wet seasons (mean = 354 m, median =354 m) than during the dry seasons (mean = 319 m, median =314 m; $W = 81.0$, $p = 0.029$). There were no significant differences in total distance travelled between the wet seasons (mean = 1,864 km, median = 2,208 km) and the dry seasons (mean = 1,625 km, median = 1,635 km; $W = 99.0$, $p = 0.122$; Table S11).

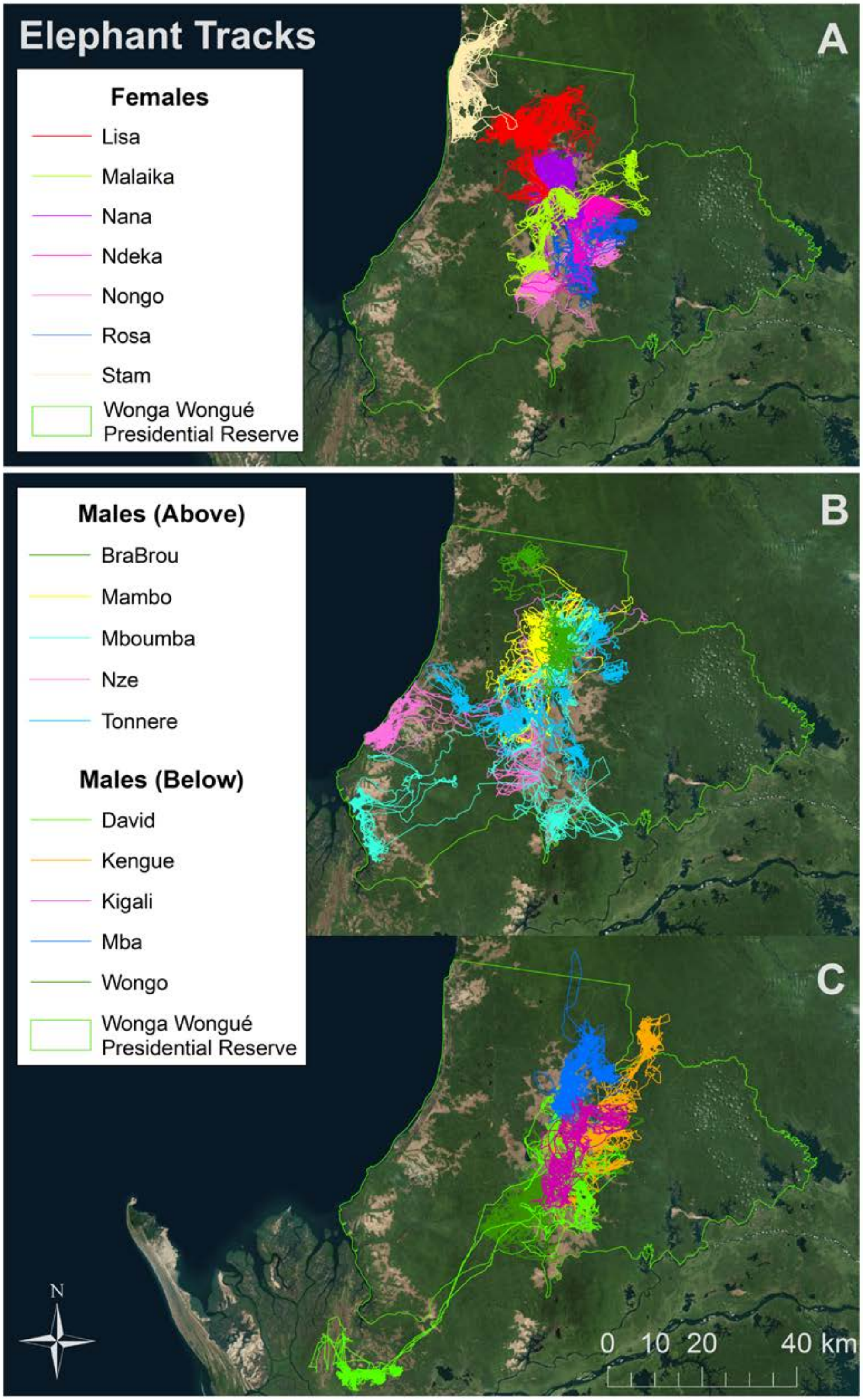

Figure 4. Map of movement tracks for 17 Wonga Wongué elephants (Female N=7, Male N=10), with tracks of (A) female elephants and (B-C) male elephants.

Table 1. Comparisons of total track distance, MCP and KUD home ranges for each elephant.

			Area of home range (km^2)		
Elephant Name	**Sex**	**Total distance traveled (km)**	**100% MCP**	**95% MCP**	**95% KUD**
Nana	F	4,393	239	174	155
Rosa	F	2,883	260	220	192
Ndeka	F	3,198	286	122	105
Stam	F	4,295	314	177	172
Nongo	F	2,754	397	348	217
Lisa	F	3,828	447	308	254
Malaika	F	2,219	534	430	388
Kigali	M	2,430	306	263	247
BraBrou	M	2,189	395	372	245
Mba	M	4,535	427	229	147
Kengue	M	4,128	615	506	512
Mambo	M	3,812	723	533	374
Wongo	M	4,020	731	492	388
Tonnerre	M	2,504	1,030	932	788
Nze	M	3,750	1,425	819	700
David	M	3,773	1,745	1,467	1,229
Mboumba	M	3,843	2,253	2,047	1,913
Female Mean		**3,367**	**354**	**254**	**212**
Male Mean		**3,498**	**965**	**766**	**654**
Mean		**3,444**	**713**	**555**	**472**

Male elephants had significantly larger home ranges than female elephants, regardless of the method used to model home ranges (full MCP: Mann-Whitney: $W = 9.0$, $p = 0.009$; 95% MCP: $W = 7.0$, $p = 0.005$; 95% KUD: $W = 11.5$, $p = 0.025$). Average home ranges of males ranged from 965 km^2 (median = 727 km^2) for full MCP, to 766 km^2 (median = 520 km^2) for 95% MCP, to 654 km^2 (median = 450 km^2) for KUD (Figures 5-6). Average home ranges of females ranged from 354 km^2 (median = 314 km^2) for full MCP, to 254 km^2 (median = 220 km^2) for 95% MCP, to 212 km^2 (median = 192 km^2) for KUD (Figures 5-6). Comparing across methods, full MCPs estimated the greatest home range areas as they use all location points, followed by 95% MCPs due to outlier removal, and finally KUD ranges, as they more closely fit the spatial data (Table 1). See Supplemental Materials for results of different outlier removal methods for MCP (Table S12) and different probabilities of utilization for KUD (Table S13) home ranges.

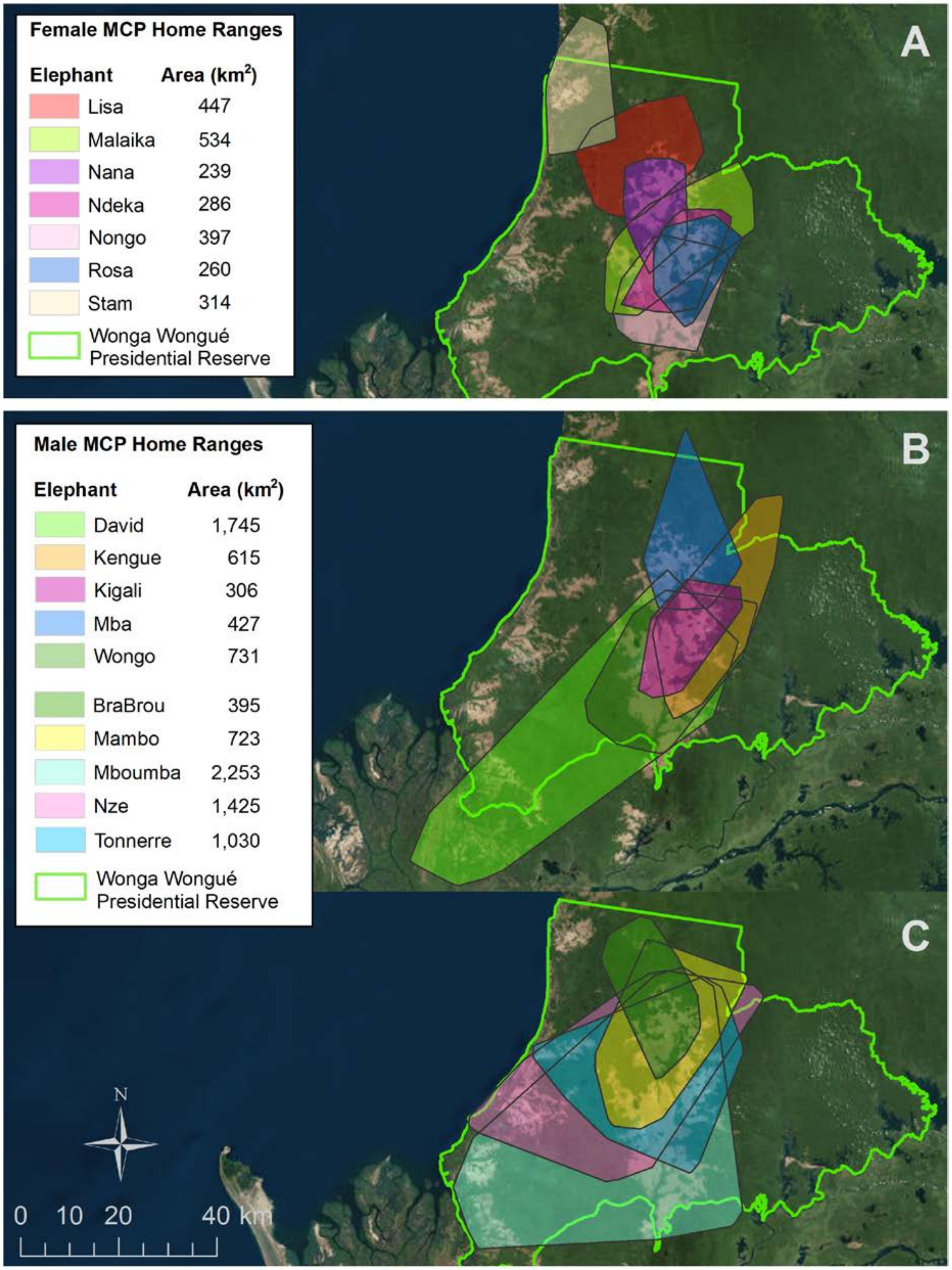

Figure 5. Minimum convex polygon home ranges for forest elephants in WW using all GPS points from Nov. 4, 2015 to March 4, 2017, with home ranges of (A) female elephants and (B-C) male elephants.

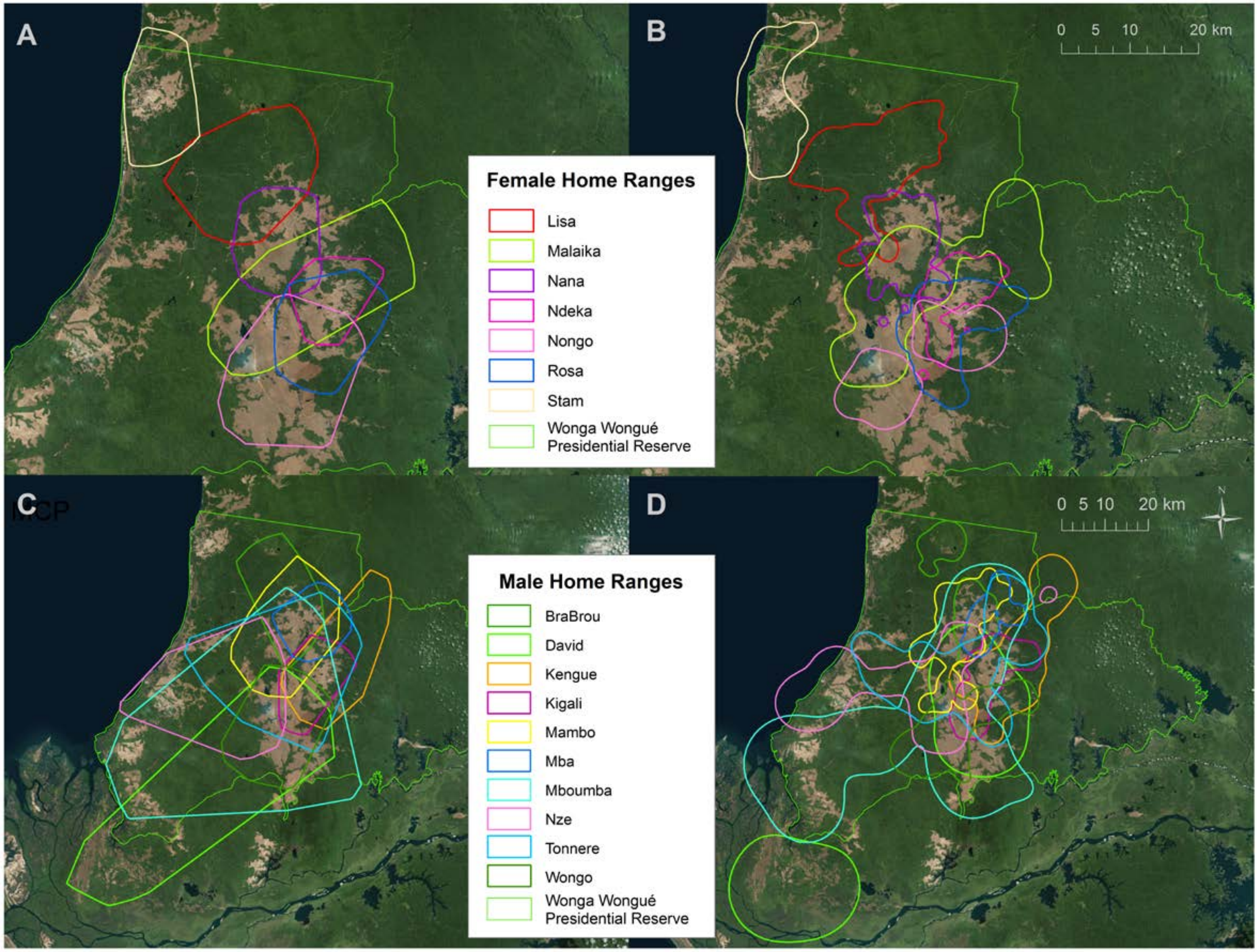

Figure 6. 95% MCP and 95% KUD home ranges for forest elephants in WW, including (A) MCP home ranges for females, (B) KUD home ranges for females, (C) MCP home ranges for males, and (D) KUD home ranges for males.

Male elephants (mean = 712 km^2, median = 542 km^2) covered significantly greater MCP home range areas than females (mean = 261 km^2; median = 205 km^2) during the dry season (Mann-Whitney: $W = 14.0$, $p = 0.043$), but not the wet season (males: mean = 734 km^2; median = 529 km^2; females: mean = 259 km^2; median = 259 km^2; $W = 18.0$, $p = 0.109$). There was no significant difference in MCP areas of all elephants between dry and wet seasons ($W = 157.0$, $p = 0.683$) (Table S14).

Female elephants tended to have less overlap in home ranges with other females compared to male elephant, whose home ranges overlapped with both males and females. On average, 67% of female elephants' home ranges overlapped with other females, whereas 86% of female elephants' home ranges overlapped with males. On average, 89% of male elephants' home ranges overlapped with other collared males.

Elephants exhibited core areas within home range areas where they spent more time, possibly due to greater resource availability, social interactions, or individual preferences. To visualize core home ranges, I present kernel density rasters and time density graphs for one female elephant, Ndeka, and one male elephant, Mboumba (Figures 7-10). Ndeka's core habitat area was in the northernmost region of her home range (Figure 7). She displayed highest resource use in the areas of forest surrounding the exposed chalk landmark of Petit Bam Bam (Figure 8). Mboumba's core habitat areas consisted of a primary cluster of two areas in the southwest of his home range, as well as a few smaller areas in the central and southeast areas of his home range (Figure 9). He displayed highest resource use in the southwest cluster of core areas, in the forested region between the estuary and the southwest savanna (Figure 10). See Supplemental Materials for kernel density surfaces and time density graphs for remaining elephants (Figures S4-S18).

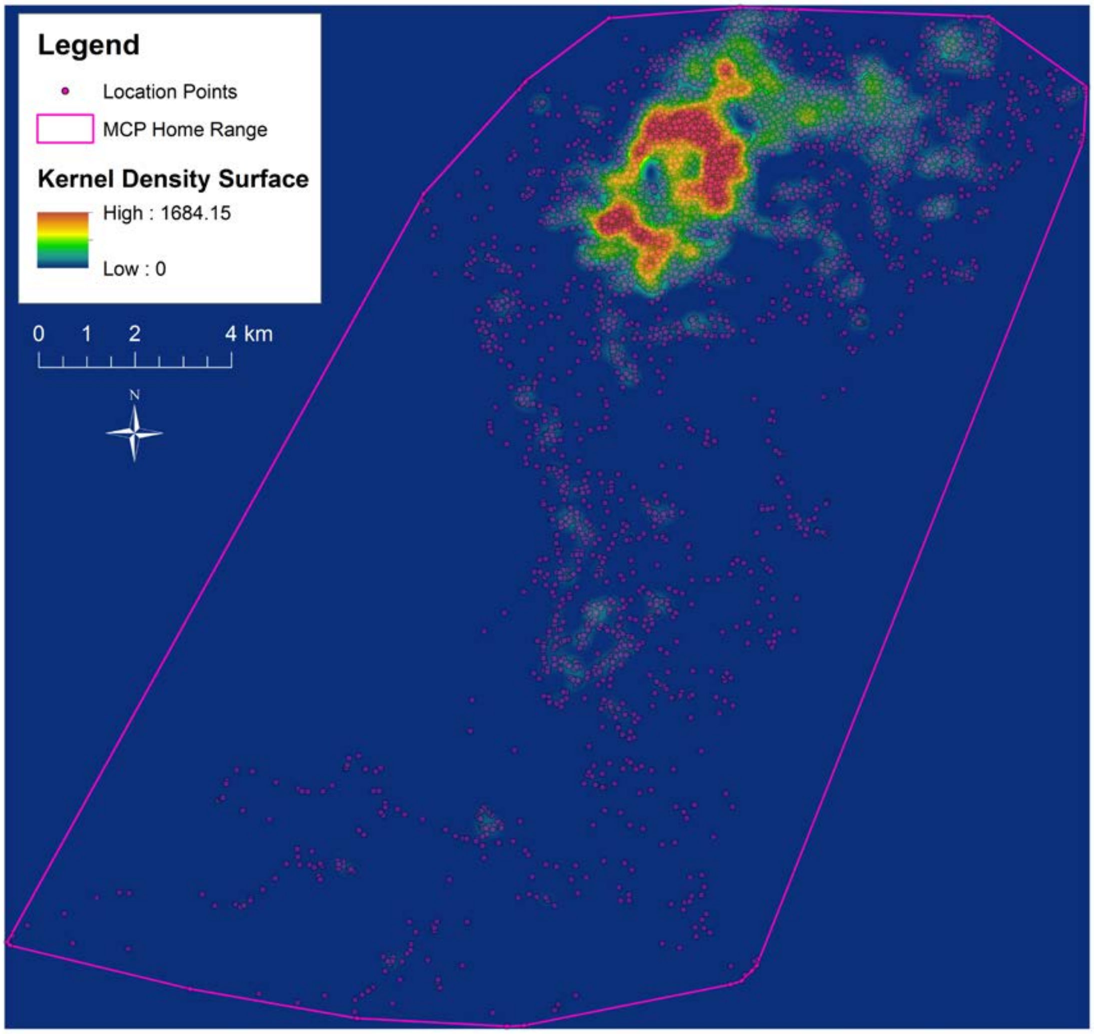

Figure 7. Kernel Density surface for female elephant, Ndeka, exhibiting core home range areas. Location points and MCP home range are displayed for context. Warmer colors represent higher values of the kernel density surface, indicating greater habitat use.

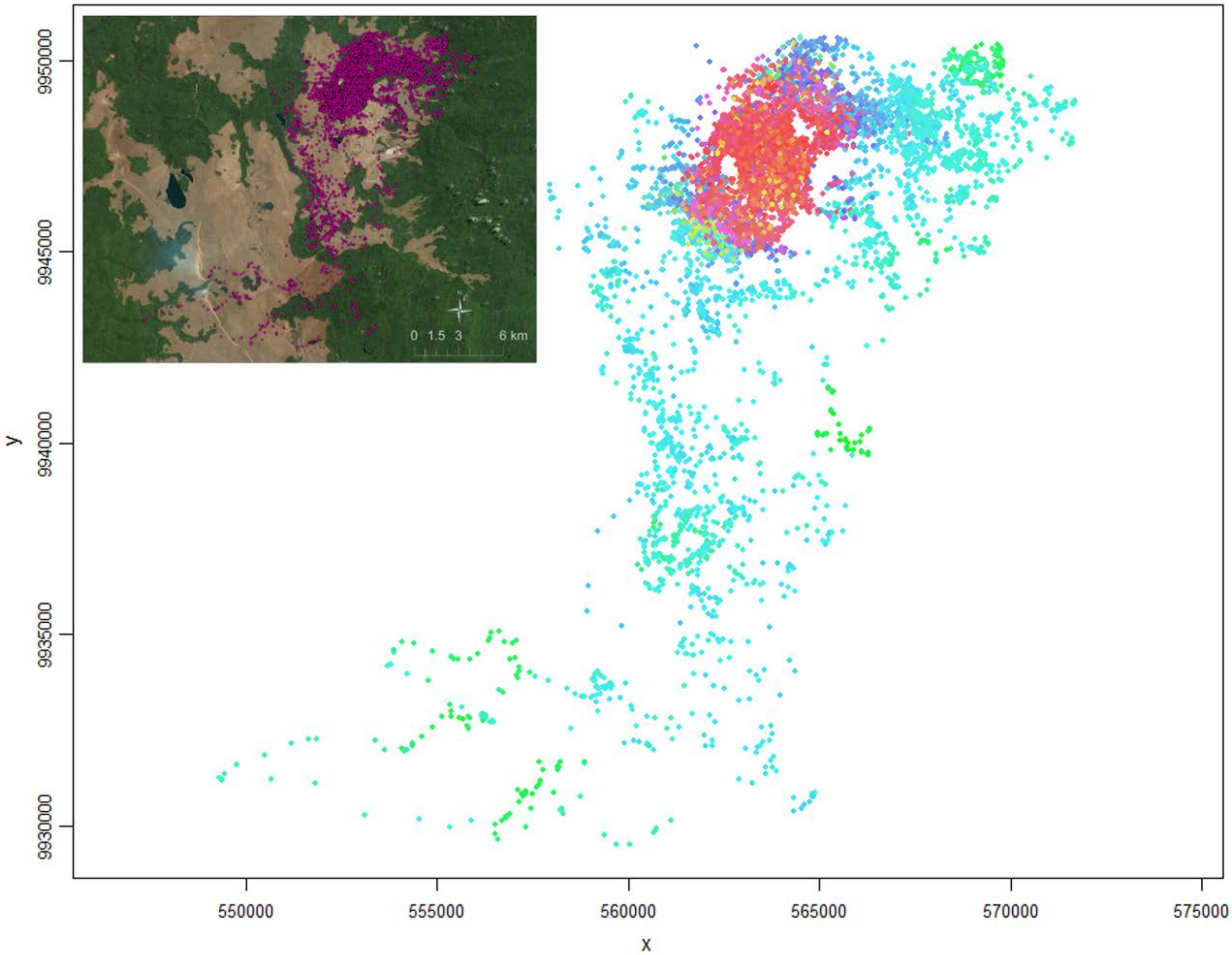

Figure 8. Time density map for Ndeka. Inset displays land cover for context. Warmer colors represent high visitation rate and low duration of visit, indicative of greater movement in and out of compact hulls, for example foraging behavior. Cooler colors represent low visitation rate and high duration of visit (as a result of elongated hulls), indicative of more directed movement through the landscape.

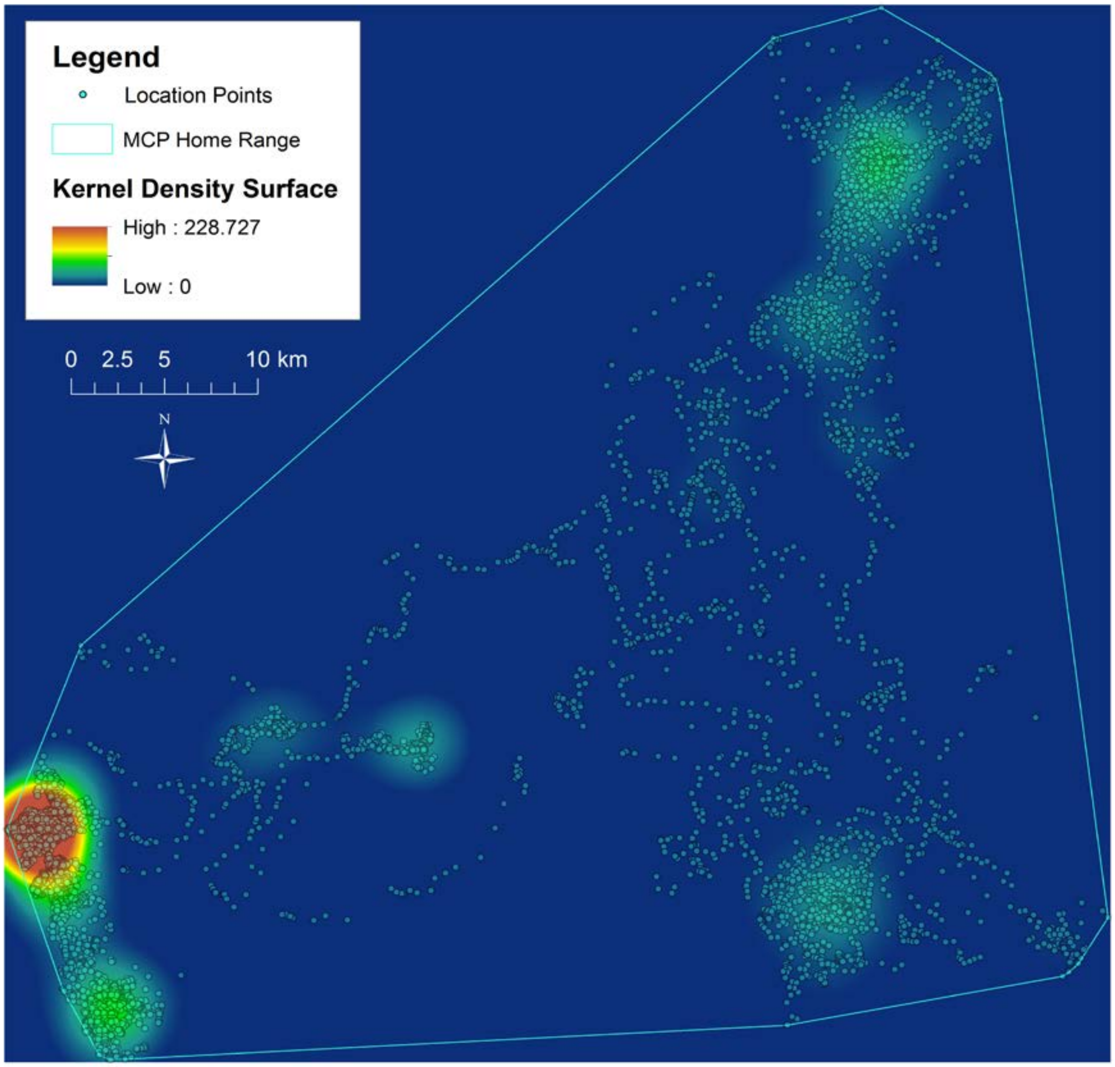

Figure 9. Kernel Density surface for male elephant, Mboumba, exhibiting core home range areas. Location points and MCP home range are displayed for context. Warmer colors represent higher values of the kernel density surface, indicating greater habitat use.

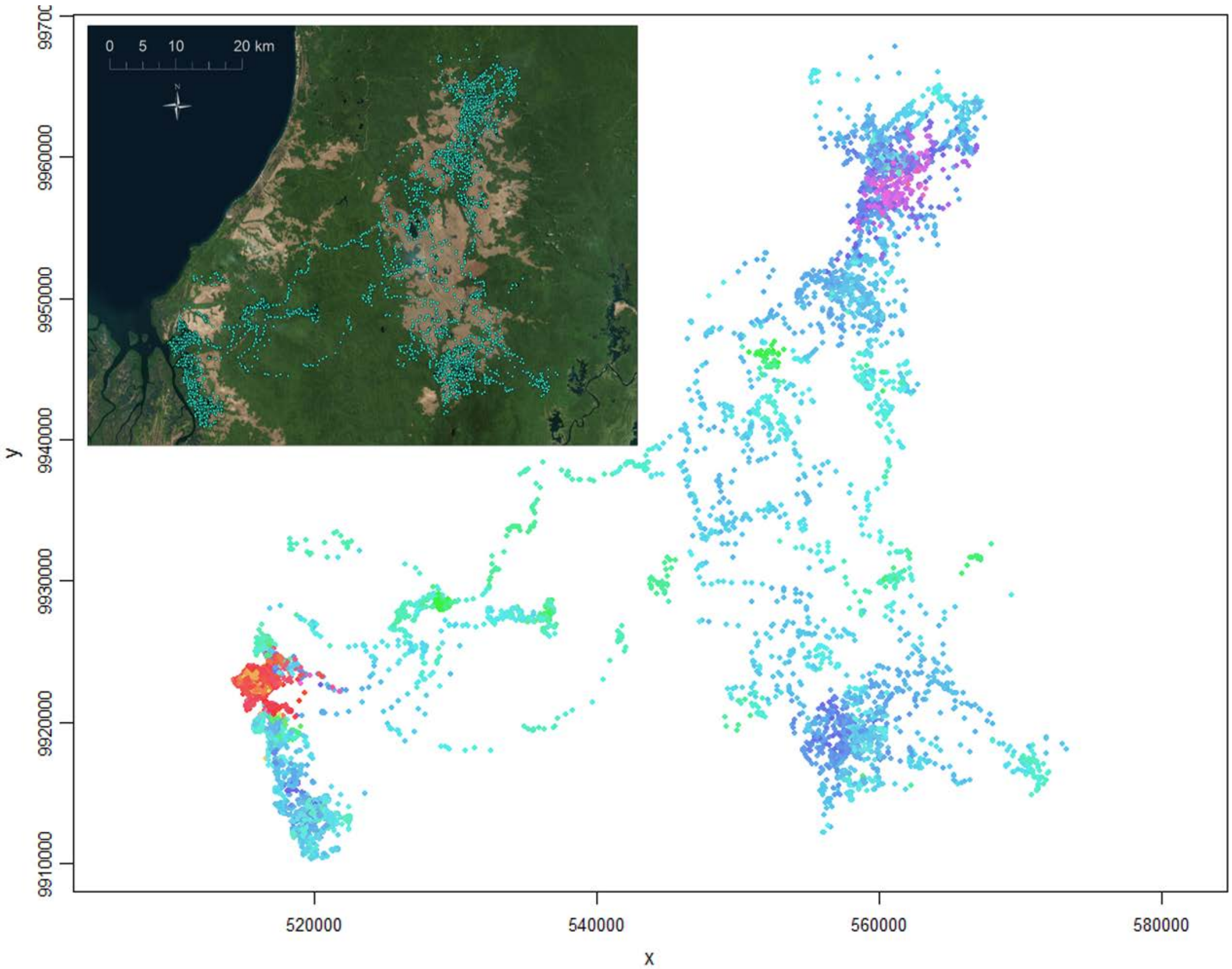

Figure 10. Time density map for Mboumba. Inset displays land cover for context. Warmer colors represent high visitation rate and low duration of visit, indicative of greater movement in and out of compact hulls, for example foraging behavior. Cooler colors represent low visitation rate and high duration of visit (as a result of elongated hulls), indicative of more directed movement through the landscape.

Elephant Habitat Use

Forest elephants spent 62% of their time in forests and 33% in savannas. Elephants tended to spend more time in forest relative to savanna during all seasons except for the short wet season (October 3- December 6), where approximately equal proportions of locations were located in forest and savanna (Figure 11). Season significantly affected the proportion of points located in forest (ANOVA: $F_{3,64}$ = 4.2, p = 0.009), such that elephants spent significantly more time in forest during the long dry season relative to the short wet season (Figure 11). Similarly, season significantly affected the proportion of points located in savanna ($F_{3,64}$ = 3.8, p = 0.014), such that elephants spent significantly more time in savanna during the short wet season relative to the long dry season (Figure 11). During the long dry season, elephants tended to spread across the landscape, with six elephants inhabiting the peripheries of the reserve. During the short wet season, forest elephants congregated in the central savanna of WW, with only two elephants near the periphery of the reserve (Figure 12).

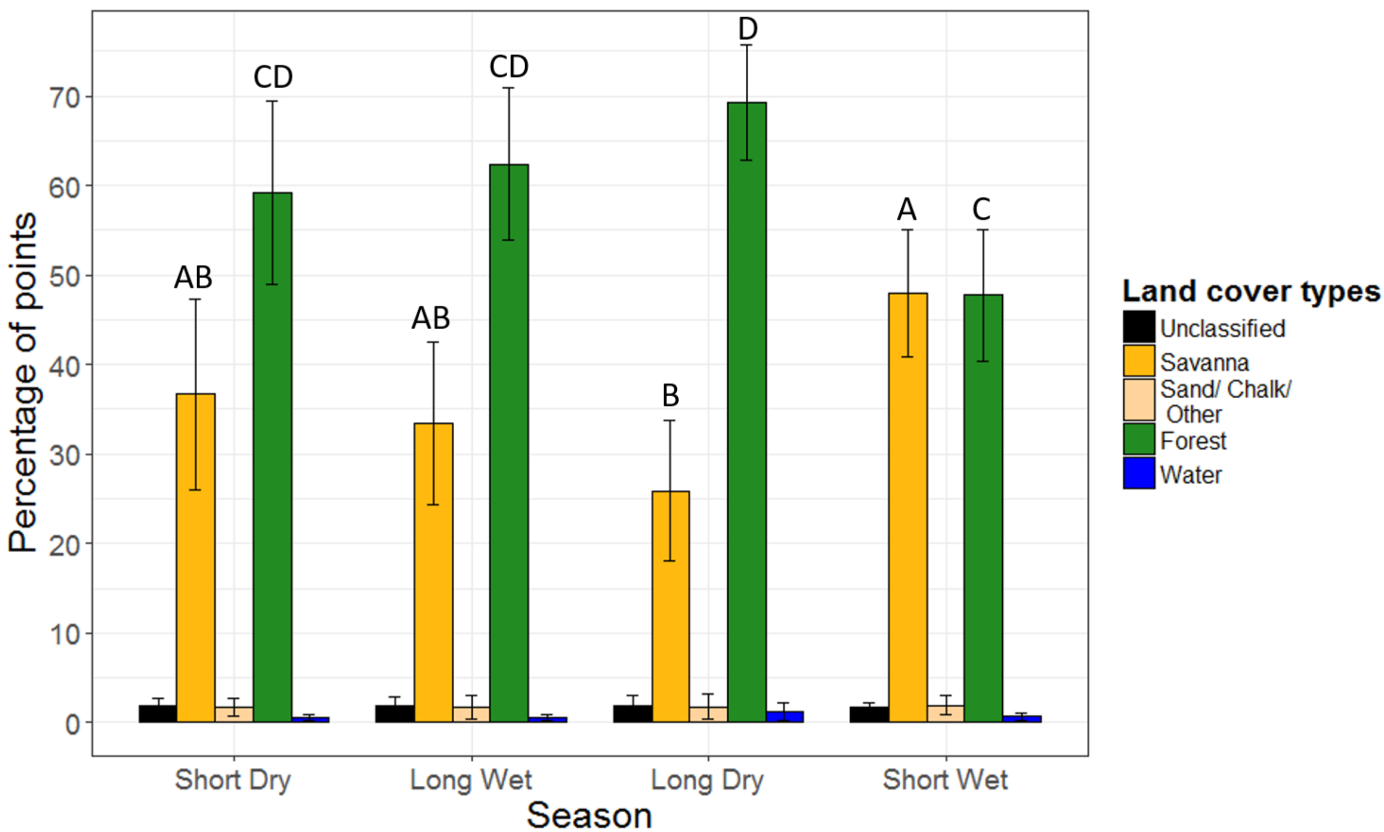

Figure 11. Percentage of elephant locations in each land cover type by season. Pairwise comparisons with different letters indicate significant differences in proportion of use by elephants across seasons within land cover type. Error bars represent 95% confidence intervals. Elephants spent more time in forest than savanna in all seasons except for the short wet season.

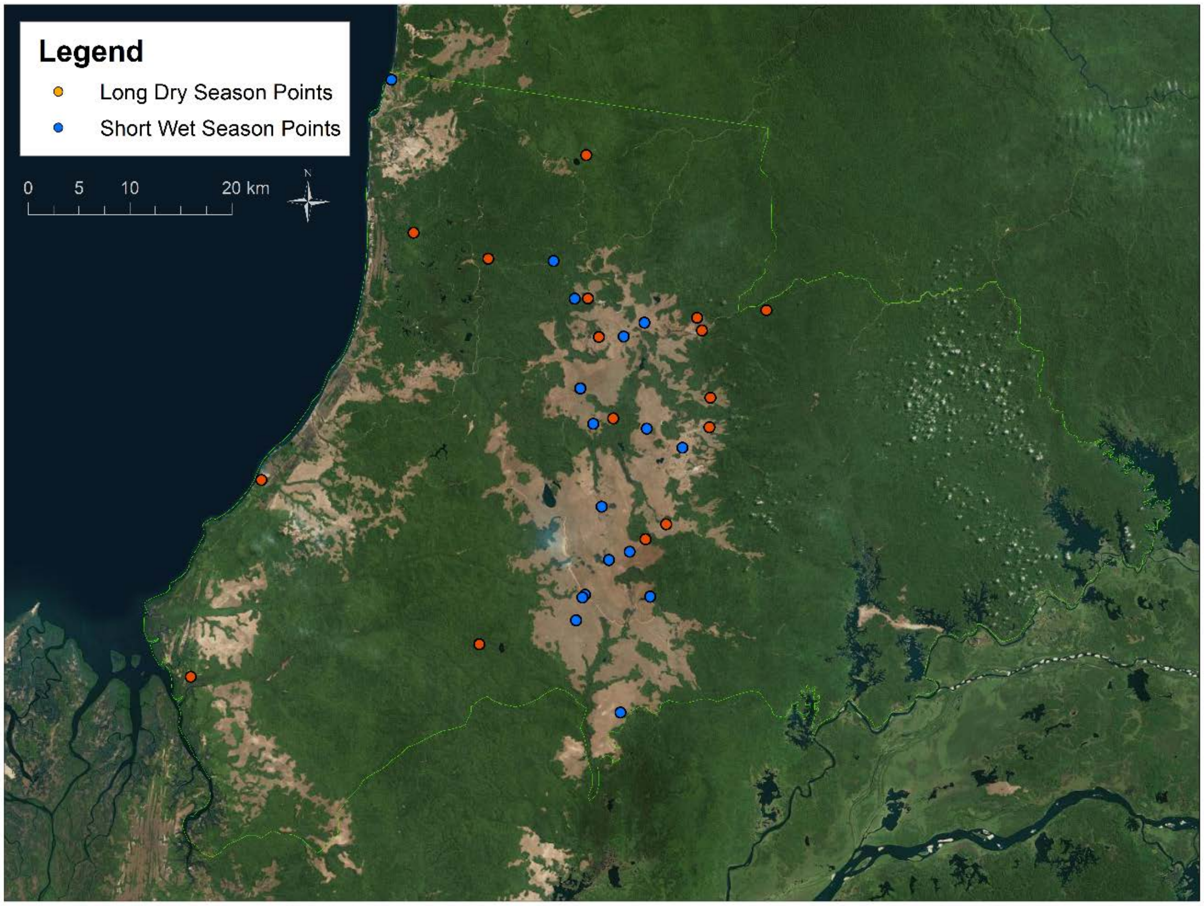

Figure 12. Elephant locations at midpoints of the long dry season (July 20, 2016) and the short wet season (November 3, 2016), demonstrating that elephants congregated in the central savanna during the short wet season.

During daytime hours when sun exposure and temperatures are highest, elephants spent more time in forest than savanna. Time of day significantly affected the proportion of points located in forest (ANOVA: $F_{3,64} = 24.4$, $p = < 0.001$). Elephants spent significantly more time in forest from 6:00-12:00 than any other time of day; they also spent significantly more time in forest from 12:00-18:00 than 18:00-24:00 (Figure 13). During nighttime hours when sun exposure and temperatures decrease, elephants spent significantly more time in savanna than forest ($F_{3,64} = 19.3$, $p < 0.001$), with elephants spending the most time in the savanna between 18:00-24:00 (Figure 13).

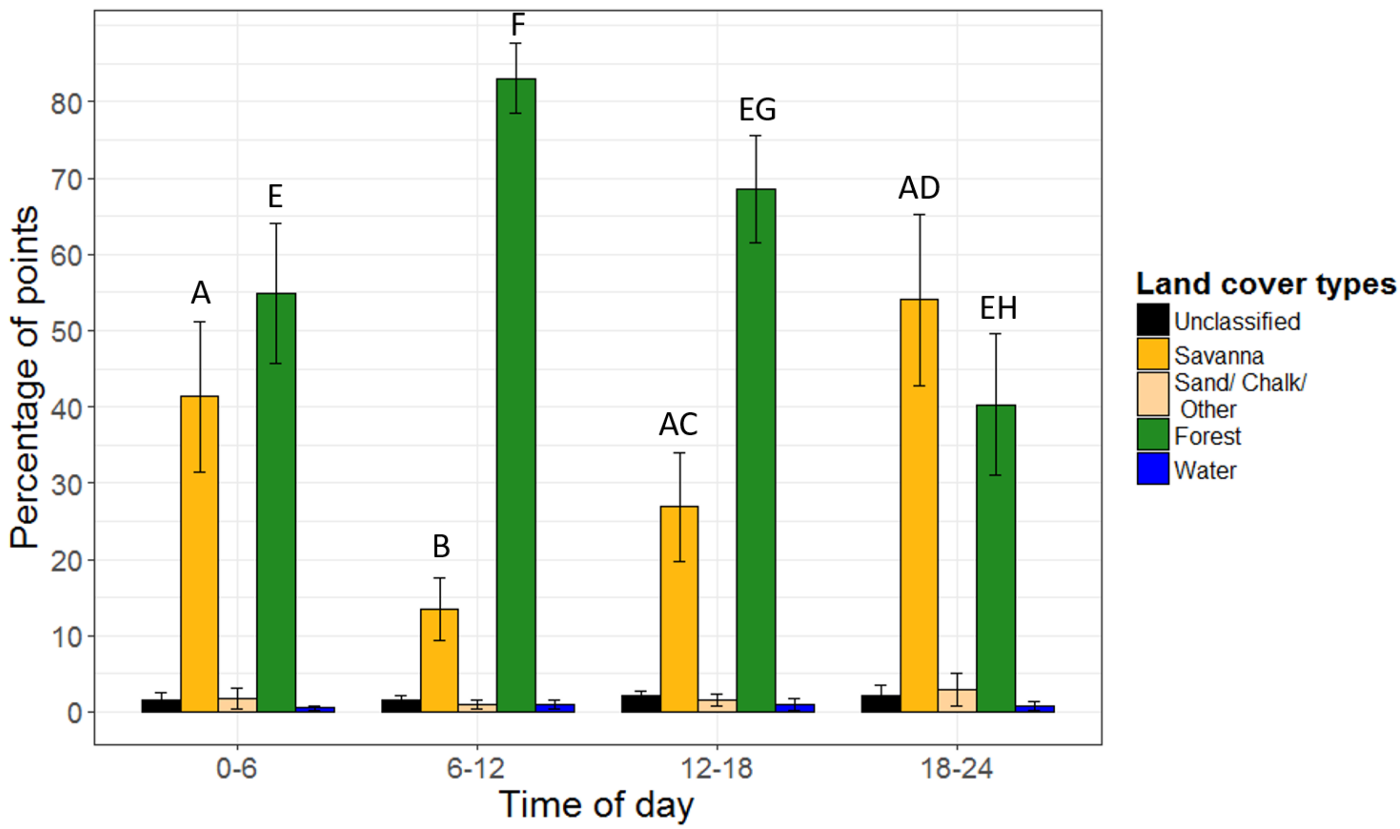

Figure 13. Percentage of elephant locations in each land cover type by time of day. Pairwise comparisons with different letters indicate significant differences in proportion of use by elephants across time periods within land cover type. Error bars represent 95% confidence intervals. Elephants spent more time in the savanna during late evening hours than daylight hours.

Male and female elephants did not differ significantly in terms of their average distance from water (Mann-Whitney: $W = 38.0$, $p = 0.813$), distance from roads ($W = 35.0$, $p = 1.000$), or distance from villages ($W = 37.0$, $p = 0.887$; Tables 2-3). All elephants tended to be within approximately 5 km of a water source (mean = 1.86 km, SD = 1.36) or a road (mean = 2.01 km, SD = 1.76; Figures S19-S20), as water sources are plentiful and roads are protected within the park boundary. Although male and female elephants did not differ in their average distance from villages, three male elephants noticeably ventured within 5 km of villages (Figure S21). There were no significant differences in the average distance of elephants from water between dry and wet seasons ($W = 124.0$, $p = 0.496$; Table S15).

Table 2. Average distance to the nearest roads and villages by elephant.

Elephant	Sex	Average distance from water (km)	Average distance from roads (km)	Average distance from villages (km)
Stam	F	1.09	2.80	11.29
Nongo	F	1.42	2.24	23.88
Rosa	F	1.46	1.57	21.99
Nana	F	1.98	1.12	24.51
Lisa	F	2.08	2.46	17.02
Malaika	F	2.16	2.88	26.23
Ndeka	F	3.77	1.18	25.18
Nze	M	0.82	2.28	7.87
Mboumba	M	1.31	2.68	11.29
Mambo	M	1.45	1.34	22.76
Tonnerre	M	1.49	2.14	21.63
Mba	M	1.51	1.49	28.33
Kengue	M	1.58	1.69	26.01
BraBrou	M	1.74	0.69	24.21
Wongo	M	2.13	3.14	25.03
David	M	2.71	3.12	9.06
Kigali	M	2.90	1.38	24.68
Mean		**1.86**	**2.01**	**20.36**

Table 3. Mean and median distances of elephants to nearest water, roads, and villages by sex.

	Distance to Water (km)		**Distance to Roads (km)**		**Distance to Villages (km)**	
Sex	Mean	Median	Mean	Median	Mean	Median
F	1.99	1.98	2.04	2.24	21.44	23.88
M	1.76	1.54	1.99	1.91	20.09	23.48

Drivers of Elephant Movements

The most important variables for predicting forest elephant habitat use during the dry seasons were distance to villages, distance to streams, slope, and EVI (Table 4). The strongest predictor of elephant presence was vegetation, where the odds of elephant presence increased by 4.1 times with each one-unit increase in EVI. Distance to village had the next strongest effect, where elephant presence was less likely as distance to village increased. Distance to stream and slope had significant but less strong, positive effects on elephant presence. Elephants had relatively low occupancy of the central savanna relative to forest during this season (Figure 14).

The most important variables for predicting forest elephant habitat use during the wet seasons were distance to villages, distance to streams, distance to roads, and EVI (Table 4). Again the strongest effect was the positive effect of vegetation with an increase of over 95 times in odds of elephant presence with each one-unit increase in EVI. The next strongest effect was distance to stream, which also had a positive effect on elephant presence. Distance to road and distance to village had significant but weaker negative effects on elephant presence. The wet season prediction surface demonstrates the relatively low presence of elephants in the central savanna compared to forest during this season, but the gradient of elephant presence is less steep than for the dry season model (Figure 14). Comparing the two prediction surfaces, elephants are much more restricted in habitat use during the dry season, with their presence being much higher in the forests surrounding the savannas. In the wet season, they tend to spread out and use the park and its periphery more evenly.

Table 4. Coefficients for forest elephant generalized linear mixed models (GLMMs) in dry and wet seasons. Habitat models consisted of GLMM models of elephant presence in relation to distance to village, road, stream, and slope and EVI, with a binomial probability distribution and logit-link. Estimates are log-odds ratios.

Dry Season

Variable	**Estimate**	**SE**	***Z***	***p***	
Intercept	-0.613	0.137	-4.475	$p < 0.001$	***
Distance to village (km)*	-0.264	0.043	-6.130	$p < 0.001$	***
Distance to stream (km)*	0.060	0.025	2.406	0.0161	*
Slope (m)*	0.046	0.024	1.930	0.0536	·
Enhanced Vegetation Index (EVI)	1.410	0.280	5.033	$p < 0.001$	***
Mean model accuracy across 5 *k*-folds: 53.9%					

Wet Season

Variable	**Estimate**	**SE**	***Z***	***p***	
Intercept	-2.010	0.245	-8.222	$p < 0.001$	***
Distance to village (km)*	-0.083	0.036	-2.311	0.021	*
Distance to stream (km)*	0.185	0.025	7.526	$p < 0.001$	***
Distance to road (km)*	-0.090	0.025	-3.618	$p < 0.001$	***
Enhanced Vegetation Index (EVI)	4.556	0.546	8.351	$p < 0.001$	***
Mean model accuracy across 5 *k*-folds: 55.4%					

*standardized to *Z*-score for analysis

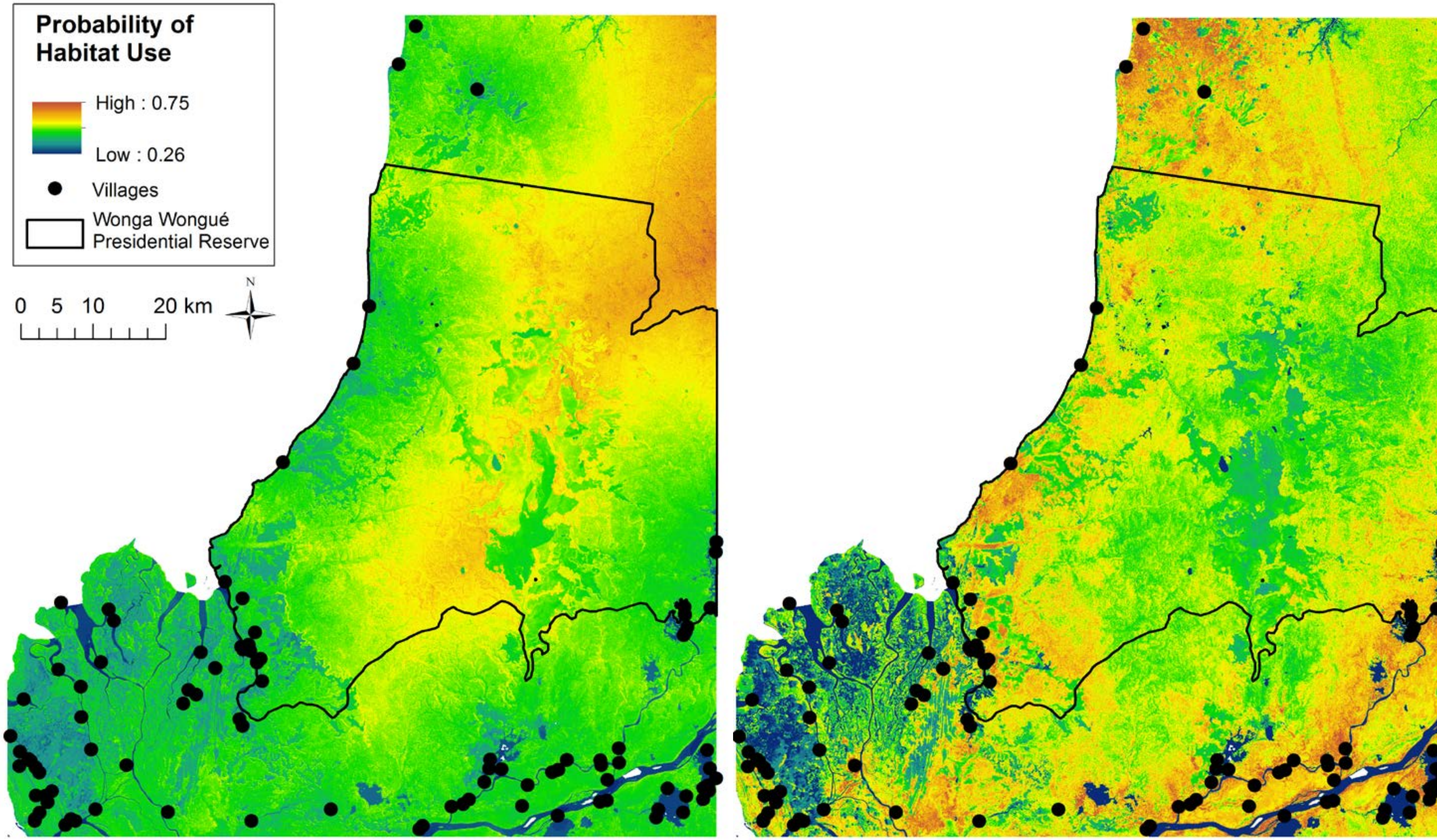

Figure 14. Prediction surfaces derived from GLMMs of elephant presence/pseudoabsence relative to environmental and anthropogenic variables. Forest elephants are more restricted in habitat use during the dry season (left), with higher elephant presence in forests around the central savanna. In the wet season (right), they tend to spread out and use the entire park and its periphery.

Discussion

To my knowledge, this is first study of the movement ecology of forest elephants in a forest-savanna matrix. By quantifying the movements and home ranges of 17 elephants in the Wonga Wongué Presidential Reserve, Gabon, we found forest elephants spend most of their time in forest, but selectively use the savanna during nighttime hours and during the short wet season, when new grass shoots provide good browse. Nearly all of the elephants used the large central savanna, with several males traveling up to 110 km to and from the savanna to the peripheries of the reserve. Of the 17 forest elephants, 11 (seven males, four females) displayed multiple core home range areas, with at least one in the central savanna and one in surrounding forests (Figures S7-S21). Savanna habitat is likely important for elephant resource use and social interactions, similar to the use of bais (forest clearings) for forest elephant social gatherings (Wrege et al. 2012; Turkalo et al. 2013). Management has largely eradicated poaching from WW, allowing forest elephants to range freely in the reserve. Therefore, environmental factors, such as food, water, and habitat, drive elephant movements more than the avoidance of anthropogenic distrubance. While previous collaring studies have mainly focused on the importance of human impacts, such as unprotected habitat or roads, on forest elephants, this study demonstrates that environmental variables influence elephant movements when they are not threatened by poaching. Forest elephants did not avoid villages and even spent more time near villages when a village was located in their home range. Human-elephant conflict is most likely along the populated peripheries of WW; thus conservation monitoring and law enforcement should be focused in these areas to protect both people and forest elephants.

Elephant Movements and Home Ranges

Both male and female forest elephants can travel approximately 7-8 km per day and 3,000 km annually. Using distance travelled between consecutive points, I found peaks of elephant movements occurred around dawn and dusk, likely representing movements from the savanna to the forest in the morning and from the forest to the savanna in the evening. While this finding concurs with activity patterns found in savanna elephants (Loarie et al. 2009), it contrasts with the diurnal activity patterns of a female elephant in Congo, that was most active between 12:00-21:00, with a peak at 15:00 (Blake et al. 2001). The authors suggested that elephants can remain active during the day because forest cover affords protection from the heat. While the

Blake et al. (2001) study only involved a single elephant, it may suggest that activity patterns vary by site and with environmental conditions and disturbance. Thus, the activity patterns of WW elephants may be influenced by the warmer, open savanna habitat, with elephants in more contiguous forest having different activity patterns.

Hourly, daily, and total distances moved by forest elephants were greatest during the wet seasons. Elephants may travel shorter distances during the dry season to stay near perennial water sources during times of relative water scarcity. Alternatively, fruiting of trees largely corresponds with the wet seasons in Gabon (White, 1994), and may account for the longer movements as elephants "tag-line" to preferred fruiting tree species (Terborgh et al. 2016). WW has similar species composition to the coastal forest of Petit Loango in Gabon, where *Sacoglottis gabonensis* occurs at relatively high stem density of 13.4 large stems (greater than 10 cm diameter at breast height) per hectare compared to other Central African sites (Morgan, 2009). During the long dry season, *Sacoglottis gabonensis* fruits are abundant in WW, and are the most common fruit found in forest elephant dung (pers. observation). Elephants may not need to move far to find a fruiting tree of this preferred species during the dry season.

While male and female elephants did not differ in total distances moved or distance between consecutive points, they did differ significantly in home range areas. MCP home range areas for WW forest elephants ranged from 239 km^2 to 2,253 km^2, with males averaging 965 km^2 and females averaging 354 km^2—greater and less than 546.8 km^2, the average home range from a study of forest elephants at six sites in Gabon, Congo, and Central African Republic (Blake et al. 2008). Male elephants may have larger home ranges than females because they are more likely to engage in exploratory movements outside core areas of habitat use—even outside park boundaries—to find forage and mates. In addition, males are often solitary and have more fluid social interactions uncontrained by offspring (Schuttler et al. 2014), whereas female elephants are more likely to be in a small family group with dependent offspring, and thus stay in a specific, known territory for reliable resources.

Other studies of forest elephants have found home ranges vary widely across sites. A single female elephant in Congo had an MCP home range of 880 km^2 (Blake et al. 2001); whereas three female elephants in an oil concession in southwest Gabon covered an average home range of 211.7 km^2, perhaps constricted by human presence (Kolowski et al. 2010). The more extensive study of 28 forest elephants across Central Africa found highly variable average home range sizes across protected areas in Gabon. Of note, six female elephants in Loango National Park had an average MCP of 75.6 km^2, four elephants (2 male, 2 female) in Ivindo National Park had an average MCP of 623.2 km^2, and 4 elephants (1 male, 3 female) in Minkébé had an average MCP of 568.2 km^2 (Blake et al. 2008). Another study of six females in Loango National Park derived an average 95% kernel home range of only 51.7 km^2 (Schuttler et al. 2012). From this small number of studies, it appears that with the exception of Loango, where home range areas are spatially confined, forest elephants across Gabon have relatively similar home range areas of about 500 to 600 km^2. Forest elephants in Loango may exhibit smaller home ranges due to the large lagoon in the northern part of the park, which together with the western coastal border limits their movements. In WW, male elephants also exhibited greater overlapping areas with both males and females, whereas female elephants maintained more separate home ranges. This finding is consistent with the observation of minimally overlapping home ranges of the six females in Loango (Schuttler et al. 2012).

Elephant Habitat Use

Forest elephants spend most of their time in the forest, but spend up to a third of their time in savanna. On average, female elephant home ranges consisted of 30% savanna and 68% forest, and male elephant home ranges consisted of 20% savanna and 78% forest. Across seasons, elephants spent more time in forest except for the short wet season, when they tended to congregate in the central savanna. Similarly, studies on savanna elephants have shown that elephants select habitats with greater tree cover in the dry season but not the wet season (Roever et al. 2012; Ngene et al. 2010). Following prescribed burns at the end of the long dry season, rainfall stimulates grass growth, attracting elephants that browse on the young shoots. During the short wet season, elephants visit the savannas during the nighttime, moving into the forest during daylight hours where they are shielded from the sun and high temperatures in the savanna (Kinahan et al. 2007). This nighttime use of savannas in WW is consistent with previous research on bais: observations of forest elephants at Dzanga-Sangha Bai in Central African Republic showed that 79% of visits to the clearing occurred at night (Wrege et al. 2012). Using forest habitat during the daytime could be an evolutionary adaptation to avoid predation or hunting, which has persisted through modern-day poaching pressures. Given the lack of poaching in WW over the last few years, and the apparent willingness of elephants to approach villages and roads, movements between forest and savanna are probably more related to environmental than anthropogenic factors.

Female elephants tended to stay closer to the central savanna with the exception of one female, Stam, who remained in the northwest region of the park. While most of the males also stayed fairly close to the central savanna, half of them travelled great distances—up to 110 km—from the central savanna to core home range areas at the peripheries of the park. Males may return periodically to the large central savanna as a social gathering place, similar to bais, where breeding females are more accessible (Turkalo et al. 2013; Wrege et al. 2012).

Forest elephants did not demonstrate significant differences in terms of average distances to water, roads, or villages between sexes or between seasons. In stark contrast to savanna elephants (Chammaille-Jammes et al. 2013), forest elephants have easy access to water sources such as lakes, ponds, and streams that do not dry up seasonally and are plentiful across the landscape, including during the dry season. While water availability may be the main limitation for savanna elephants, phenology and distribution of fruiting trees may be more important in influencing forest elephant movements (Schuttler et al. 2012). Although elephants avoid unprotected roads in areas where poaching and human disturbance is high (Blake et al. 2008), a study of four elephants in a protected oil concession in Gabon found them to be located just 516 m from roads on average (Kolowski et al. 2010). Forest elephants in WW maintained an average distance of 2 km from roads, but this distance may largely be an artefact of the low density of roads in the large wilderness area of WW. Both male and female elephants crossed roads often, with males averaging 503 crossings and females averaging 342 crossings. Forest elephants crossed the secondary, unpaved roads of WW at significantly higher speeds than non-crossing movements, consistent with previous findings on protected road crossings (Blake et al. 2008).

Forest elephants did, however, demonstrate a proclivity to approach villages at the edges of the reserve. Male elephants were more likely to approach villages than females, probably to forage on manioc crops. Villagers from Gongoué, on the west coast of WW, witnessed a collared male elephant -- likely Nze -- raiding their crops. Monitoring the distance of elephants from villages is important to assess the severity of crop raiding in the periphery of WW and to identify target areas for conflict mitigation (Graham et al. 2009; Guerbois et al. 2012). Repeated crop raiding can motivate villagers to poach elephants through retaliatory killing. Poachers killed the elephant, David, in February 2017, southwest of the park boundary 5 km from the nearest village. It is not yet clear whether the killing of David was in response to crop raiding, or motivated by the ivory trade. The poachers removed his tusks, suggesting the latter.

Drivers of Elephant Movements

Forest elephants movements are more limited in habitat use during the dry season, with higher likelihood of elephant presence in the forests around the central savanna and very low likelihood of elephant presence in the central savanna. In the wet season, they tend to spread out and use the entire park and its periphery more evenly. The most significant driver of elephant movements in WW during both dry and wet seasons was vegetation, where elephants preferred areas with higher levels of vegetation, which afford cover and browse. When villages were nearby, elephants tended to spend time near to them, contrary to the hypothesis that elephants would avoid villages. Elephants may be attracted to villages because of easy access to crops in plantations.

During the wet season, elephants were more likely to be present at greater distances from perennial water sources, indicating decreased water limitation and greater movement away from streams. Elephants were also more likely to be close to roads during the wet season, in contrast to the hypothesis that elephants would avoid roads. The well protected secondary roads in WW do not appear to hinder elephant movements. Elephants were more likely to found at higher slopes during the dry season, consistent with previous research suggesting that elephants avoid steep slopes in the wet season, perhaps due to injury risk on steep muddy slopes (Ngene et al. 2009; Roever et al. 2013).

Conservation and Management Implications

Even though this is the second-largest study of GPS-collared forest elephants, most of the statistical tests conducted suffer from a low sample size of 17 elephants. As more elephants are fitted with GPS collars, sample size will improve allowing us to draw robust conclusions about forest elephant movements and habitat use. In addition, as existing collared elephants transmit more data across multiple years, we can gain further insight into seasonal movement patterns over a larger temporal scale. There is still an enormous amount to be learned about the movement ecology and behavior of forest elephants.

Multiple ecological questions pertaining to specific food resources arise from this study, and could be addressed in future research efforts. For example, how might fruiting tree phenology, particularly during the wet seasons, determine seasonal patterns of forest elephant movements? And, how do prescribed burns performed by park management affect resource availability/quality and subsequent movements for forest elephants? Fire stimulates growth of new grass, a high-nutrient food resource for elephants and other herbivores (Hopcraft et al. 2010). Grass can be a major part of forest elephant diets (Tchamba & Seme, 1993); however, research has not been conducted on the use of grasslands in Central Africa by forest elephants. In addition, while briefly examining overlapping home range areas, this study does not encompass social interactions and behavioral aspects of forest elephant movements. This is an area ripe for future studies addressing questions regarding genetic relationships of kin group members, social group fluidity, and the influence of communication and learning on location/resource memory.

This study has demonstrated unique challenges in the conservation of forest elephants. The distinct interaction of forest elephants with savanna landscapes calls for continued management of savannas through prescribed burns to maintain openness and continual grass turnover. Whereas managers of savanna elephant populations are often concerned with water availability, this is not a key management issue in humid tropical forests. The interior of WW appears to be well protected from poachers, but human-elephant conflict is likely at the boundaries of the park, particularly during the wet seasons. Thus, increased conservation monitoring and law enforcement should be focused on the periphery of the park, near villages with potential crop raiding issues during the wet seasons. Future GPS-tracking efforts should focus on elephants located in the periphery of the park, particularly males, to evaluate their movements in and out of the park and their interactions with villages. Specifically, repeat crop raiders or “problem elephants” could be collared to set up an early warning system where park management and/or villages receive SMS text alerts when the elephant approaches within a certain distance of their plantations (Wall et al. 2014). To the extent possible, park management should increase efforts to communicate with villagers about the nature of the GPS monitoring program as well as invest in feasible methods to prevent elephants from crop raiding.

In the future, forest elephants in multiple-use areas between protected areas should be fitted with GPS collars. Comparing elephant habitat use inside, outside, and near the borders of protected areas will help to assess the anthropogenic impacts on forest elephant movements and habitat use in Gabon. Additionally, expanding habitat modeling to multiple-use areas and generating subsequent prediction surfaces of habitat use will allow future studies to examine connectivity between parks. Maximizing connectivity between parks will preserve genetic diversity, limit local extirpations, and maintain dispersal pathways of plant and animal species. Connectivity analyses will be a critical tool to inform ANPN on strategies to maintain movement corridors, and to assess the capacity of the protected area network in Gabon to conserve forest elephant populations.

Movement ecology has greatly improved our understanding of forest elephant movements in WW and informed specific management recommendations for the reserve to maintain its forest elephant population. But there is still much to discover about how forest elephants select habitats and interact with landscapes on which humans also depend. Future studies of elephant movement and habitat use are necessary to improve our current understanding of forest elephant behavior and ecology. Addressing this knowledge gap will allow us to better manage elephants' resources and threats to ensure that they remain an integral component of Central African forests.

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Supplementary Materials

Table S1. Seventeen forest elephants collared in Wonga Wongué Presidential Reserve monitored from November 4, 2015 to March 4, 2017. Table sorted by sex and ID code.

Elephant Name	ID Code	Sex	Date Collared	Date Start Hourly Pings	Total GPS Points
Rosa	Duke01	F	10/23/2015	11/4/2015	10,759
Nana	Duke02	F	10/26/2016	11/4/2015	10,922
Lisa	Duke04	F	10/22/2015	11/4/2015	10,015
Ndeka	Duke06	F	10/26/2015	11/4/2015	10,875
Stam	Duke09	F	10/29/2016	11/4/2015	9,309
Nongo	Duke16	F	4/30/2016	05/12/2016	6,892
Malaika	Duke20	F	4/29/2016	05/12/2016	6,790
Kengue	Duke03	M	10/23/2015	11/4/2015	10,233
Mba	Duke05	M	10/25/2015	11/4/2015	10,467
Mambo	Duke07	M	10/24/2015	11/4/2015	10,668
Mboumba*	Duke08	M	10/25/2015	11/4/2015	10,543
David*	Duke10	M	10/24/2015	11/4/2015	10,241
Wongo	Duke11	M	10/28/2016	11/4/2015	10,876
Nze	Duke12	M	10/28/2016	11/4/2015	10,417
BraBrou	Duke19	M	4/30/2016	05/12/2016	6,630
Tonnerre	Duke31	M	4/29/2016	05/12/2016	6,489
Kigali	Duke32	M	4/30/2016	05/12/2016	6,629

*Mboumba's GPS collar ceased transmission on February 12, 2017. He has not been relocated, suggesting potential collar failure.

* Poachers killed the elephant, David, whose last GPS transmission was on February 22, 2017. Field teams located the carcass with ivory and head removed, and the GPS collar in a nearby swamp.

Table S2. Landsat scene metadata.

Scene ID	Orientation	Date Taken	Time Taken	Product Level
LC81860602015179LGN00	Northern	2015-06-28	09:33:24	1T
LC81860612015179LGN00	Southern	2015-06-28	09:33:48	1T
LC81860602016070LGN00	Northern	2016-03-10	09:33:54	1T
LC81860612016070LGN00	Southern	2016-03-10	09:34:18	1T

Table S3. Landsat 8 OLI/TIRS Bands.

Band Number	Purpose	Wavelength (µm)	Spatial Resolution (m)
Band 1	Ultra Blue (coastal/aerosol)	0.43 - 0.45	30
Band 2	Blue	0.45 - 0.51	30
Band 3	Green	0.53 - 0.59	30
Band 4	Red	0.64 - 0.67	30
Band 5	Near Infrared (NIR)	0.85 - 0.88	30
Band 6	Shortwave Infrared (SWIR) 1	1.57 - 1.65	30
Band 7	Shortwave Infrared (SWIR) 2	2.11 - 2.29	30
Band 8	Panchromatic	0.50 - 0.68	15
Band 9	Cirrus	1.36 - 1.38	30
Band 10	Thermal Infrared (TIRS) 1	10.60 - 11.19	100* (30)
Band 11	Thermal Infrared (TIRS) 2	11.50 - 12.51	100* (30)

*Thermal bands resampled to 30m

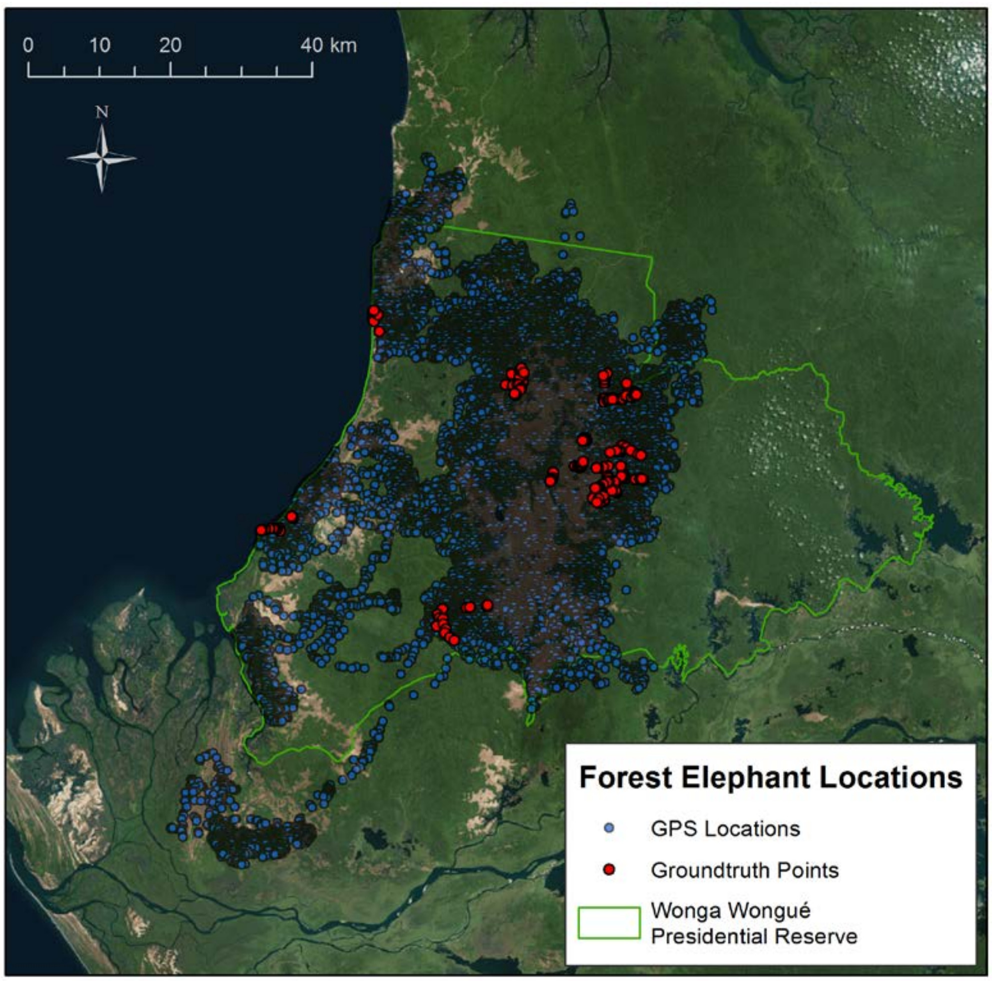


Figure S1. GPS locations of 17 elephants (blue) in Wonga Wongué Presidential Reserve and 220 ground truth points (red) collected between June and July 2016.

Table S4. Description of ground truth points collected from June 6, 2016 to July 21, 2016.

Descriptive Statistics		**Ecosystem Type**	**Number of points**
Number of points	220	Forest	151
Number of individual elephants followed	8	Savanna	52
Average positional dilution of precision (PDOP)	1.63	Swamp	6
Average error (m)	8.27	Beach	4
Average canopy height (m)	17.34	Mangroves	4
Average canopy cover (%)	97.0	Transitional	3

Table S5. Original classes of regions of interest (ROIs) and number of pixels in training sets for each tile. Swamp and mangrove pixels were excluded from analysis due to poor separability from forest.

Class	**Training Pixels (North)**	**Training Pixels (South)**	**Validation Points (Total)**
Savanna	338	141	97
Forest	151	35	82
Water	137	105	79
Sand/ Chalk/ Other	24	25	-

Table S6. Environmental variables of interest included in habitat modeling.

Category of Interest	**Raster Layers**
Human Influence	Distance to secondary roads (km) Distance to villages (km)
Terrain characteristics	Elevation (m) Slope (m)
Vegetation characteristics	Land Cover Type Classification Enhanced Vegetation Index (EVI) Tasselled Cap Transformation (TCT) Greenness
Openness/Exposure	Focal Forest Tasselled Cap Transformation (TCT) Brightness
Water sources	Distance to streams (km) Tasselled Cap Transformation (TCT) Wetness

Table S7**.** Confusion matrices in pixels and percentages for three main land cover types of interest. Matrix diagonals show correctly classified pixels.

	Ground Truth (Pixels)			
Classification	**1- Savanna**	**3- Forest**	**4- Water**	**Total**
Savanna	93	4	0	97
Forest	0	82	0	82
Water	0	0	78	78
Total	93	86	78	257

	Ground Truth (Percent)			
Classification	**Savanna**	**Forest**	**Water**	**Total**
Savanna	100.00%	4.65%	0.00%	37.74%
Forest	0.00%	95.35%	0.00%	31.91%
Water	0.00%	0.00%	100.00%	30.35%
Total	100.00%	100.00%	100.00%	100.00%

Table S8. Total track distance summaries for 17 GPS-collared forest elephants in WW.

Elephant Name	Sex	Total distance (km)	Average distance per day (km)	Average distance per hour (m)
Malaika*	F	2,219	7.50	312
Nongo*	F	2,754	9.30	388
Rosa	F	2,883	5.93	247
Ndeka	F	3,198	6.58	274
Lisa	F	3,828	7.88	328
Stam	F	4,295	8.84	368
Nana	F	4,393	9.04	377
BraBrou*	M	2,189	7.40	308
Kigali*	M	2,430	8.21	342
Tonnerre*	M	2,504	8.46	352
Nze	M	3,750	7.72	322
David	M	3,773	7.76	323
Mambo	M	3,812	7.84	327
Mboumba	M	3,843	7.91	329
Wongo	M	4,020	8.27	345
Kengue	M	4,128	8.49	354
Mba	M	4,535	9.33	389
Female Mean		**3,367**	**7.87**	**328**
Male Mean		**3,498**	**8.14**	**339**
Mean		**3,444**	**8.03**	**334**

*Elephants with GPS transmission starting on May 12, 2016 instead of November 4, 2015 had fewer points and therefore shorter total distances.

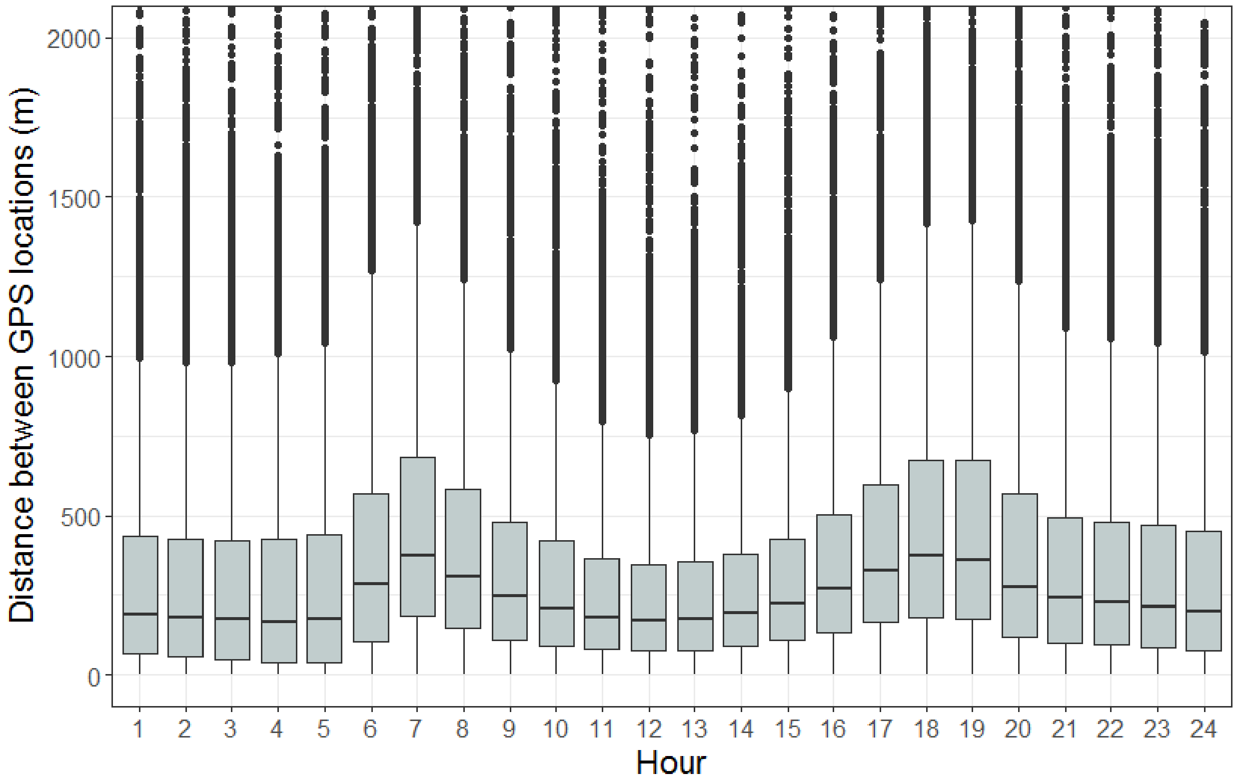


Figure S2. Boxplots showing distances moved between consecutive GPS points for all hours of the day. Elephants exhibited peak movement times between 6:00 and 9:00 and between 17:00 and 20:00. The y-axis was limited to 2000 m to better illustrate the boxplots, rather than the outliers.

Table S9**.** Statistics for distance between consecutive points by hour of the day.

Hour	**Mean distance traveled (m)**	**Minimum distance traveled (m)**	**Maximum distance traveled (km)**
1	325	0	7.31
2	317	0	5.11
3	312	0	4.57
4	308	0	6.20
5	318	0	4.96
6	413	0	16.79
7	521	0	16.44
8	452	0	7.10
9	369	0	7.02
10	324	0	5.95
11	285	0	4.92
12	277	0	6.85

Hour	**Mean distance traveled (m)**	**Minimum distance traveled (m)**	**Maximum distance traveled (km)**
13	269	0	7.76
14	295	2	7.29
15	332	0	8.09
16	382	0	7.21
17	458	2	5.21
18	516	3	6.94
19	515	0	6.39
20	433	0	7.06
21	384	0	7.12
22	371	0	6.11
23	350	0	6.74
24	336	0	7.98

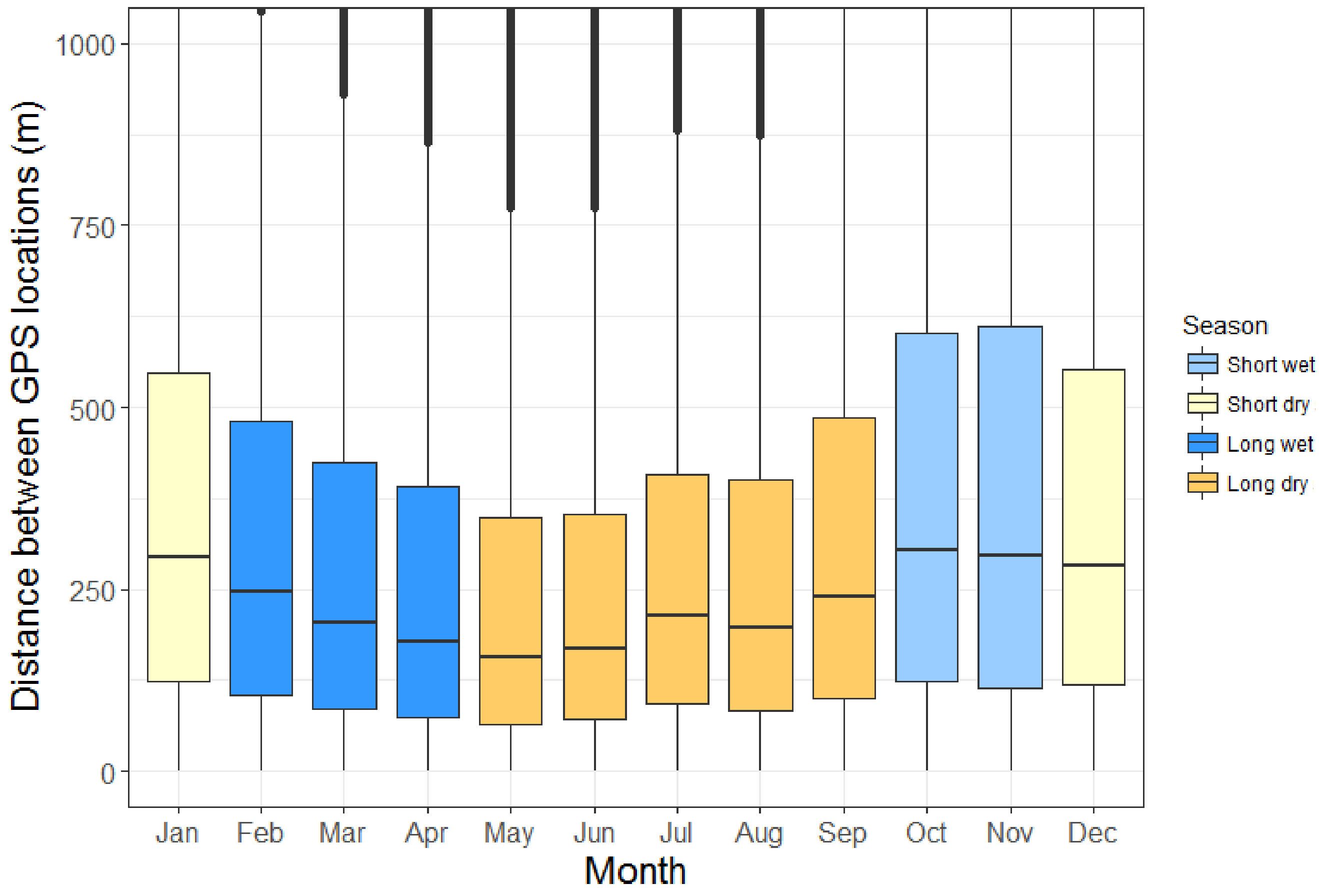


Figure S3. Boxplots showing distributions of distance between consecutive GPS points by month. Elephants exhibited greatest movement speeds during the short-wet season. The y-axis was limited to 1000 m to better illustrate the boxplots, rather than the outliers.

Table S10. Statistics for distance between consecutive points by month.

Month	**Mean distance traveled (m)**	**Minimum distance traveled (m)**	**Maximum distance traveled (km)**
Jan	411	0	7.98
Feb	358	0	16.79
Mar	328	0	7.29
Apr	297	0	5.76
May	284	0	7.31
Jun	275	0	6.20
Jul	314	0	6.42
Aug	315	0	8.09
Sep	364	0	6.41
Oct	453	0	6.11
Nov	455	0	7.28
Dec	424	0	6.94

Table S11. Distance metrics for each elephant summarized by dry and wet seasons.

Elephant	Sex	Total distance (km)		Average distance per day (km)		Average distance per hour (m)	
		Dry	Wet	Dry	Wet	Dry	Wet
Malaika	F	1,205	1,030	6.62	8.88	276	370
Rosa	F	1,284	1,630	5.71	6.20	238	258
Ndeka	F	1,292	1,916	5.74	7.29	239	304
Nongo	F	1,635	1,129	8.98	9.73	374	406
Lisa	F	1,684	2,208	7.48	8.40	312	350
Stam	F	1,945	2,388	8.64	9.08	360	378
Nana	F	1,957	2,473	8.70	9.40	362	392
BraBrou	M	1,289	910	7.08	7.84	295	327
Nze	M	1,388	2,432	6.17	9.25	257	385
Kigali	M	1,463	978	8.04	8.43	335	351
Mambo	M	1,568	2,302	6.97	8.75	290	365
Tonnerre	M	1,577	941	8.66	8.11	361	338
David	M	1,680	2,235	7.47	8.50	311	354
Wongo	M	1,697	2,374	7.54	9.03	314	376
Mboumba	M	1,843	2,111	8.19	8.03	341	334
Kengue	M	1,961	2,230	8.72	8.48	363	353
Mba	M	2,150	2,399	9.56	9.12	398	380
Female Mean		**1,572**	**1,825**	**7.41**	**8.43**	**309**	**351**
Male Mean		**1,662**	**1,891**	**7.84**	**8.55**	**327**	**356**
Mean		**1,624**	**1,863**	**7.66**	**8.50**	**319**	**354**

Table S12. Area of MCP home ranges in square kilometers for different percentages of points after outlier removal (80 – 100% of all points). Table sorted by sex, then 95% MCP area.

		Area of MCP Home Range (km^2)				
Sex	**Elephant**	**80%**	**85%**	**90%**	**95%**	**100%**
F	Ndeka	46	64	90	122	286
F	Nana	97	115	141	174	239
F	Stam	133	142	155	177	314
F	Rosa	143	162	196	220	260
F	Lisa	162	185	233	308	447
F	Nongo	235	290	320	348	397
F	Malaika	358	381	407	430	534
M	Mba	111	132	170	229	427
M	Kigali	198	214	236	263	306
M	BraBrou	241	325	357	372	395
M	Wongo	291	317	365	492	731
M	Kengue	448	465	473	506	615
M	Mambo	221	324	434	533	723
M	Nze	191	482	615	819	1,425
M	Tonnere	683	780	858	932	1,030
M	David	1,077	1,356	1,436	1,467	1,745
M	Mboumba	1,502	1,634	1,910	2,047	2,253

Table S13. Area of KUD home ranges in square kilometers for different probability levels of elephant utilization (80 – 95%). Table sorted by sex, then 95% KUD area.

		Area of KUD Home Range (km^2)			
Sex	**Elephant**	80%	85%	90%	95%
F	Ndeka	38	50	69	105
F	Nana	85	100	121	155
F	Stam	95	112	134	172
F	Rosa	115	133	156	192
F	Nongo	109	130	161	217
F	Lisa	128	155	194	254
F	Malaika	208	246	298	388
M	Mba	79	94	115	147
M	BraBrou	106	131	171	245
M	Kigali	148	171	201	247
M	Mambo	180	225	285	374
M	Wongo	183	222	280	388
M	Kengue	265	322	399	512
M	Nze	248	341	479	700
M	Tonnere	459	535	636	788
M	David	580	713	900	1,229
M	Mboumba	985	1,204	1,494	1,913

Table S14. 100% MCP home range areas for WW by elephant and season.

Elephant	Sex	Dry MCP area (km^2)	Wet MCP area (km^2)
Ndeka	F	113	242
Rosa	F	177	259
Stam	F	188	312
Nana	F	205	193
Lisa	F	343	374
Nongo	F	392	138
Malaika	F	409	294
Nze	M	164	1,424
Kigali	M	306	199
Mba	M	333	163
BraBrou	M	359	96
Kengue	M	451	557
Mambo	M	632	501
Wongo	M	697	587
Tonnerre	M	811	384
David	M	1,425	1,512
Mboumba	M	1,946	1,918
Female Mean		**261**	**259**
Male Mean		**712**	**734**
Mean		**527**	**538**

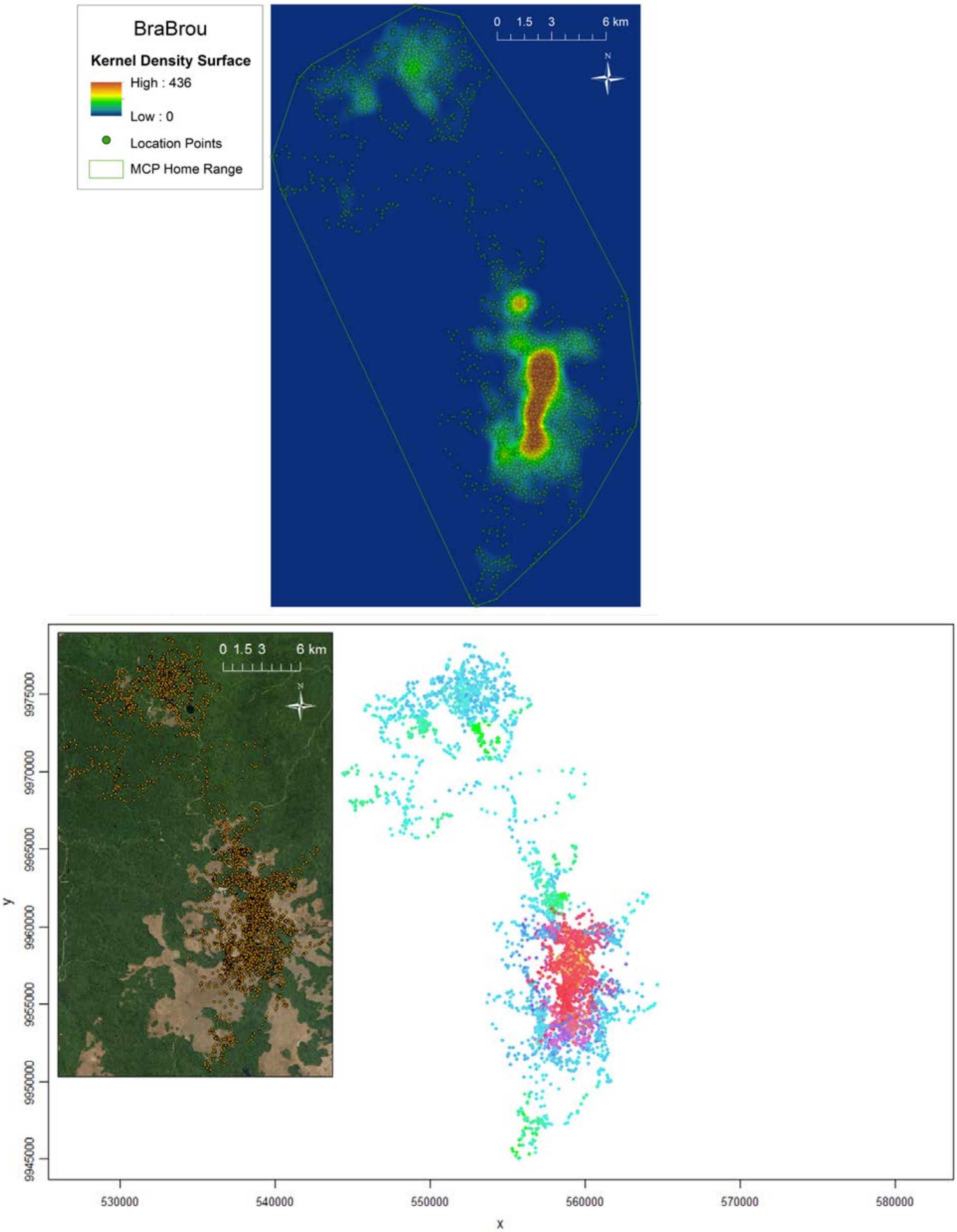


Figure S4. Kernel density surface (above) and time density graph (below) showing core home range areas for the elephant, BraBrou. Points, MCP home range, and land cover are shown for context.

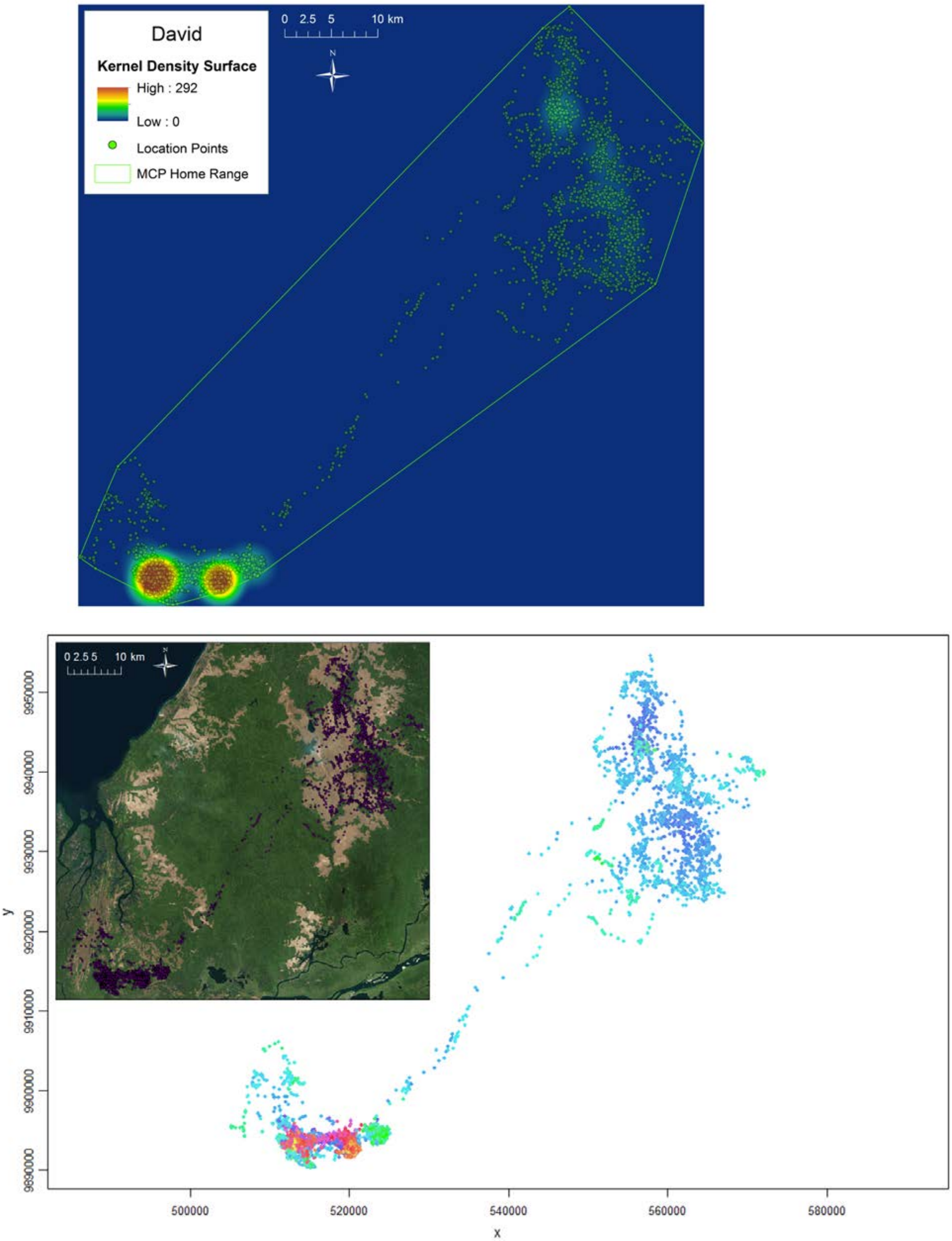


Figure S5. Kernel density surface (above) and time density graph (below) showing core home range areas for elephant, David. Points, MCP home range, and land cover are shown for context.

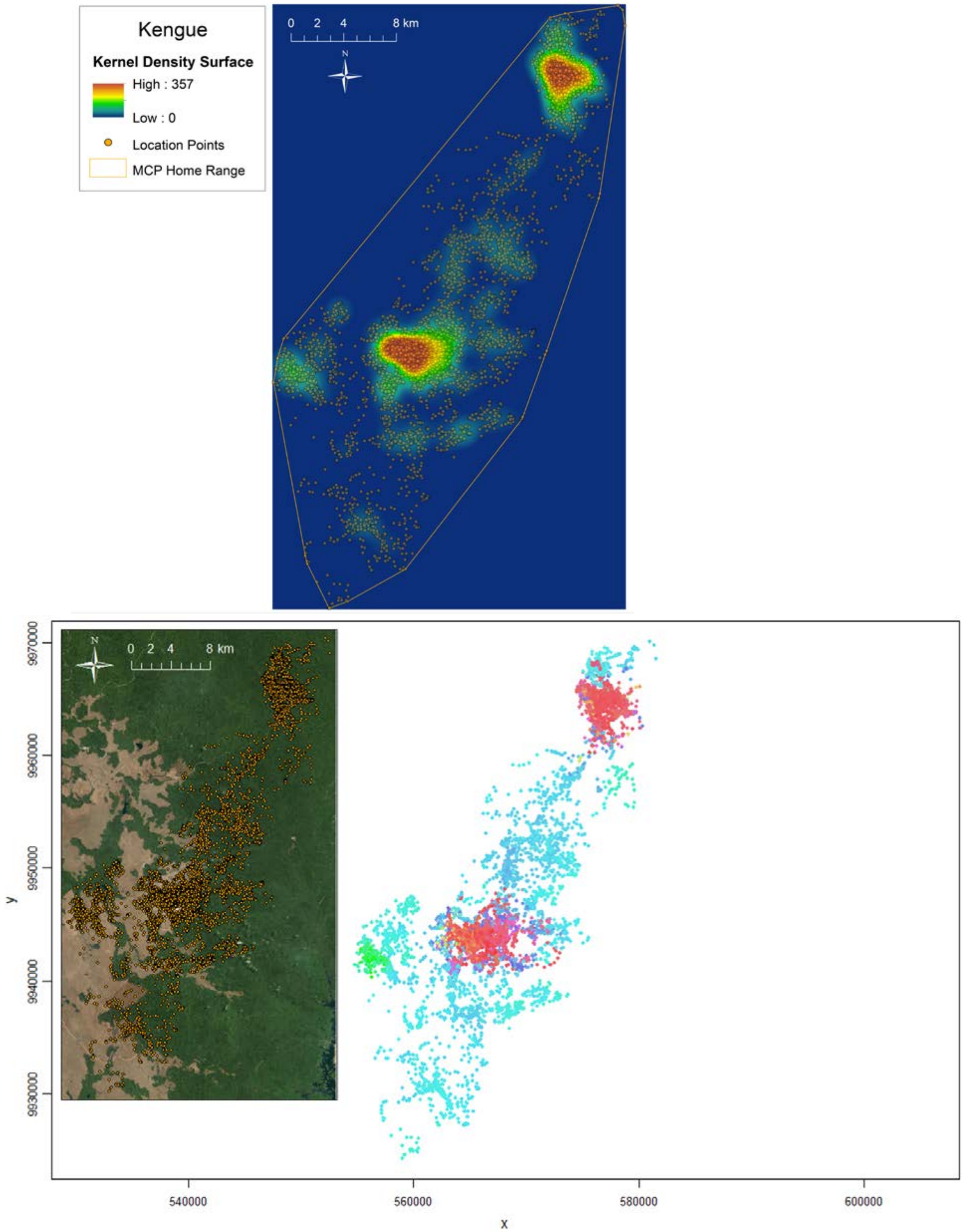


Figure S6. Kernel density surface (above) and time density graph (below) showing core home range areas for Kengue. Points, MCP home range, and land cover are shown for context.

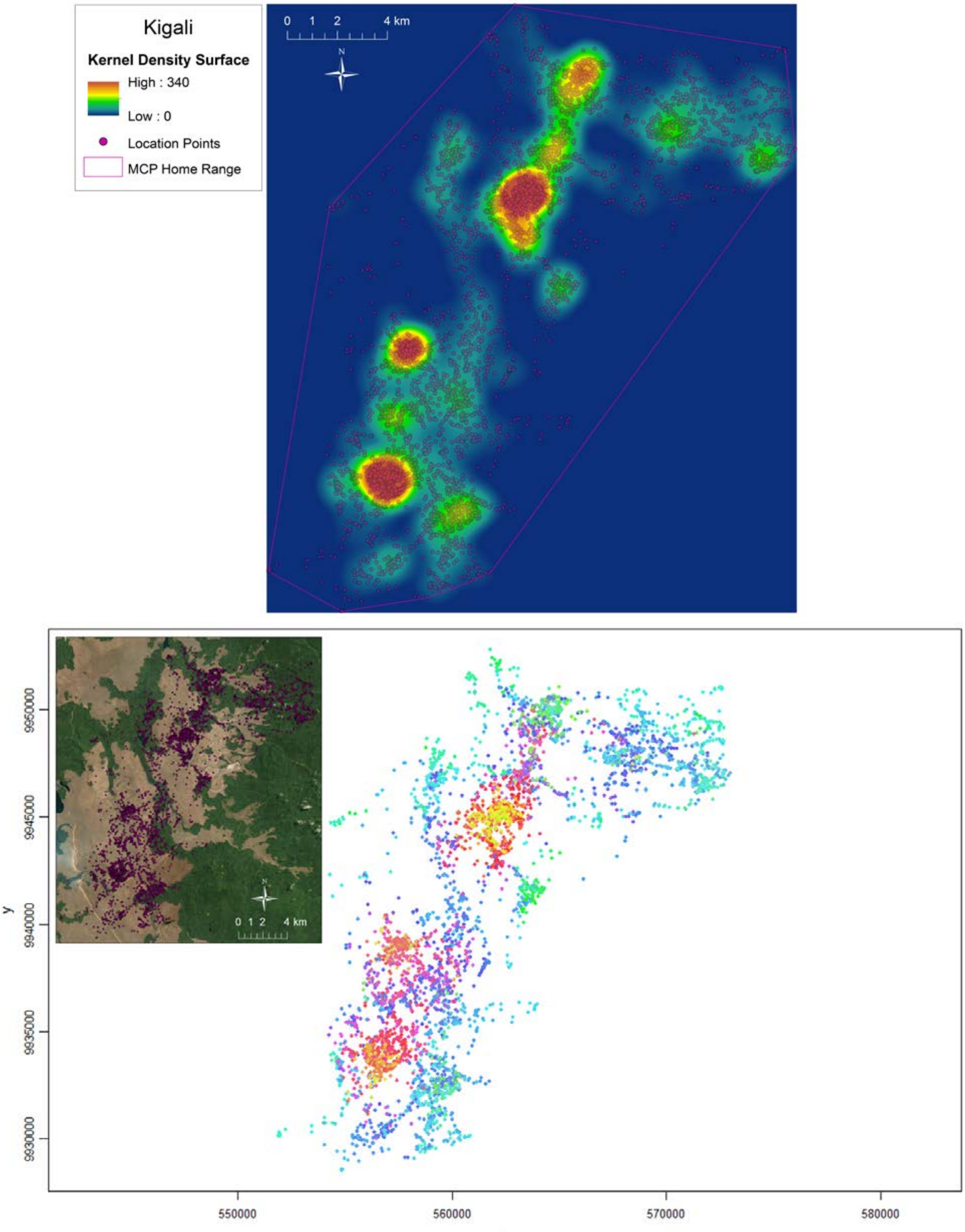
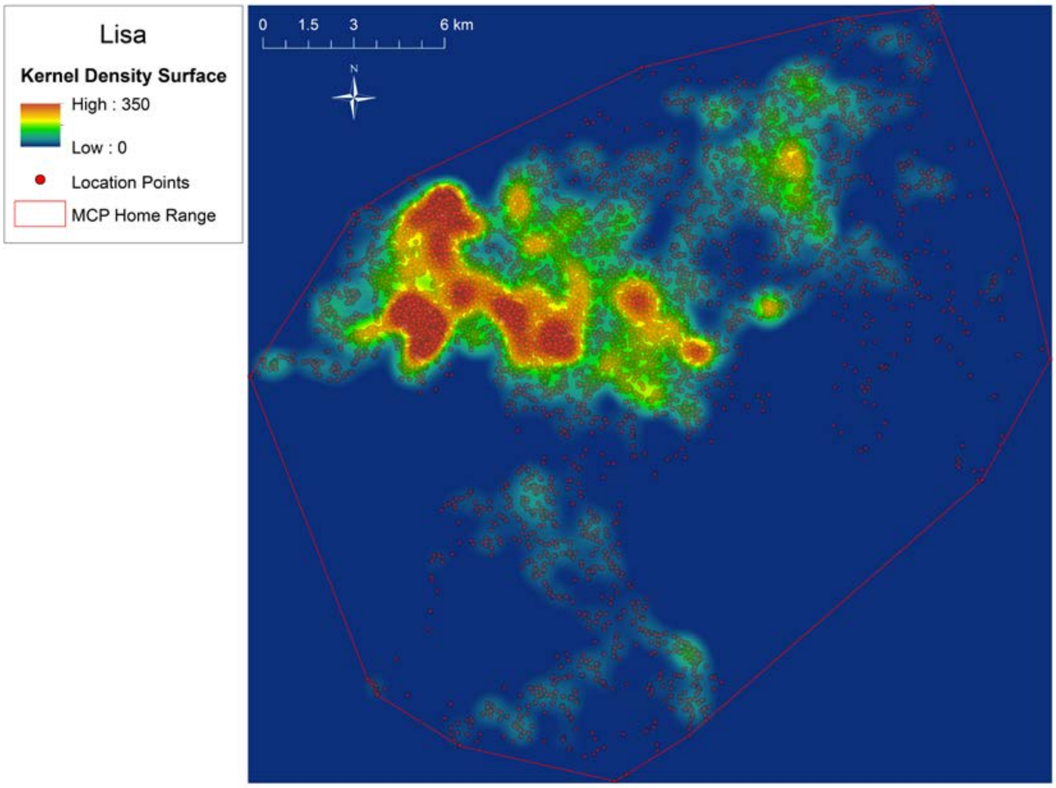


Figure S7. Kernel density surface (above) and time density graph (below) showing core home range areas for Kigali. Points, MCP home range, and land cover are shown for context.



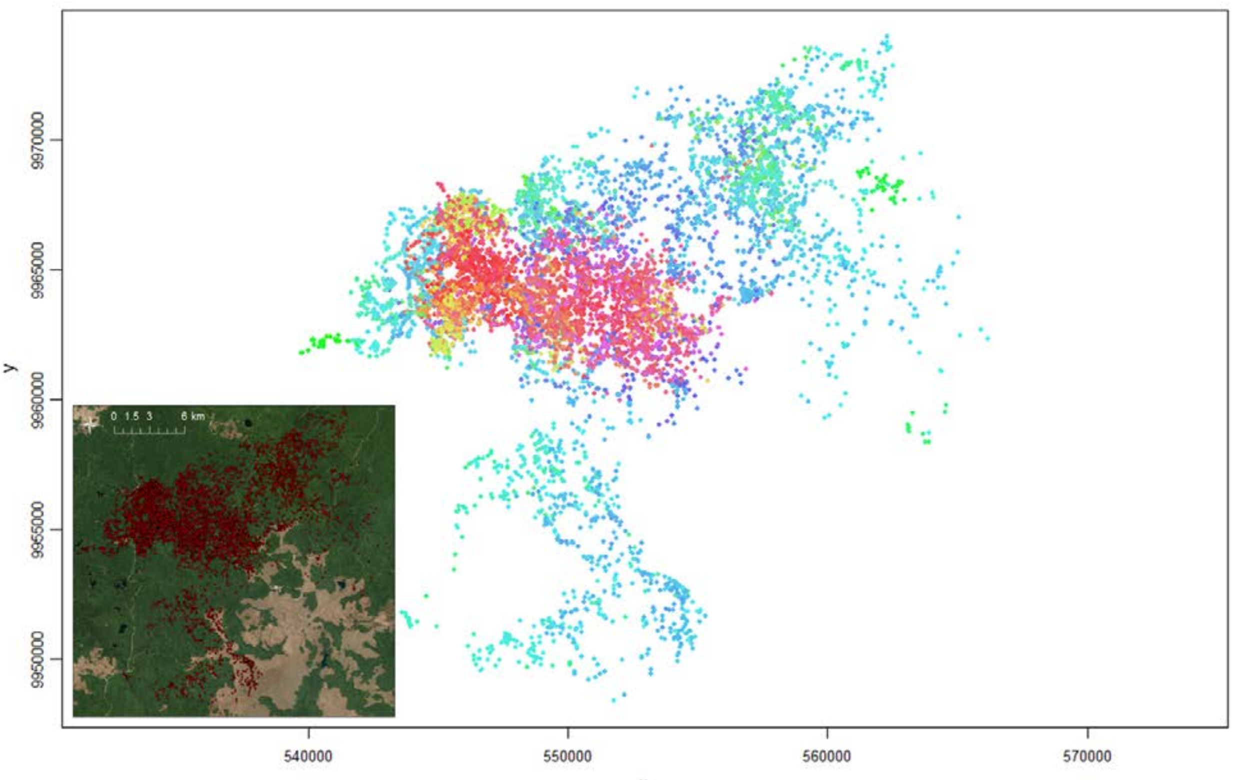


Figure S8. Kernel density surface (above) and time density graph (below) showing core home range areas for Lisa. Points, MCP home range, and land cover are shown for context.

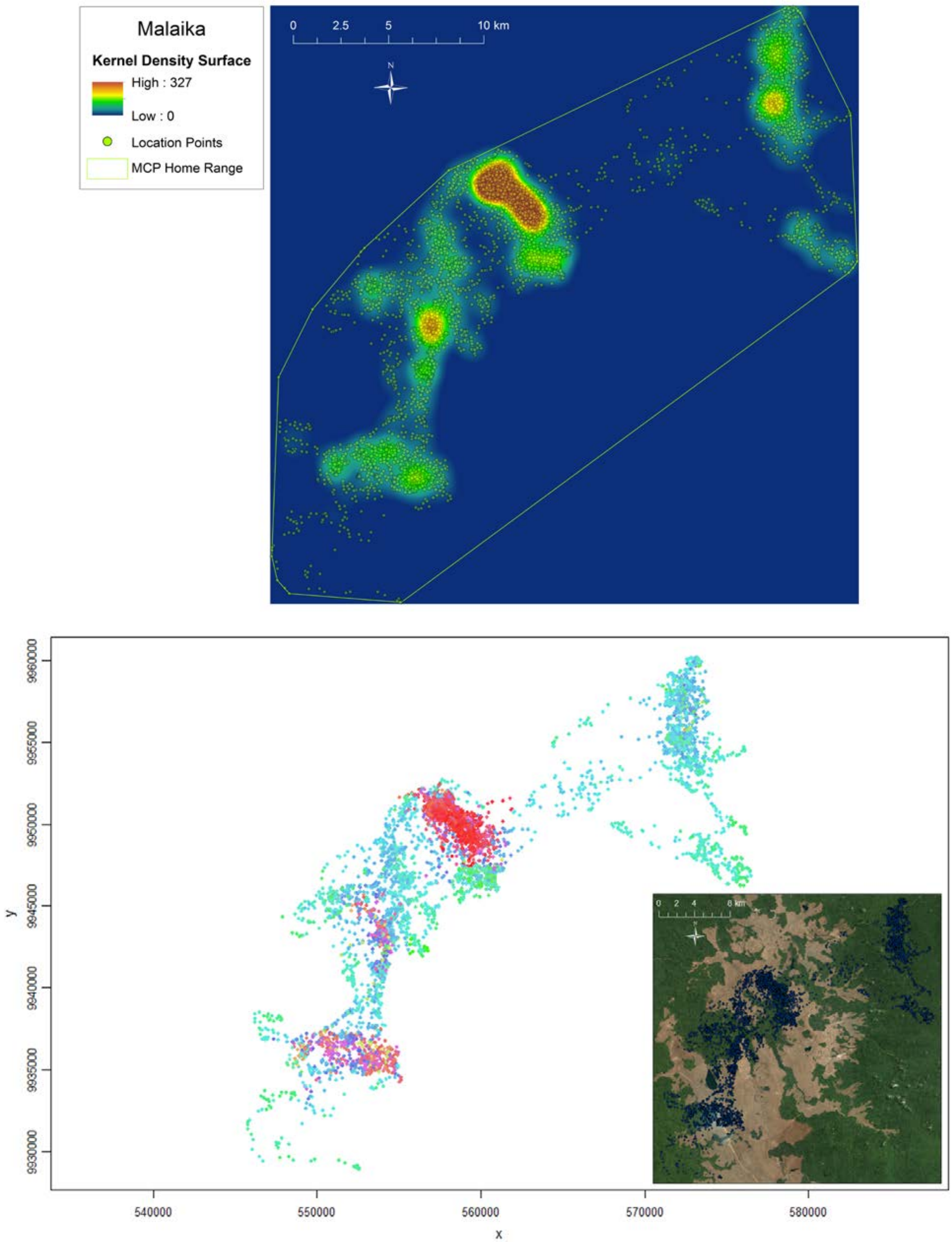
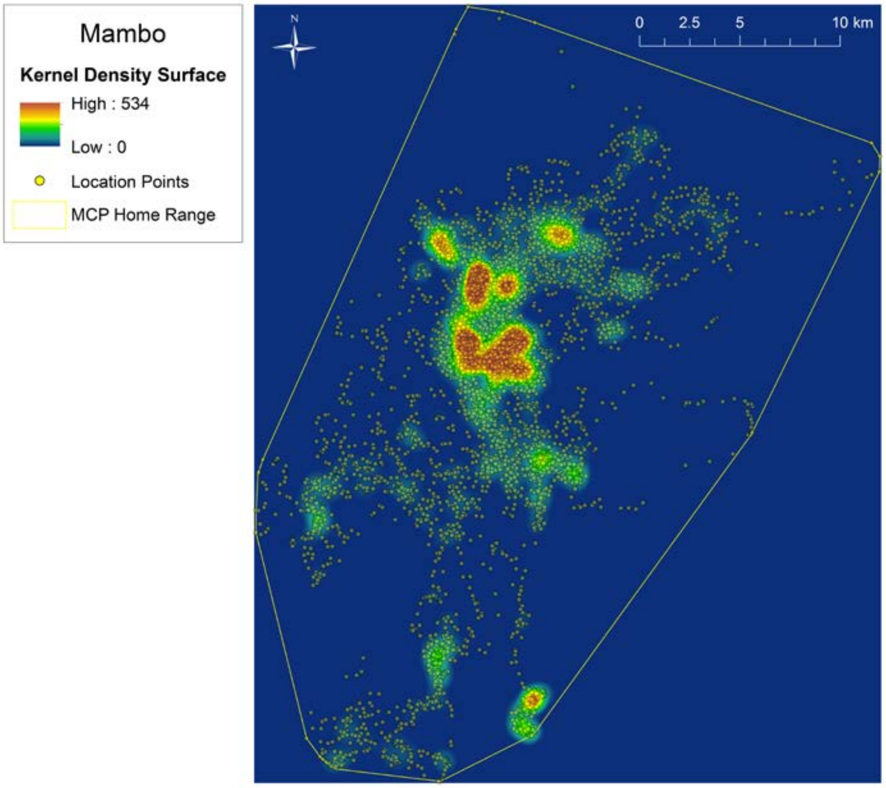


Figure S9. Kernel density surface (above) and time density graph (below) showing core home range areas for Malaika. Points, MCP home range, and land cover are shown for context.



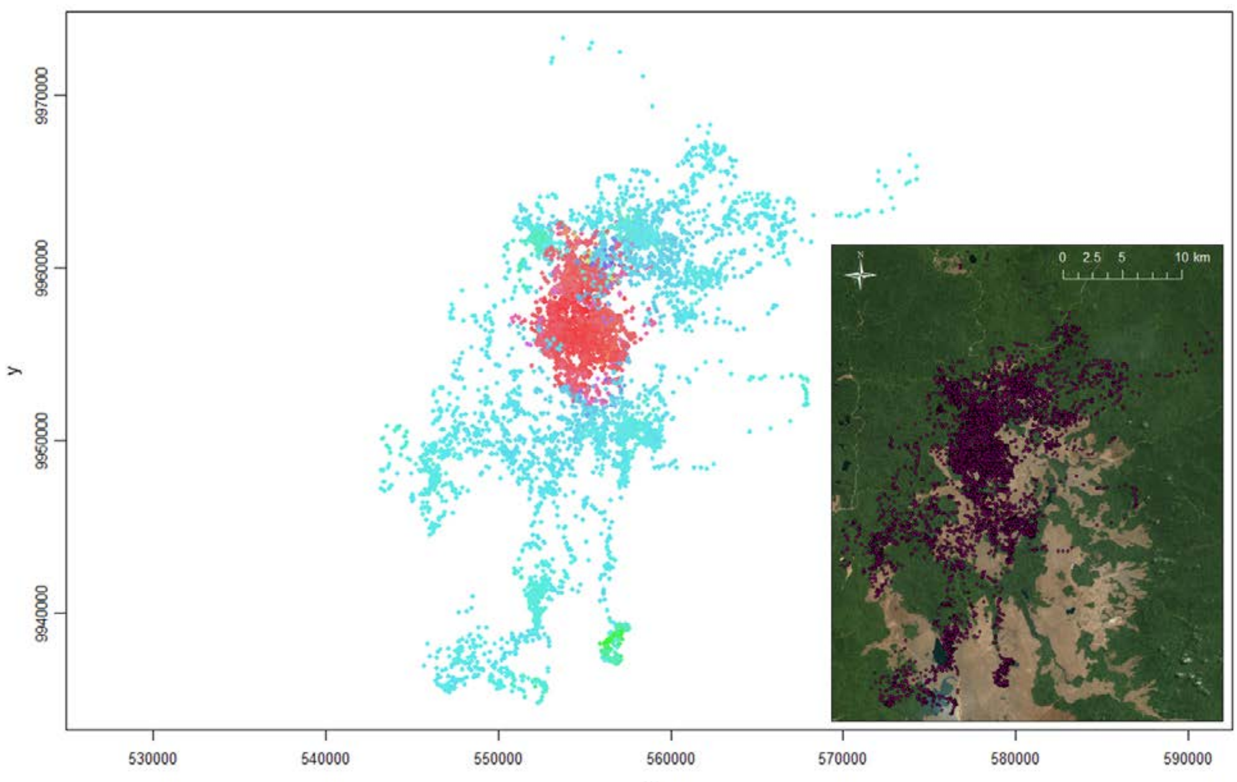
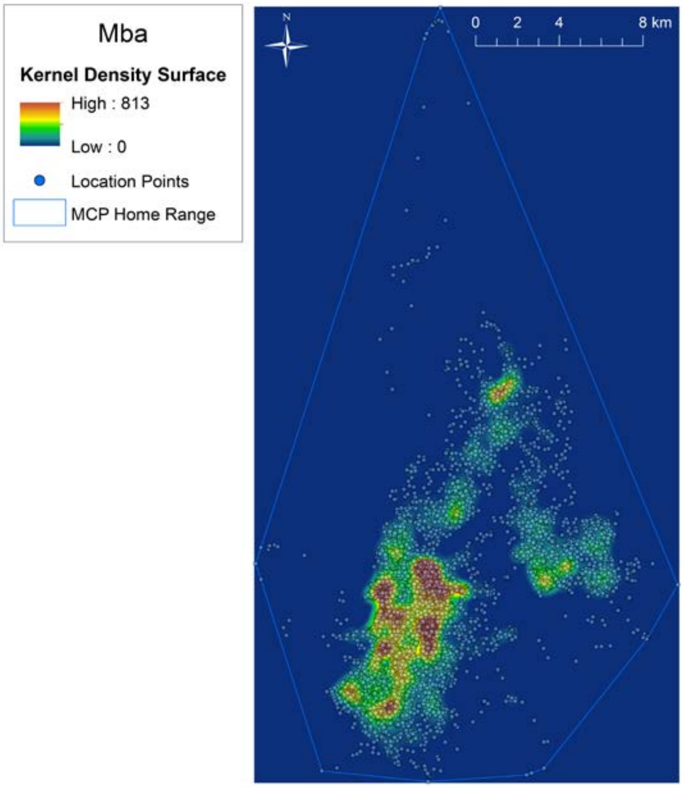


Figure S10. Kernel density surface (above) and time density graph (below) showing core home range areas for Mambo. Points, MCP home range, and land cover are shown for context.



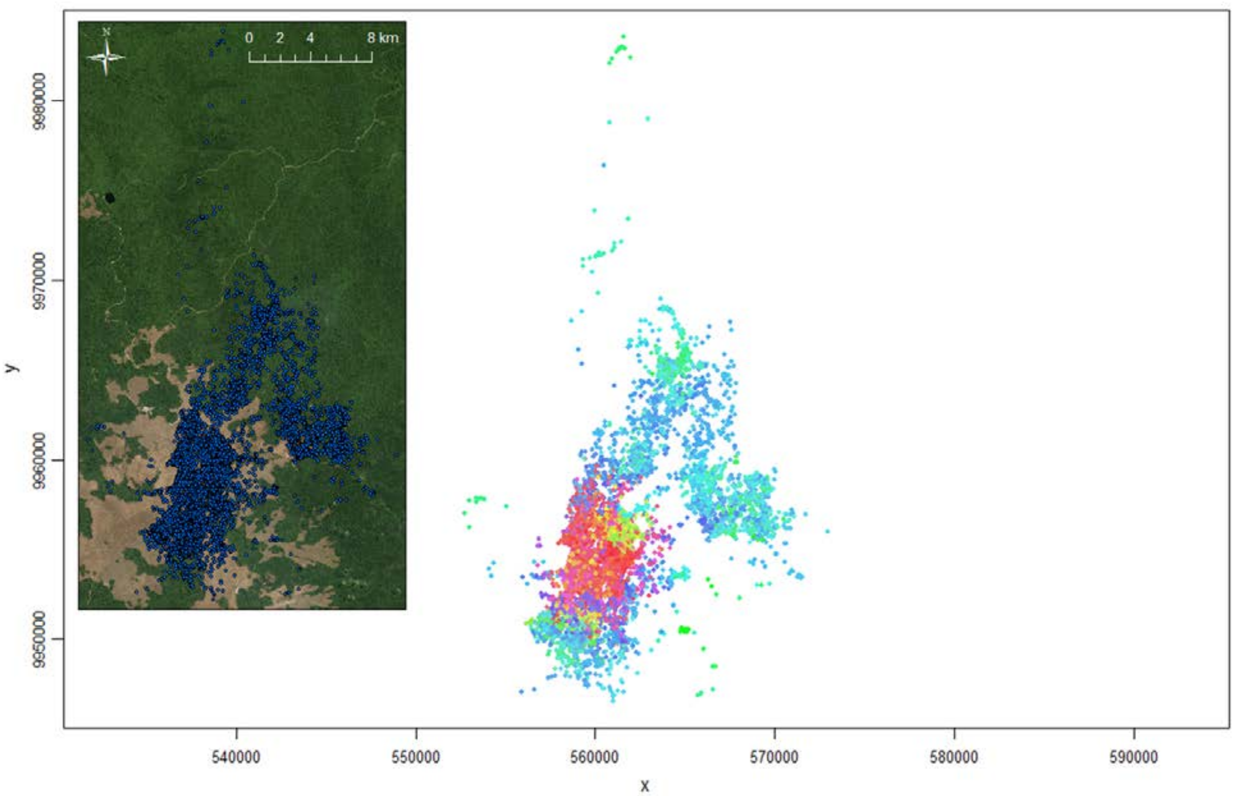
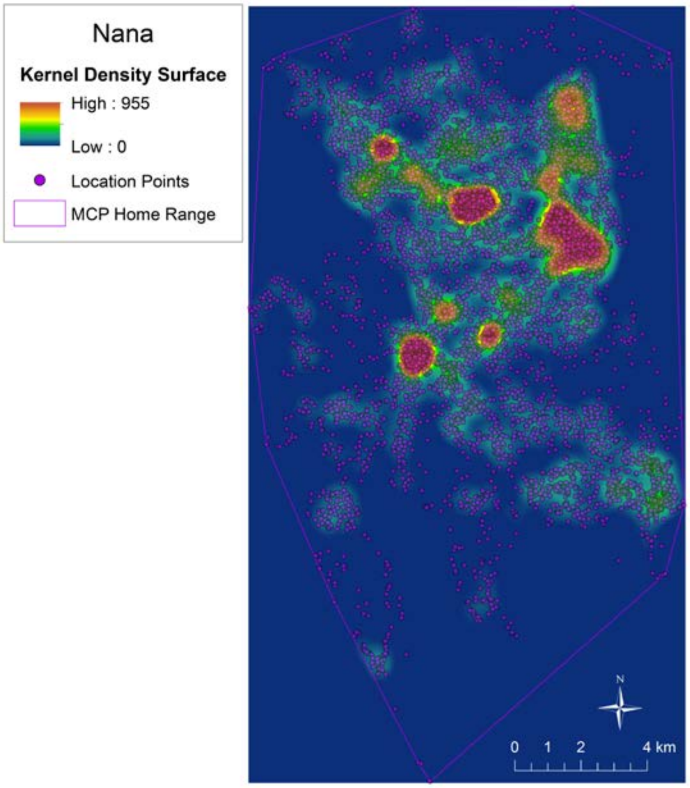


Figure S11. Kernel density surface (above) and time density graph (below) showing core home range areas for Mba. Points, MCP home range, and land cover are shown for context.



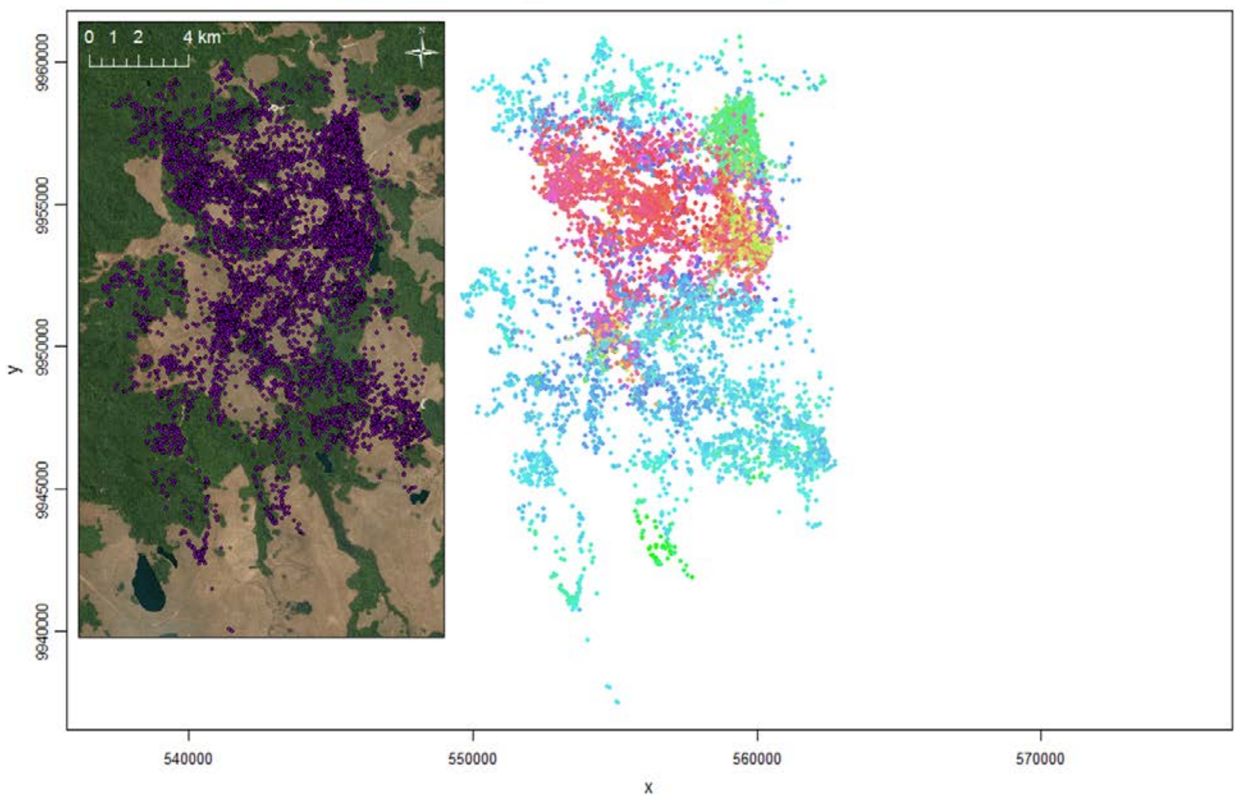


Figure S12. Kernel density surface (above) and time density graph (below) showing core home range areas for Nana. Points, MCP home range, and land cover are shown for context.

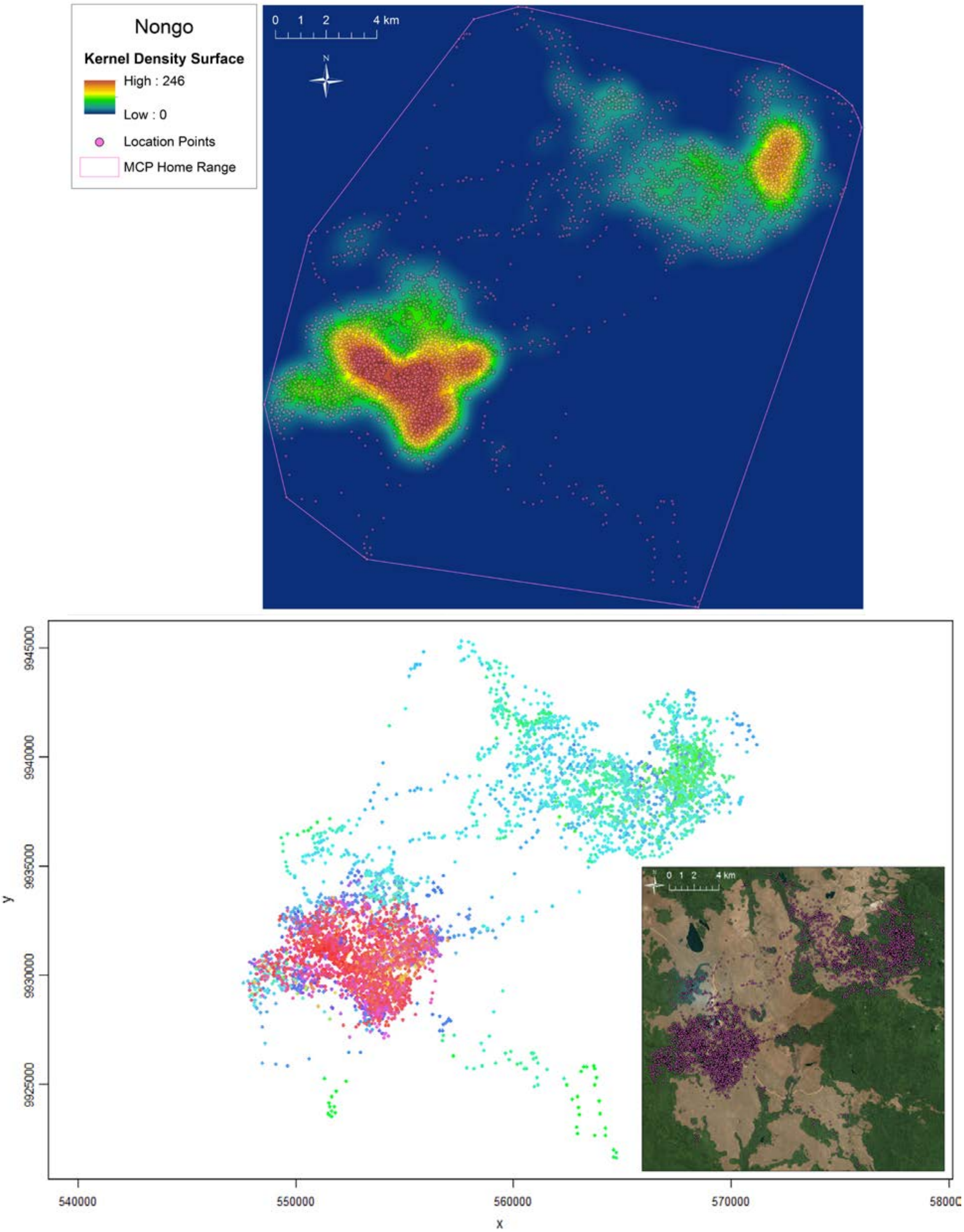


Figure S13. Kernel density surface (above) and time density graph (below) showing core home range areas for Nongo. Points, MCP home range, and land cover are shown for context.

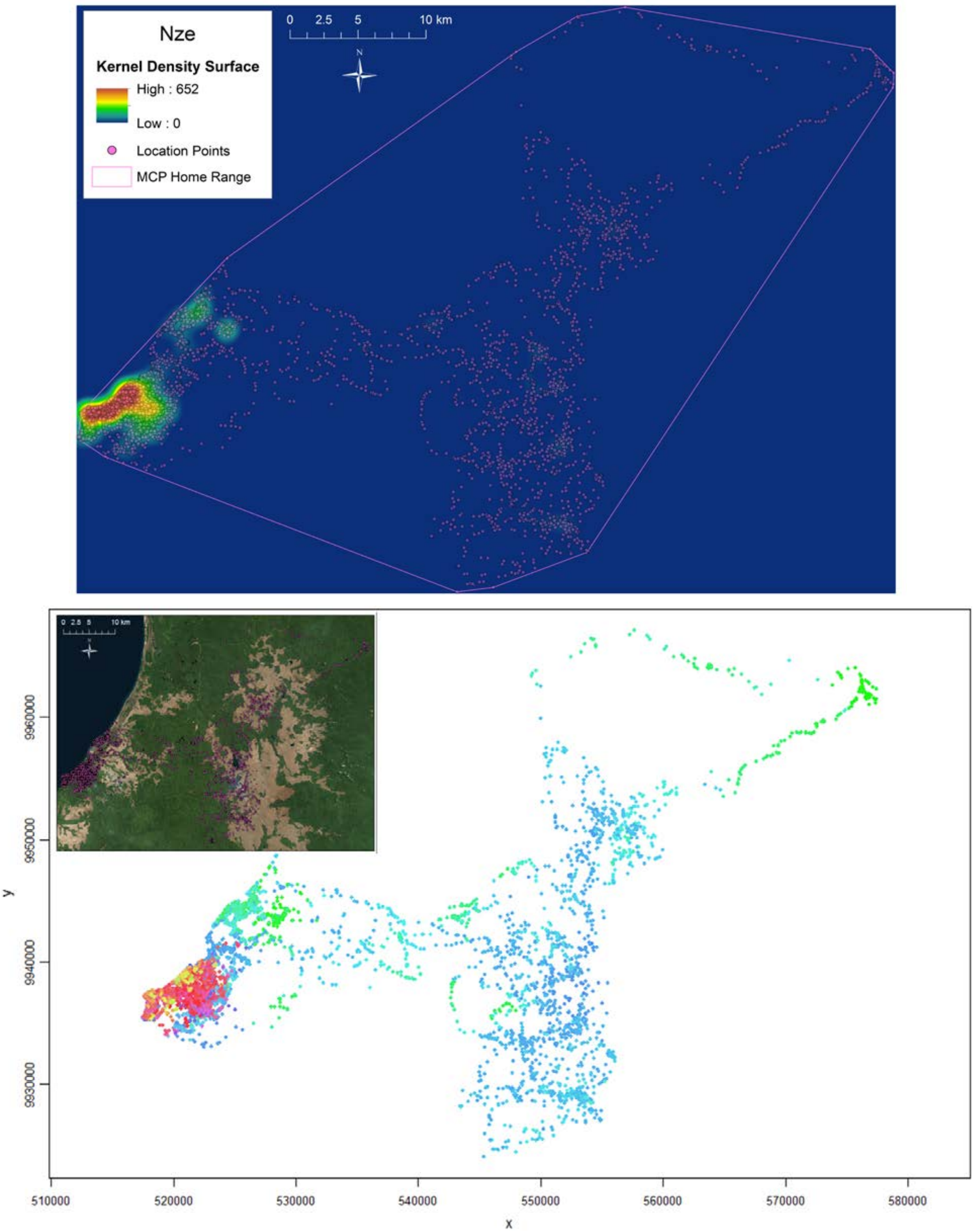


Figure S14. Kernel density surface (above) and time density graph (below) showing core home range areas for Nze. Points, MCP home range, and land cover are shown for context.

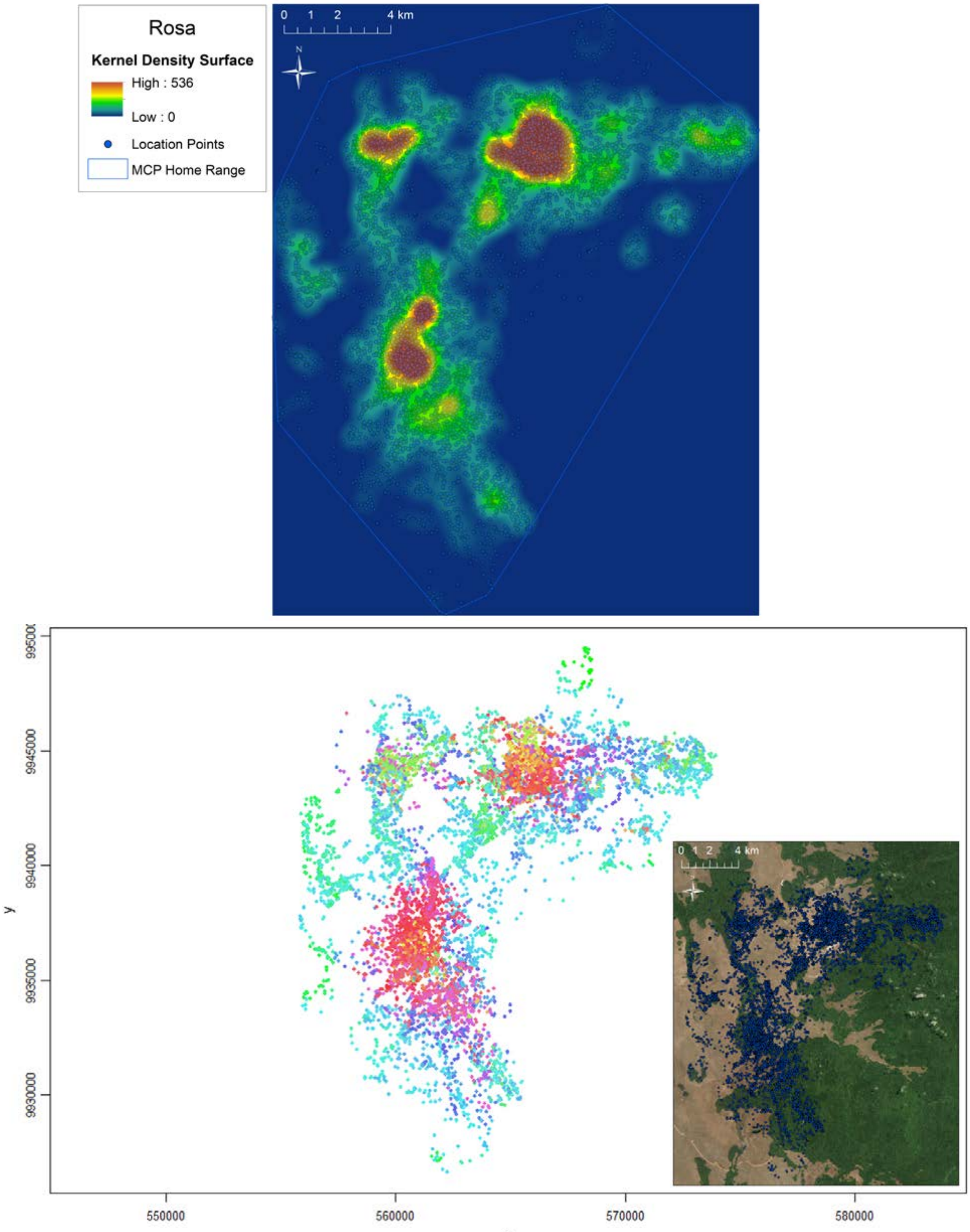
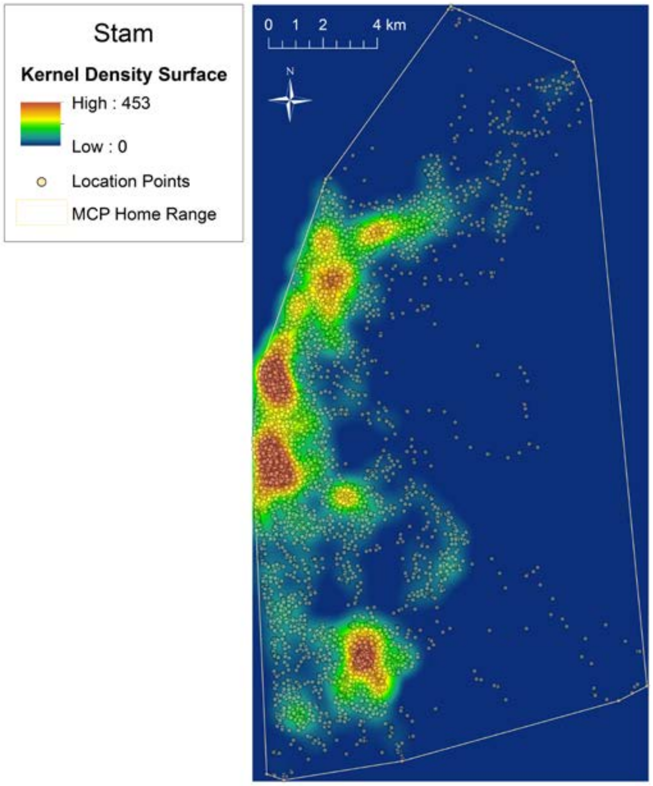


Figure S15. Kernel density surface (above) and time density graph (below) showing core home range areas for Rosa. Points, MCP home range, and land cover are shown for context.



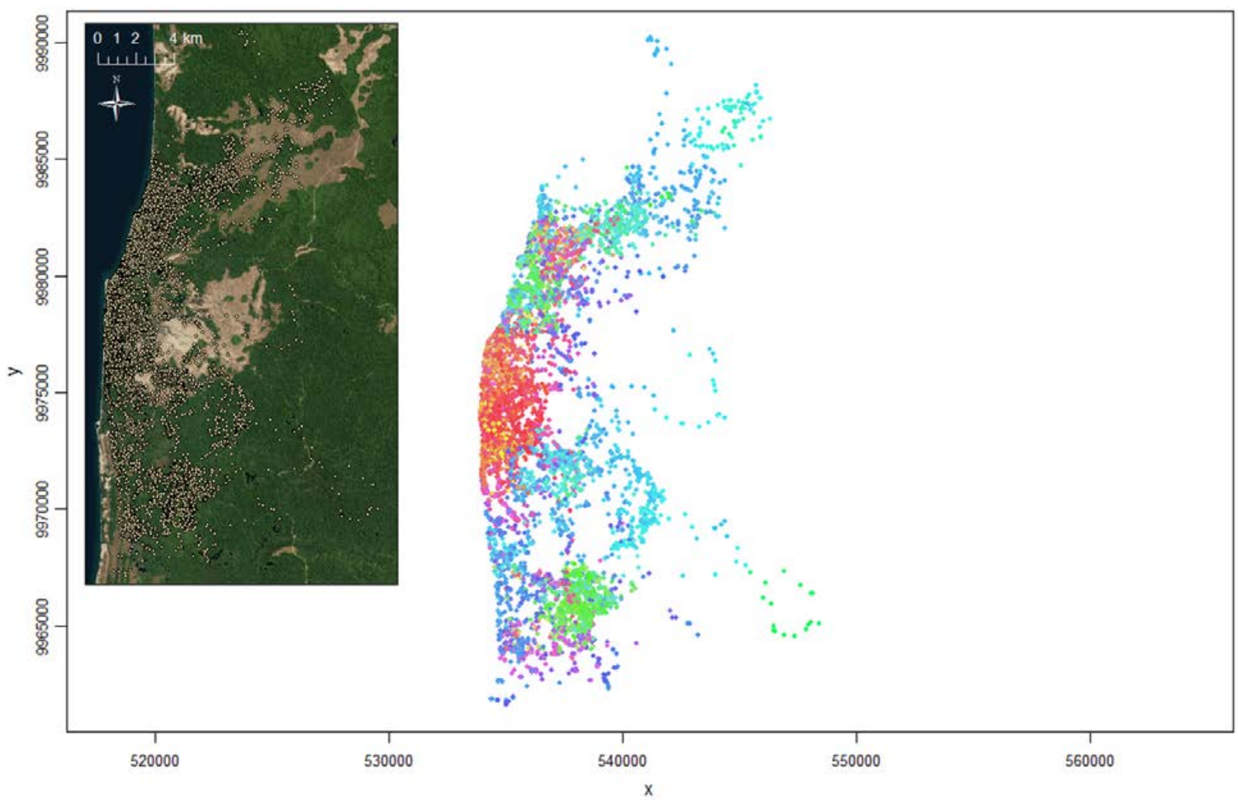


Figure S16. Kernel density surface (above) and time density graph (below) showing core home range areas for Stam. Points, MCP home range, and land cover are shown for context.

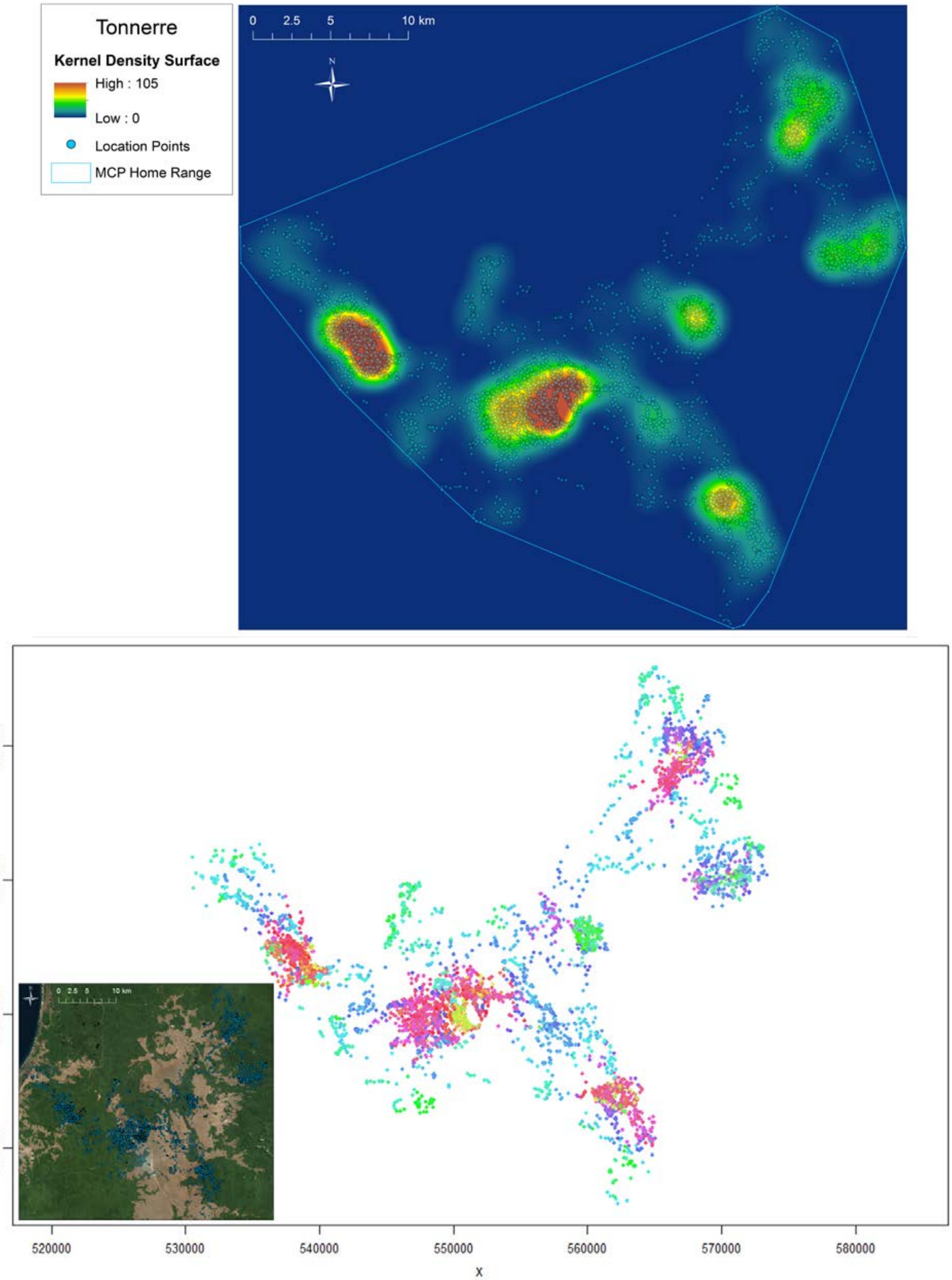


Figure S17. Kernel density surface (above) and time density graph (below) showing core home range areas for Tonnerre. Points, MCP home range, and land cover are shown for context.

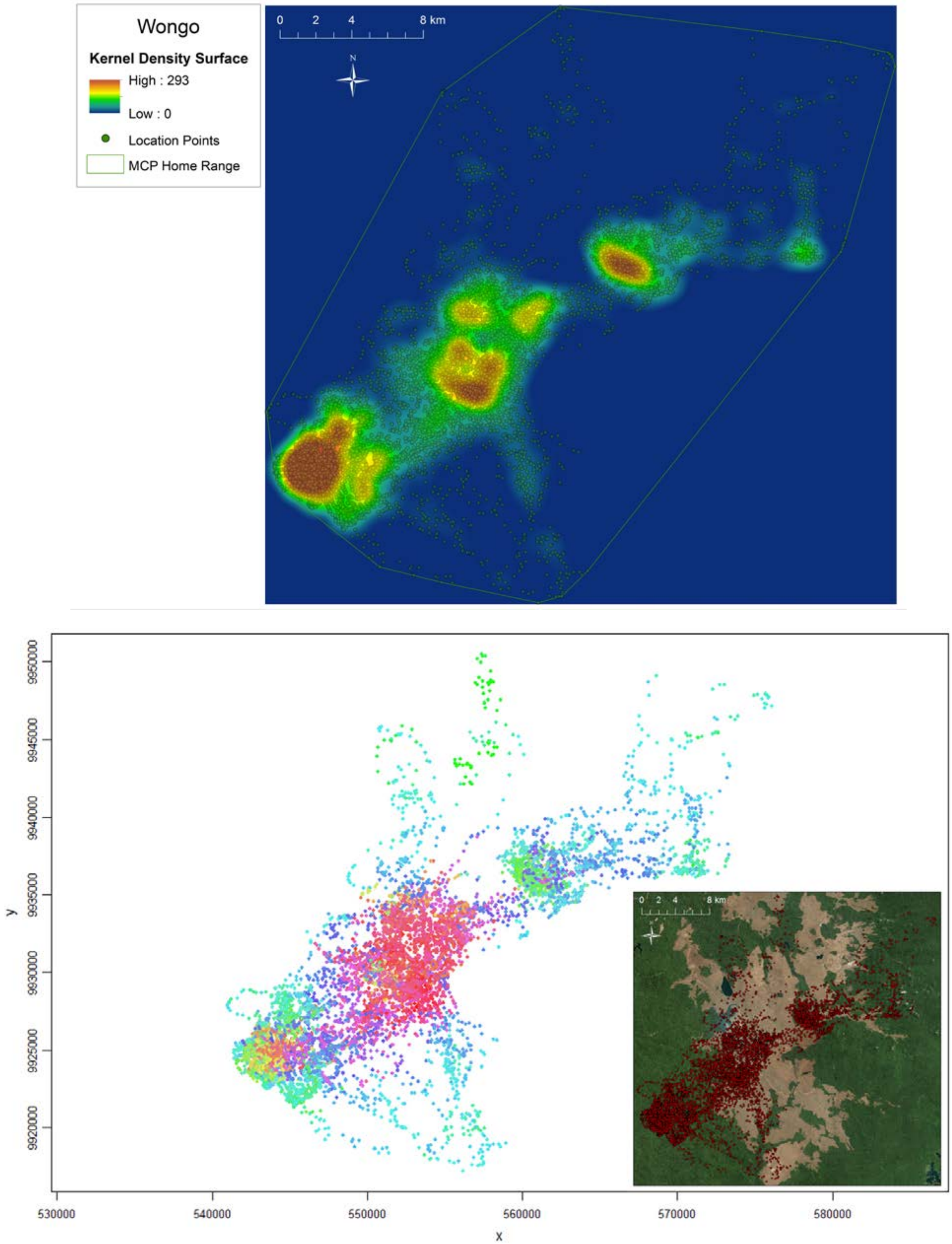
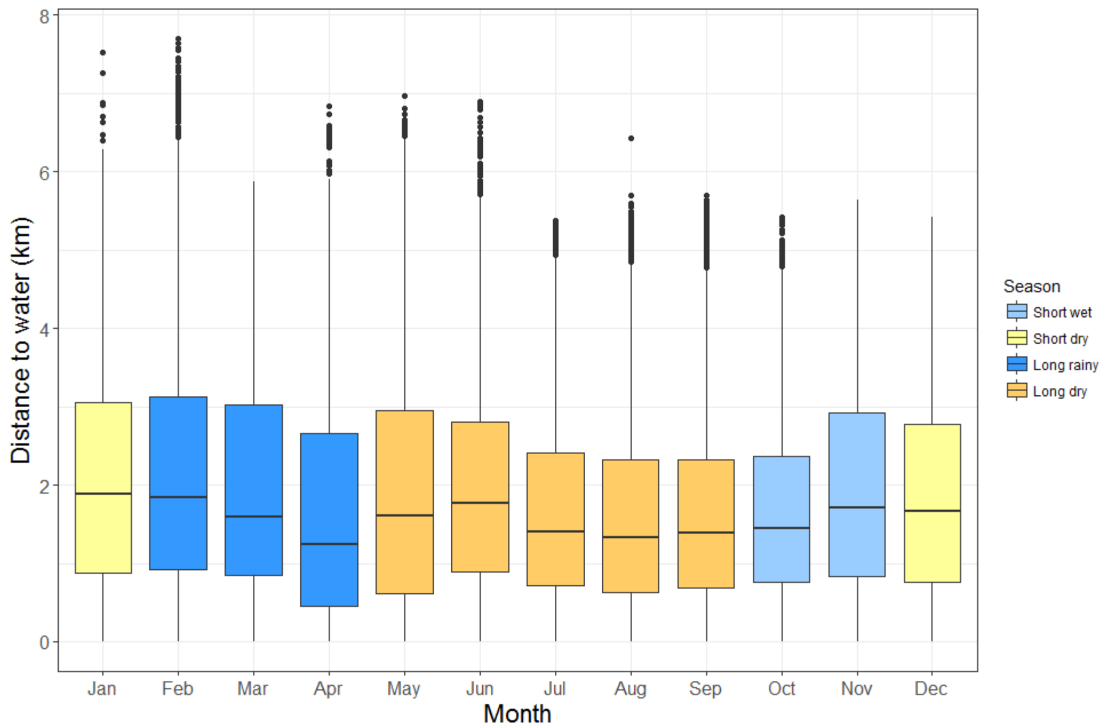


Figure S18. Kernel density surface (above) and time density graph (below) showing core home range areas for Wongo. Points, MCP home range, and land cover are shown for context.



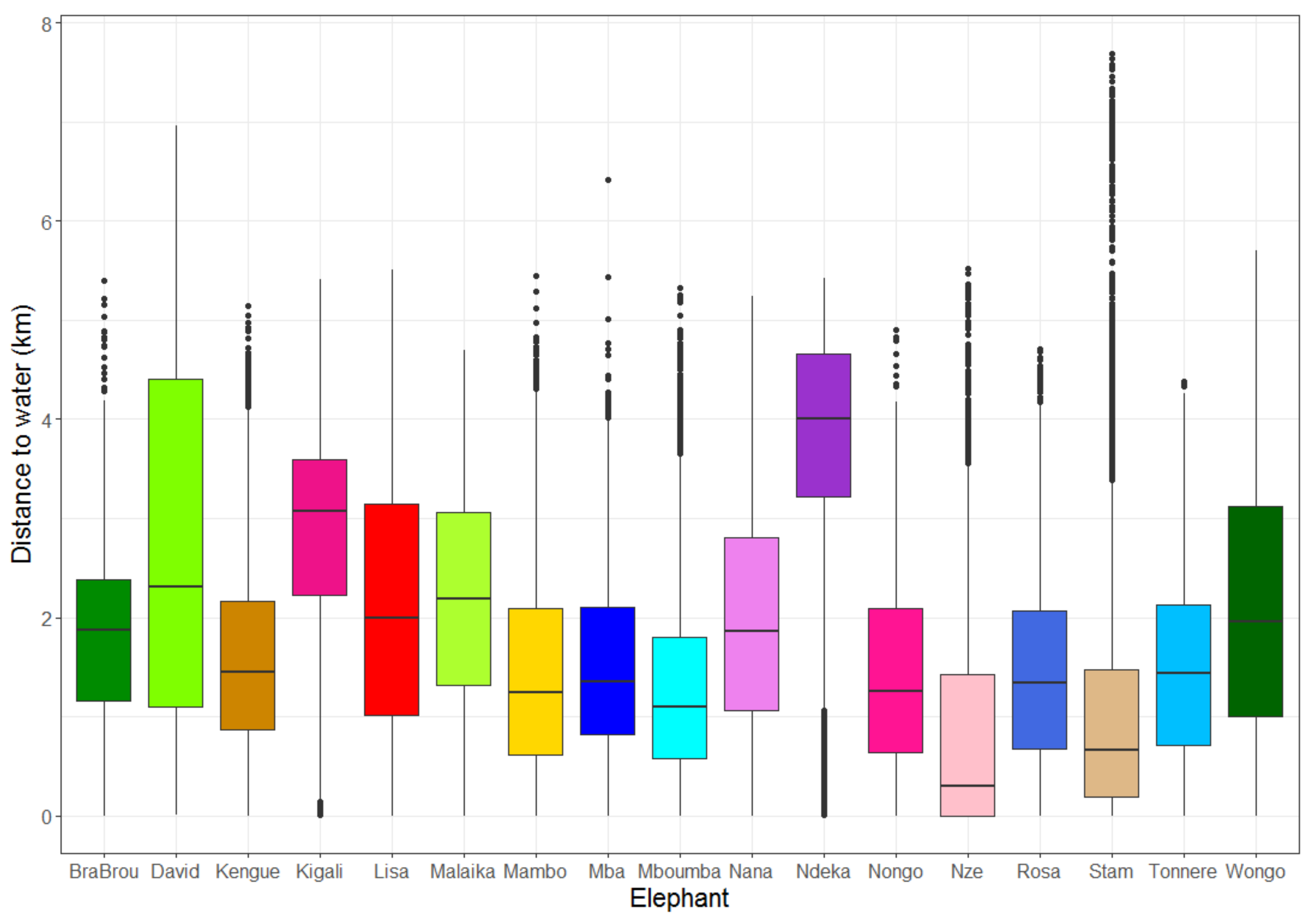


Figure S19. Distance to nearest water by month (above) and by elephant (below).

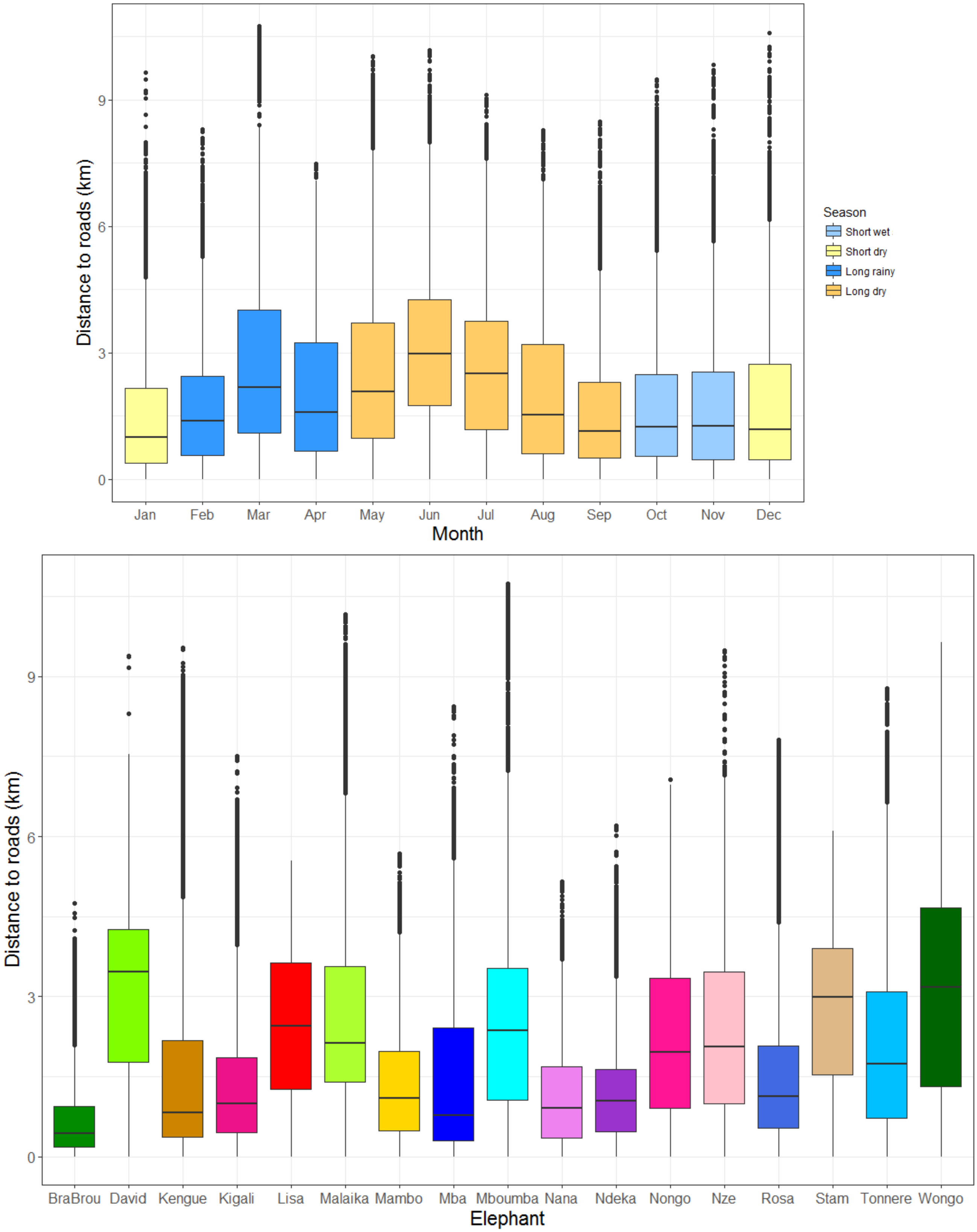


Figure S20. Distance to nearest roads by month (above) and by elephant (below).

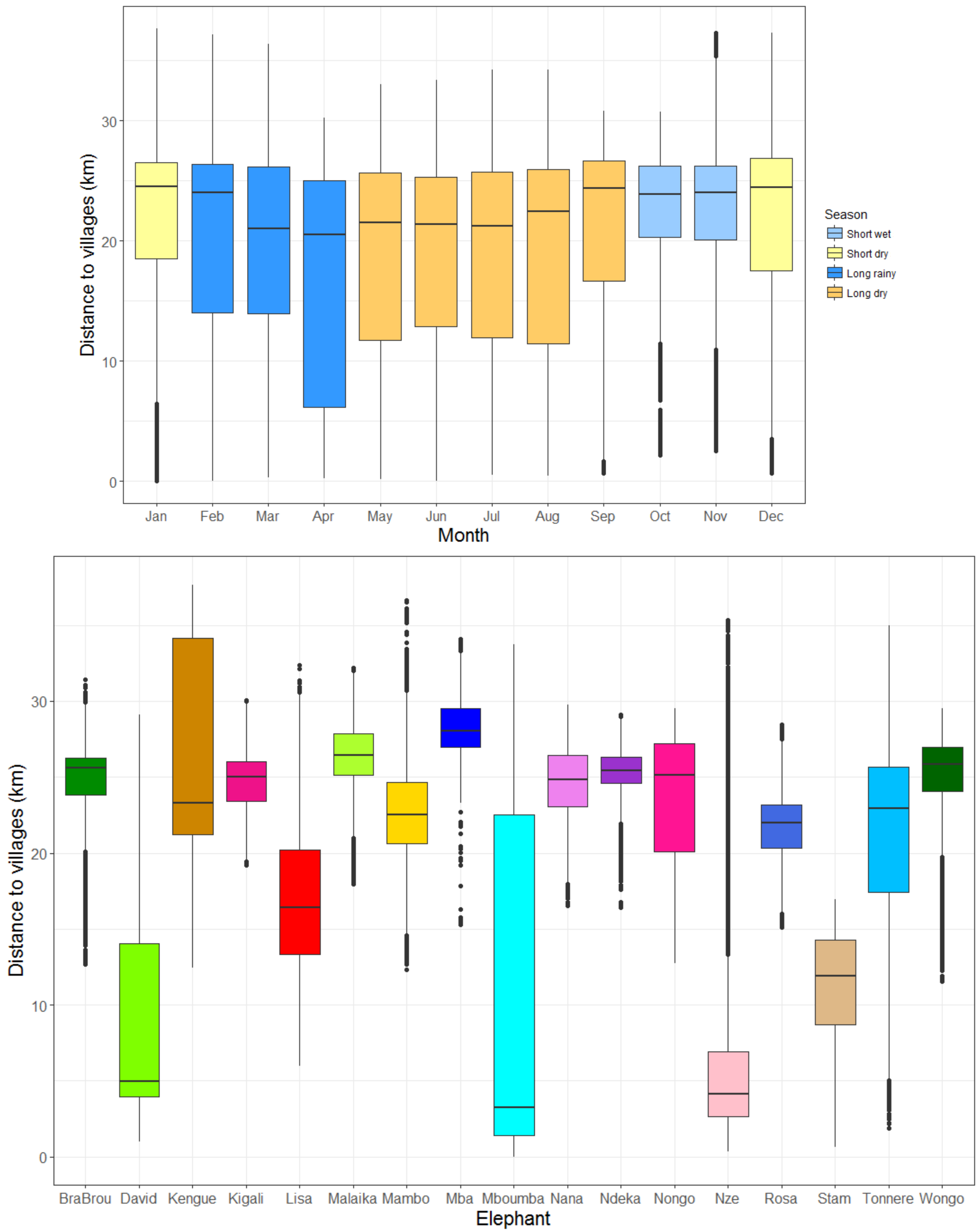


Figure S21. Distance to nearest villages by month (above) and by elephant (below).

Table S15. Descriptive statistics for average distance to water by elephant and season.

Elephant	Sex	Dry seasons average distance to water (km)	Wet seasons average distance to water (km)
Stam	F	0.79	1.34
Rosa	F	1.40	1.51
Lisa	F	1.83	2.29
Nana	F	2.02	1.94
Malaika	F	2.09	2.28
Ndeka	F	3.80	3.74
Nze	M	0.57	1.03
Mboumba	M	1.13	1.48
Mambo	M	1.30	1.58
Mba	M	1.33	1.65
Tonnere	M	1.49	1.48
Nongo	M	1.53	1.25
BraBrou	M	1.55	2.05
Kengue	M	1.61	1.55
Wongo	M	2.27	2.00
David	M	2.46	2.92
Kigali	M	2.93	2.85
Female Mean		**1.99**	**2.18**
Male Mean		**1.65**	**1.80**
Mean		**1.77**	**1.94**