Movement patterns of forest elephants (*Loxodonta cyclotis* Matschie, 1900) in the Odzala-Kokoua National Park, Republic of Congo.

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Abstract

African forest elephants (*Loxodonta cyclotis* Matschie, 1900) are ecological engineers that play a fundamental role in vegetation dynamics. The species is of immediate conservation concern, yet it is relatively under-studied. To narrow this knowledge gap, we studied the drivers of daily movement patterns (linear displacements) of forest elephants —characterised by a set of geographical, meteorological and anthropogenic variables— in the Odzala-Kokoua National Park, Republic of Congo. Explicitly, we used conditional random forest to model and disentangle the main environmental factors governing the displacements of six forest elephants, fitted with GPS-collars and tracked over 16 months. Results indicated that females moved further distances than males, while the presence of roads or human settlements disrupted elephant behaviour resulting in faster displacements. Forest elephants moved faster along water courses and through forest with understory dominated by Marantaceae forests and bais, but moved slower in savannahs. Finally, flood-prone areas —described by elevation and accumulated precipitation— and higher temperatures prevented longer displacements. We expect these results to improve the knowledge on the species movements throw different habitats, which would benefit its conservation management.

Key words: Central Africa; distance to road; elephant gender; linear displacements; GPS telemetry; seasonal behaviour.

1 INTRODUCTION

Forest elephant (*Loxodonta cyclotis* Matschie, 1900) movement and feeding behaviour (pollarding, peeling and trampling) modify forest structure, controlling the availability of resources for other organisms (Poulsen et al., 2018), and maintaining habitats with open canopy such as bais — forest clearings— (Fishlock, 2010; Metsio Sienne, Buchwald, & Wittemyer, 2014; Turkalo, 2013). A reduction in the abundance of forest elephants can alter plant communities and ecosystem function (Poulsen et al., 2018), which may have implications for the entire ecosystem due to cascading effects. Central Africa holds the main part of African forest elephant populations, although they are currently enduring a pronounced increase in poaching activities, particularly in Gabon and Congo, where the bulk of the entire population exist (Breuer, Maisels, & Fishlock, 2016; Gobush, Mutayoba, & Wasser, 2008; Maisels et al., 2013; Poulsen et al., 2017), but also in eastern Democratic Republic of Congo, south-eastern Cameroon and south-western Central African Republic (Wasser et al., 2015). From 2006 until the present, a severe decline in elephant numbers has been detected due to a surge in ivory poaching to the extent that the increasing human-elephant conflict and habitat loss have been overshadowed in importance (Convention on International Trade in Endangered Species of Wild Fauna and Flora - CITES, 2016). The Republic of Congo still hosts large populations of forest elephants, although there is concern there regarding the illegal ivory trade (Milliken, Burn, Underwood, & Sangalakula, 2013; Wittemyer et al., 2014). Nonetheless, the estimated forest elephant population in Odzala-Kokoua National Park (hereafter OKNP) was recorded to be at about 14,000 individuals (1.0 elephant per km^2) (Blake et al., 2007) and it is still one of the highest densities for the species.

Mammal species tend to suffer from a higher risk of extinction when they have higher body mass and larger ranges, as well as when their habitat is more fragmented (Crooks et al., 2017; Gonzalez-Voyer, González-Suárez, Vilà, & Revilla, 2016; Ripple et al., 2016). Thus, aside from the commercial interest of their ivory and other anthropogenic side-effects, elephants are intrinsically at greater risk of extinction, and the study of their range, movement patterns and linear displacement throughout different landscapes are of special concern for their effective conservation. Information about mammal movement and migrations is crucial for conservation plans, but is often scarce (Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009). Apart from the distribution of food and other key resources (Johnson, Kays, Blackwell, & Macdonald, 2002), mammal movement patterns are mainly determined by interactions between individual characteristics (e.g., maturity) and weather (Elliot, Cushman, Loveridge, Mtare, & Macdonald, 2014). In order to implement effective conservation and management plans, a greater understanding is required about elephant movements across large areas and over long periods (Breuer et al., 2016; Loarie, Aarde, & Pimm, 2009). Both the distribution and movement patterns of African Savannah elephants (*Loxodonta africana* Blumenbach, 1797) have been related to land cover type (Loarie et al., 2009; Young, Ferreira, & van Aarde, 2009), weather (i.e., temperature and rainfall) (Birkett, Vanak, Muggeo, Ferreira, & Slotow, 2012; Bohrer et al., 2014), as well as elevation, slope, and the presence of water bodies (natural or artificial)(Graham, Douglas-Hamilton, Adams, & Lee, 2009). These natural features interact with human infrastructures such as fences or human settlements (Buij et al., 2007; Loarie et al., 2009), which shape elephant movement patterns. Furthermore, spatial movements were shown to influence survival and reproduction rates in savannah elephants (Goldenberg, Douglas-Hamilton, & Wittemyer, 2018). But, while determinants of elephant distribution and movement patterns have been extensively studied for Savannah elephants (Bohrer et al., 2014; Buij et al., 2007; de Knegt et al., 2011; S. Z. Goldenberg, Douglas-Hamilton, Daballen, & Wittemyer, 2016; Shifra Z. Goldenberg et al., 2018; Young et al., 2009), relatively little is known about the ecology of the forest elephant largely due to the difficulties of undertaking direct observations of them in rainforests.

Previous studies suggest that forest elephants prefer to move at night (Kuwong, 2014; Turkalo, Wrege, & Wittemyer, 2013), probably conditioned by the schedules of human activities, and that seasonal displacements of forest elephants are a result of the distribution and fruiting patterns of diet tree species (Blake, 2002; Mills et al., 2018; Short, 1983; White, 1992). In addition, elephants are known to use bais for access to minerals (Metsio Sienne et al., 2014), while these sites also function as social arenas where elephants exhibit aggregations (Fishlock, 2010; Turkalo et al., 2013). It is also known that elephants benefit from herbaceous vegetation in recently logged forests (Clark, Poulsen, Malonga, & Elkan, 2009; Stokes et al., 2010) and positively select for this vegetation type during specific seasons (Mills et al., 2018). By contrast, non-surveyed roads outside protected areas — which are not patrolled to control hunting or poaching— are formidable barriers to elephant displacements (Blake et al., 2008; Laurance et al., 2006). Finally, it has been reported that elephant abundance and distribution varies seasonally, depending on the water-forest matrix, the forest-grassland matrix, and the distribution and phenology of fruit trees (Blake, 2002; Mills et al., 2018; Schuttler, Blake, & Eggert, 2012).

The goal of this study is to disentangle the main environmental drivers governing the daily linear displacements of forest elephants in the OKNP. Specifically, we hypothesise that forest elephants stay near areas of high resource abundance (mainly food and shelter), away from human disturbances, and perform long-distance seasonal displacements to satisfy their ecological and behavioural requirements; thus a suite of interactions between natural and anthropogenic variables drive their displacements and whether they stay put or migrate. To test this hypothesis we: i) employed GPS collars to collect information on OKNP elephant spatial movements, ii) gathered data on geographic (e.g., elevation or slope), meteorological (e.g., rainfall and temperature) and anthropogenic (e.g., distance to villages and roads) variables for the study period, iii) and used Conditional Random Forest (CRFs, Carolin Strobl, Boulesteix, Zeileis, & Hothorn, 2007) to determine the most relevant variables influencing elephant daily displacements.

2 MATERIALS AND METHODS

2.1 Study area

The OKNP (Figure 1; 00°23'-01°10'N, 014°39'-015°14'E) is located 850 km north of Brazzaville, Republic of Congo, and is geographically placed between the Batéké Plateau and the northern Congo forests (Mbete, Ngokaka, Ntounta, & Vouidibio, 2010). The highest elevations are found in the W and NE of the park, while the main basin that drains the park flows towards the SE. Of its total area of 13,600 km^2, six percent of the park surface is covered by savannah (Aveling & Froment, 2001). Nevertheless, this area is described as a forest-savannah mosaic, with dense gallery forest along the deeper river valleys, and savannah areas dominated by grass species (family Graminae), with scattered fire-resistant shrubs (Bermejo, 1999). Today, it is the oldest and largest protected area in the country and is a Biosphere Reserve. The remainder of the park is composed of Congolian evergreen forests and semi-deciduous transitional forest, Marantaceae forest, swamp forests and secondary forests found along roads and abandoned settlements and clearings. At OKNP, agriculture is forbidden, although some subsistence farming (manioc, corn, peanut) takes place on its outskirts, triggering some human-elephant conflicts in the Park and its surroundings (Boukoulou et al., 2012). Some tourist activity exists in the central part of the park, mainly between the savannah of Mboko and the Lango bai and, as such, there are some buildings in this area: hangars, a small dock, a small airstrip and two groups of accommodation buildings where most of the tourist activities occur.

[Figure 1 here]

2.2 Elephant movements data collection

We immobilized eight adult elephants and fitted them with GPS collars (African Wildlife Tracking) following methods in Blake, Douglas-Hamilton, & Karesh (2001), between November and December 2014. All International and Congolese guidelines for the care and use of animals were followed. Collar #9 stopped working before being fitted and collar #2 (Female 2) apparently stopped working a few days after the capture; consequently, this elephant was not considered in the analyses. The remaining six collars worked properly, taking up to one fix per hour. From 22 November 2014 until 11 April 2016, a database of 14,780 fixes was obtained for the six elephants, which roamed across the southern part of the park (Figure 1). On average, collars failed to transmit 47.6% of fixes, resulting in a mean of 6 (3–13) fixes per day (see Figure B1 in supplementary material for a graphical depiction about the distribution of fixes per month). The failure of data transmission was exacerbated under dense forest canopy; thus, the longer an individual spent under the forest canopy or other types of dense land cover, the fewer the fixes collected (D'Eonet al., 2002), This situation partly determined the selection of the modelling technique used in this study (see section 2.4). In general, the temporal distribution of fixes and intervals between them show marked differences between different tracking devices and consequently render an uneven temporal distribution (Loarie et al., 2009). This deficiency is usually addressed by removing the most inaccurate fixes and by averaging the positions to one fix at a standard time step (e.g., every 8 or 24h de Knegt et al., 2011; Loarie et al., 2009). However because we used only one type of tracking device, we did not remove any locations to avoid losing data for forest and dense land cover types, which were of particular interest. Nonetheless, we standardised the location of each elephant in 24h time steps to calculate the daily linear displacement (km/24h). We averaged the values of the coordinates (X, Y) of the fixes collected every 24h. Environmental variables were assigned at the site of mean 24h fixes, whereas the daily linear displacement was calculated by summing half the distance from this site to both the previous and subsequent locations of mean 24h fixes respectively.

2.3 Environmental covariates

The OKNP is characterised by an annual rainfall of 1,200 mm, spread over two rainy and two dry seasons (Mbete et al., 2010). Therefore, we assigned elephant locations to: Short Dry (Dec–Feb), Short Rainy (Mar–May), Long Dry (Jun–Aug), and Long Rainy (Sep–Nov) seasons (see Figure B1 in supplementary material for a graphical depiction about the distribution of fixes per season). We obtained daily rainfall and temperature data from the GSOD (Global Surface Summary of the Day) website maintained by the NOAA (National Oceanic and Atmospheric Administration) within the United States Department of Commerce. Four meteorological stations surrounding the OKNP were selected (i.e., the meteorological stations located at Kellé, Makoua, Ouésso and Souanké). The meteorological variables used were the maximum, minimum and mean temperature (Max., Min. and Mean, respectively), precipitation, as well as the moving average (MA) for the 30 preceding days for these four variables, in order to better describe the two rainy and dry seasons (Table 1). These variables were calculated for each meteorological station and were interpolated at each mean 24h fix. However, the reliability of the values collected each station for the mean 24h fix is inversely proportional to the distance between them and the mean 24h fix. Therefore, the interpolation was inversely weighted by the distance of the mean 24h fix to each meteorological station.

[Table 1 here]

We retrieved the Digital Elevation Model from the web site of the Consortium for Spatial Information (CGIAR-CSI) and used it to infer the slope with ESRI® ArcMap™ 10.3.0.4322. The land cover type and complementary geospatial data (roads, rivers, villages and territorial boundaries) were obtained from the Ministry of Forestry and Environment (2011). Specifically, data related to vegetation classes were derived from a satellite image (Landsat) and consisted of 15 different cover types including forested areas of different canopy cover (e.g., savannah, dense closed forest, etc.), water and flooded areas (e.g., swamp forest) and areas covered by clouds, which were eventually removed from final analyses. The land cover type assigned to each elephant location was then found at the coordinates of the mean 24 h fix. In the end, forest elephants travelled across ten out of the thirteen different land cover types (Figure 1). The distance of each daily observation to the nearest river was used as a proxy for water resource availability, and was also calculated with ESRI® ArcMap™ 10.3.0.4322. Human footprint was characterised by means of distance to villages, distance to the Lango lodge, and distance to main roads, which were calculated in the same way as the distance to rivers. Finally, we also considered the sex of each individual in the analysis. A graphical depiction of the correlations among variables can be found in the Appendix A of supplementary material.

2.4 Data analysis with conditional random forests

Gathering information on either natural or artificial features typically leads to datasets encompassing a mixture of continuous and categorical variables sampled at different scales (i.e., varying accuracies and different categorical scales; Table 1). Therefore, the relationship between the daily linear displacement by the forest elephants and the environmental predictors (natural or anthropogenic) were investigated with Conditional Random Forests (CRFs, Strobl et al., 2007). CRFs is an ensemble machine learning technique based on the aggregation of a large set of conditional inference trees (Hothorn, Hornik, & Zeileis, 2006), which has already been used to determine the most relevant drivers of extinction risk in African mammals (Di Marco et al., 2014). CRFs resolve the bias in the implementation of the original Random Forests (RFs) (Breiman, 2001) towards variables with higher accuracy (e.g., distance to rivers) over those with a low number of categories (e.g., elephant sex), balancing the role of each variable, regardless of the number of unique values or categories (Strobl et al., 2007). Consequently, CRFs allow a reliable inference of linear and non-linear effects and the relative importance of the environmental variables (Strobl, Hothorn, & Zeileis, 2009).

We developed the CRFs in *R* (R Core Team, 2015) with the *party* package (Strobl et al., 2009). Following previous studies, we were more interested in general patterns than in the behaviours of any single elephant (Loarie et al., 2009). Therefore, data were pooled and, prior to model training, the linear displacement was log transformed to reduce the influence of any particular displacement (i.e., principally to reduce the potential influence of female 4 – F4). Nevertheless, to balance the influence of each individual in the model predictions, the input data were inversely weighted by their proportion of fixes over the entire dataset. Unlike previous studies comparing decision-tree induction methodologies (Muñoz-Mas, Fukuda, Vezza, & Martínez-Capel, 2016), we did not consider beforehand the correlation between variables because CRFs correct the bias towards groups of correlated variables present in standard RFs (Strobl et al., 2007). As recommended in a number of publications (Arlot & Celisse, 2010), we performed a stratified fivefold cross-validation (i.e., each fold presented a similar proportion of cases per individual as the complete dataset) to search for the most general model using the backward variable elimination approach (May, Dandy, & Maier, 2011). The fivefold cross-validation was repeated five times (i.e., 25 models in total) (Muñoz-Mas et al., 2016) and the loss function corresponded to the weighted Mean Squared Error (MSE) to balance the influence of the different number of fixes per elephant. As a common practice (Muñoz-Mas et al., 2016), once the optimal parameters and variables were obtained, a single case-weighted CRFs was calculated without cross-validation and employing the optimal variable set. Using the final model, we evaluated the coefficient of determination (r^2), and the modelled effects and importance of the variables.

The relationship between the most relevant input variables and the daily linear displacement by forest elephants was graphically characterised with partial dependence plots (Friedman, 2001) adapting the code implemented in the package *randomForest* (Liaw & Wiener, 2002). Partial dependence plots are based on the predictions rendered by the CRFs obtained after substituting, one at a time and sequentially, the inspected variable by the different values of the variable (Muñoz-Mas, Fukuda, Pórtoles, & Martínez-Capel, 2018). Then, the resulting predictions are used to depict the effect of the inspected variable over the response variable (i.e., mean effect and/or other statistics) accounting for the effects of the other variables within the model by averaging their effects. Consequently, partial dependence plots are a useful way to visualise the marginal effect of the target variable on the response variable (Muñoz-Mas et al., 2016). Finally, the importance of the variables was examined by employing the function implemented by the *party* package (Strobl et al., 2009).

3 RESULTS

The average linear displacement per elephant (i.e., distance between standardised/mean 24h fixes) was 1.87 km per day (1.65±1.25 for males and 2.05±1.82 for females). Female 4 showed the longest displacement per day (15.4 km, during the short dry season of 2016), while female 3 showed the shortest (~0.0 km, during the short dry season of 2016). Per season, the smallest displacements (i.e., distance between standardised/mean 24h fixes) were close to zero both for males and females. Conversely, the largest distances travelled varied. The longest displacements occurred during the short dry season (i.e., 11.3 and 15.4 for males and females, respectively) whereas these values were smaller during the other seasons and did not show a clear pattern between seasons and sexes (See Appendix B for a graphical depiction of the linear displacements per month performed by each elephant).

The backward variable elimination stopped after removing six of the seventeen variables. The final variable set included nine continuous variables: the moving average of temperature and its maximum and minimum and those of precipitation (i.e., Temp. MA, Max. Temp. MA, Min. Temp. MA and Precipitation MA), distance to rivers and elevation and distance to villages, lodge and roads. It also included two categorical variables: land cover type and sex. The final model explained 61 percent of the variance (Figure 2).

[Figure 2 here]

Although interactions between variables generated a range of predictions for each permuted value, in general elephants moved furthest in the vicinity of main roads (Figure 3). Distance to roads generated the largest differences in daily displacement (i.e., from approximately 0.7 to 1.1), which is indicative of the importance of this variable (see Figure 5). Daily linear displacements were higher for fixes located near to the Lango lodge (Figure 3), which were also collected at intermediate distance to villages (i.e., between ca. 25 and 30 km); the abrupt increase in the distances moved at fixes located more than 36 km from villages correspond to a very large displacement undertaken by individual Female 4. Elevation indicated that the daily linear displacement by the elephants decreased in flood-prone areas. Daily distance increased markedly from the lowest elevation (i.e., zero level) up to 425 m a.s.l., while above this elevation, there was no effect on linear displacement. Forest elephants travelled almost irrespectively of the value of the moving average of the maximum temperature (Max. Temp. MA) up to 31.3 ºC. Above this temperature their movement decreased abruptly. The moving average of the temperature (i.e., Temp. MA) had similar effect (elephants displaced longer distances at lower temperatures), although no abrupt changes were present in this case. On the contrary, the moving average of the minimum temperature (i.e., Min. Temp. MA) presented an unclear pattern, although, overall, it can be considered to influence negatively elephant movements. Finally, the moving average of precipitation (Precipitation MA) had almost a negative linear effect so elephants moved shorter distances during periods of heavy rainfall.

[Figure 3 here]

The categorical variables selected indicated that forest elephants moved faster when moving through Marantaceae forest, bais and land cover patches classified as water, mainly flooded river flooding areas (Figure 4; left panel). Conversely, they moved more slowly in the remaining habitat types, particularly in savannahs, which is interpreted as a preference for these habitats: elephants that use savannahs may spend much time moving through slowly and grazing at a single location. Finally, with regard to elephant gender, female elephants travelled longer daily distances than males do (Figure 4; right panel).

[Figure 4 here]

The variable importance function indicated that sex and distance to roads and to lodge were the most important variables determining the daily linear displacement by forest elephants, whereas some meteorological variables (i.e., precipitation MA and Min. Temp. MA) were the least important (Figure 5). The decrease in variable importance (from sex to distance to Min. Temp. MA) was gradual.

[Figure 5 here]

4 DISCUSSION

Using the conditional random forests model, we found that elephant sex and the presence of roads or human settlements were the strongest predictors of the length and speed of elephant movements. Contrary to the main hypothesis, the tagged elephants did not clearly undertake any seasonal migration. Our model confirms that elephants in PNOK experience human disturbances. Consequently, despite taking into account the importance that touristic activities have on habitat conservation, regulating and restricting them —in time and space— to avoid human-elephant conflicts and disturbance could notably contribute to elephant conservation. We acknowledge that a larger sample size, both in duration of the study and in the number of tagged individuals is desirable to understand the ecology of the population of elephants in OKNP. Therefore, these results should be interpreted with caution as representing these six individuals and not the entire population. Nevertheless, although the r^2 of 0.61 suggests that other unmeasured variables also influence elephant movements, this value is similar to other studies employing a restricted number of individuals and input variables (Bohrer et al., 2014).

Female elephants undertook longer daytime movements than males contradicting results of previous studies (Kolowski et al., 2010; Mills et al., 2018), which we hypothesize may be first due to our low sample size for males, and secondly due to the possible reproductive status for some females and the resources they are accessing during the study period. The ecological strategies of lactating females are generally focused on the intake of sufficient water and calories to maximise milk production (for data on elephants' age estimates see Appendix A in supplementary materials). In addition, the high availability of water (de Beer & van Aarde, 2008) and the sexual dimorphism of the species, would allow males to thrive in habitats of low water availability, which also explain the relatively shorter distances travelled by our males. In any case, these differences between sexes should be interpreted with caution due to our particular small sample size for males.

With regard to the distance to roads, the partial dependence plots indicated that forest elephants did not select the vicinity of roads for resting, feeding or social purposes as has been observed in areas with controlled hunting (Kolowski et al., 2010). The use of the dirt road —the only path that supports road traffic— is restricted to the OKNP and lodge staff and to the few tourists visiting the lodge. Consequently, traffic along the road is sporadic and occurs during the daytime. Nevertheless, according to the sequence of fixes obtained during the study period, our collared elephants did not use this road for travelling, because most of movements were perpendicular to the road. Protected roads in OKNP are not a barrier for elephants' movement, as opposed to those found outside other protected areas (Blake et al., 2008). However, our results indicate that even the necessary activities performed in the park, such as eco-monitoring and anti-poaching patrolling, and the visits of small groups of tourists, affects the speed of elephant movements to some extent.

Faster displacements occurred near the lodge complex and, neglecting the long displacements of female 4 (F4) (see Figure 1), in areas between 22 and 31 km from them. It has been suggested that human activities alter elephant behaviour for short time spans (Wrege, Rowland, Thompson, & Batruch, 2010), emphasizing the possibility that park activities may cause elephants to change their behaviour. However, the lodge is located near some of the biggest bais in the park, which in turn may favour faster movements as elephants travel to habitats with abundant resources and/or for social interactions. Despite the uncertainty, near these areas it would be recommendable to perform tourist activities with special care to avoid frequent disruption to the forest elephants' normal behaviour.

Although most of the GPS locations were obtained in the same range of elevations (with the exception of female 4 – F4), below 350 m a.s.l. there was a sharp decrease in the speed of the elephants. This fact, combined with the information described in the partial dependence plots for the meteorological variables, suggests that water presence in low elevation flood plains may slow down elephant movements but also because they positively select these habitats to maintain social relationships (Fishlock, 2010; Fishlock & Lee, 2013) and to satisfy thermoregulatory needs (Kuwong, 2014). On the contrary, most of the displacements were made following the SE-NW axis of the Mambili River basin, where the edge of the riverine area facilitates their movement. Apparently, such movement patterns coincide with those described for a number of mammals that employ riparian corridors as 'highways' during their displacements (Sánchez-Montoya et al.2016), a behaviour that has also been occasionally reported for African elephants. These two phenomena related to flooded plains and movement through riverine habitats do not necessarily have to be contemporary or to occur at the same spatial scale. Notwithstanding, forest elephant at the OKNP did not perform migrations in the same way as savannah elephants do (Birkett et al., 2012; Bohrer et al., 2014), although they are still affected by weather patterns. The moving average of the maximum temperature (Max. Temp. MA) affected elephant linear displacement above 31.5 ºC resulting in an abrupt decrease in distance moved between fixes the linear displacement, which might be explained by their low surface-to-volume ratio that affects heat dissipation (Williams, 1990). Although with a less pronounced pattern, the temperature and the minimum temperature (Temp. MA and Min. Temp. MA) were positively related to activity and distance moved. Finally, precipitation was inversely related to elephant movement; during the periods of highest rainfall, the elephants moved more slowly. We hypothesise that, aside from flooding, this pattern would highlight that elephants are more inclined to rest during storms, or to seek cover and hide if they suffer major disturbances (i.e. poaching).

The study of GPS collared elephants has shed some light on the drivers of linear displacements of the forest elephant in the OKNP in regard to a suite of geographical, meteorological and anthropogenic variables. Sex, land cover and three anthropogenic, two geographic and four meteorological variables described their daily linear displacements. Despite our low sample size, the present study produced some interesting results. Previous studies found that unprotected roads have a barrier effect in elephant displacements, but not in the case of roads located inside protected areas (Blake et al., 2008; Kolowski et al., 2010; Poulsen et al., 2018; Schuttler et al., 2012). Given that our road is a protected road inside a National Park our results are consistent with these previous studies. Nevertheless, the partial dependence plots exposed a disruptive effect of its presence because our elephants moved faster near the roads. Our elephants showed a trend to move slower in savannahs than in any other habitat what perfectly agrees with what Mills et al. (2018) found at Wonga Wongué Presidential Reserve in Gabon. Contrary to what was found in the studies cited above, we did not find a strict seasonal movement pattern, characterised by sustained long unidirectional displacements, apart from the differences found for temperature and rainfall. We consider our results to be of great interest for wildlife management plans because they highlight drivers of daily movement distance for the forest elephant, which is especially relevant because daily displacements performed by elephants would be one of the factors affecting their vulnerability to poachers (Goldenberg et al., 2018). We found evidences that the activities performed during the standard operation of the park and the distribution of the different habitat patches affected the daily linear displacement of the collared elephants. Notwithstanding, the notorious importance of tourism related employment in remote rural areas (reducing poverty, improving the social welfare of local communities and promoting biodiversity conservation (Dinets & Hall, 2018; Snyman, 2012), the strict control of the tourist activity schedules and the application of especial care when performing these activities may prevent unnecessary disturbances to vulnerable fauna. Consequently, human activities and displacements within the park should be limited —in time and space— as much as possible, this would be especially important for tourist groups, by avoiding large groups of people and trying to concentrate their activities at specific places for given periods of time. Furthermore, proactive vegetation management, such as the ongoing controlled fires for savannahs' maintenance or the recovering of degraded patches could be used to encourage different activities. Overall, we expect these results to favour grounded decisions in the process of management of this endangered species.

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TABLES

Table 1. Summary and units of input variables employed in the analysis of the movement patterns with conditional random forests. MA corresponds to moving average, Min. to minimum, Qu. to Quartile and Max. to maximum.

Variable	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Linear displacement (km/24 h)	0.00	0.81	1.40	1.88	2.40	15.41
Temp. (ºC)	21.67	25.12	26.00	26.07	27.14	30.44
Max. Temp. (ºC)	23.31	29.49	31.21	30.87	32.39	35.71
Min. Temp. (ºC)	13.08	20.28	20.97	20.86	21.56	26.94
Precipitation (mm)	0.00	0.00	0.37	4.07	4.03	61.98
Temp. MA (ºC)	25.15	25.48	25.82	26.03	26.56	27.16
Max. Temp. MA (ºC)	28.60	30.30	30.98	30.88	31.64	32.25
Min. Temp. MA (ºC)	17.90	20.51	20.96	20.80	21.24	22.32
Precipitation MA (mm)	0.26	2.17	4.33	4.09	5.65	8.46
Elevation (m a.s.l.)	352.00	377.00	393.00	420.10	445.00	740.00
Slope (º)	0.00	1.08	2.21	2.40	3.58	13.91
Distance to rivers (km)	0.00	1.03	1.59	1.83	2.44	7.48
Distance to villages (km)	8.97	22.79	31.52	28.56	34.18	42.35
Distance to roads (km)	0.03	4.08	7.42	10.73	14.68	41.16
Distance to lodge (km)	0.20	6.32	11.12	14.61	17.38	63.00
Season	Short dry, short rainy, long dry & long rainy					
Land cover type	Bais, dense closed forest, forest with Marantaceae, open forest with Marantaceae, Raphia – Phoenix, savannah, swamp forest, water, woodland, woodland in regeneration + urban settlements, croplands and fallows, swamp grassland (never visited)					
Sex	Male & female					

FIGURES:

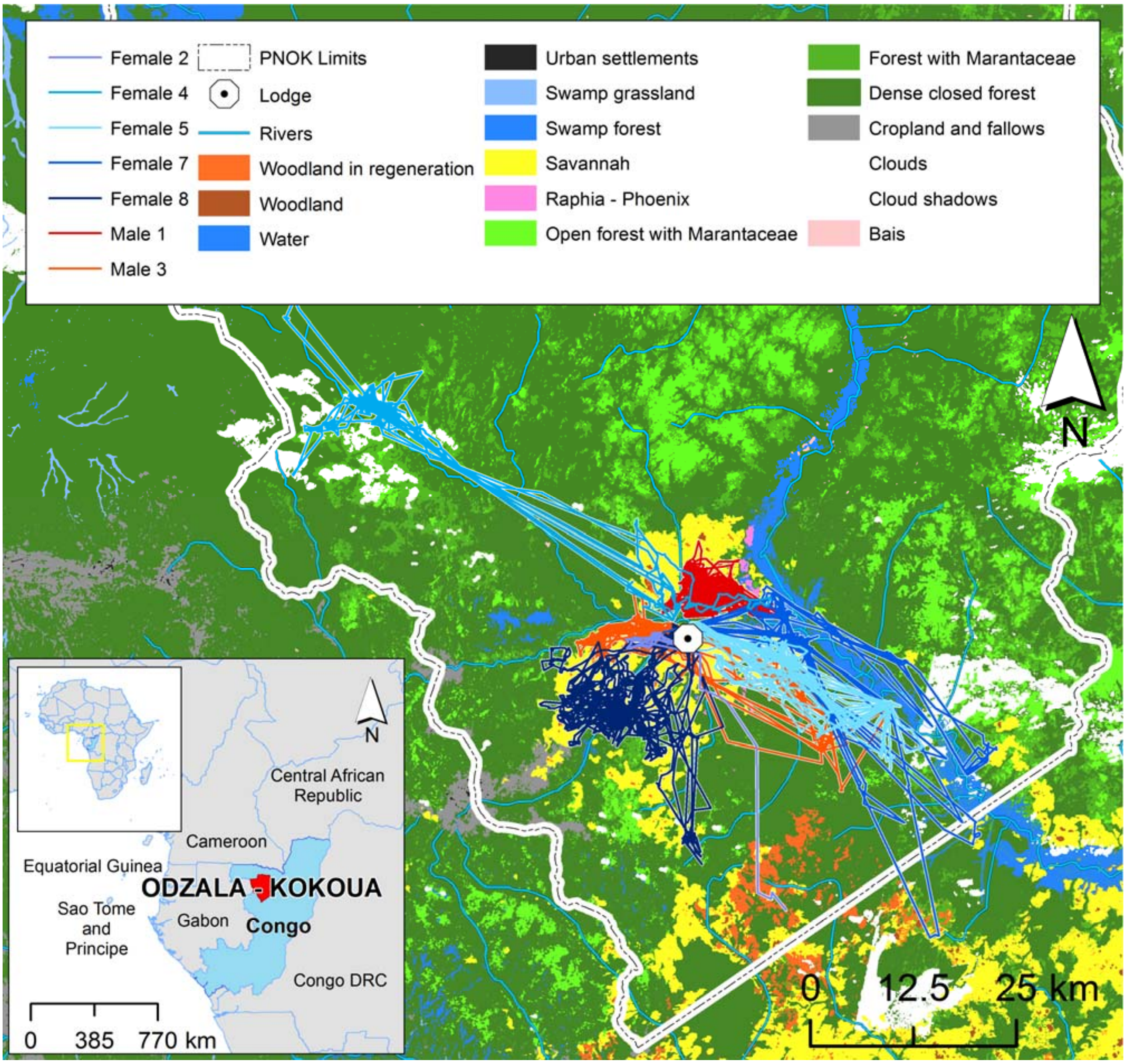

Figure 1. Location of the Odzala-Kokoua National Park (OKNP) within the African continent and general view of the elephant trajectories, land cover, rivers and villages in the environs of the OKNP.

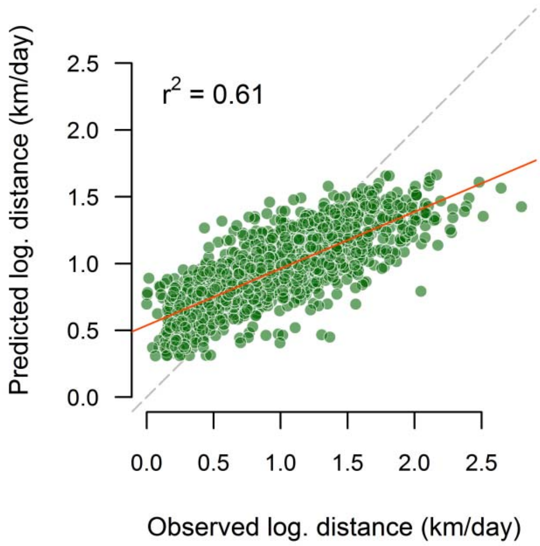

Figure 2. Observed versus predicted mean daily linear displacement by the forest elephants and coefficient of determination (r^2). The red line: obtained data, grey line: reference r = 1.

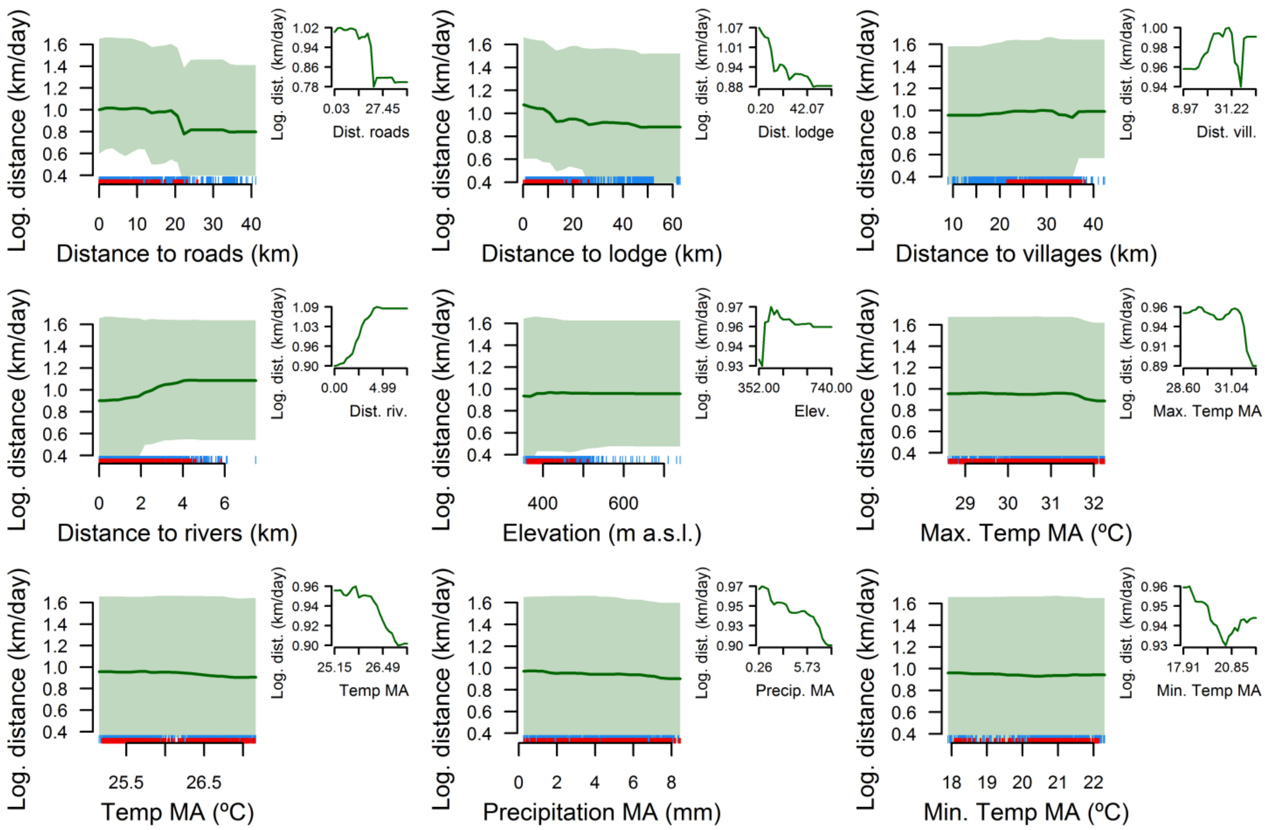

Figure 3. Partial dependence plots for the most relevant continuous variables selected during conditional random forests optimisation. MA corresponds to moving average, Min. to minimum and Max. to maximum. Tick marks represent data contained in the training dataset. Blue corresponds to females and red to males. The shaded area depicts the range of the predictions obtained for each permuted value. In order to clarify the variable effect, the mean trend (central line in the larger plots) is depicted next to main plots.

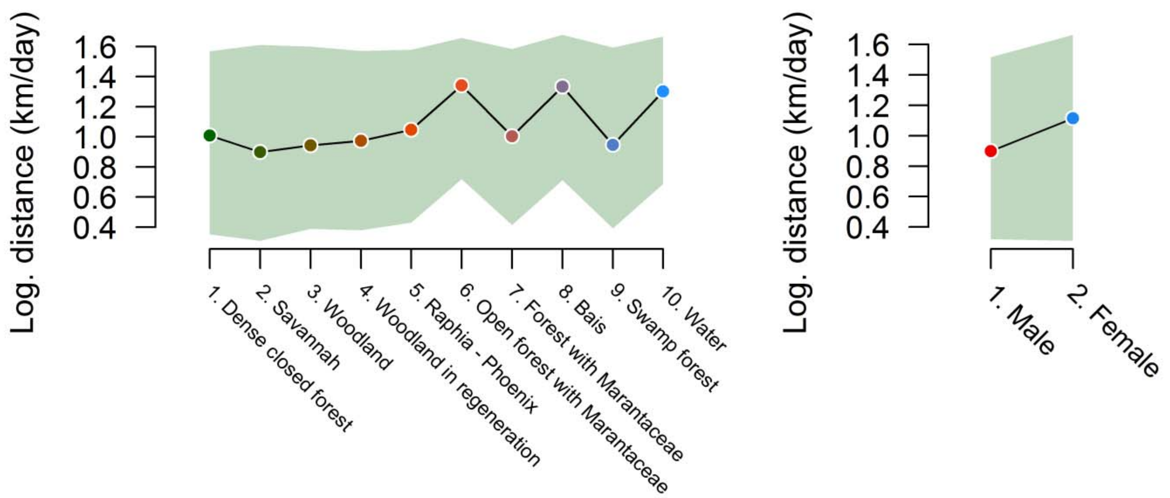

Figure 4. Partial dependence plots for the most relevant categorical variables selected during conditional random forests optimisation. The shaded area depicts the range of the predictions obtained for each permuted value. Colour code differentiates each category.

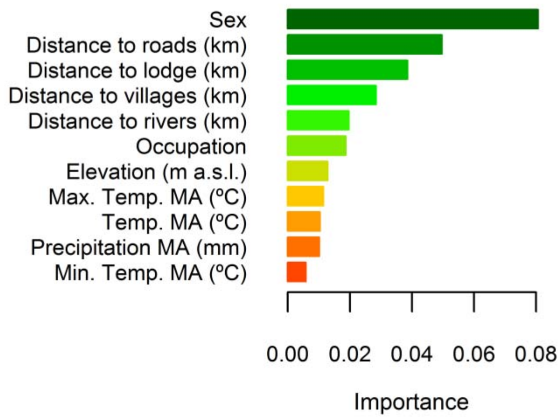

Figure 5. Variable importance obtained with conditional random forests.

Appendices

APPENDIX A – INDIVIDUALS DATA SUMMARY TABLE

Biological characteristics (age and sex) and main tracking data obtained per individual (data of the first and last fixes gathered, total number of fixes obtained and total number of days tracked) are shown in table A1.

[Table A1 Here]

APPENDIX B – CORRELATION AMONG ENVIRONMENTAL COVARIATES

The correlation among environmental variables has been characterised with a force-directed graph (Fruchterman & Reingold, 1991) (Figure A1). This graph depicts the correlation between the geographical, meteorological and anthropogenic variables, which revealed the presence of two groups of variables encompassing, the geographical and anthropogenic variables on the one hand, and the meteorological variables on the other hand. Relevant correlations were obtained for temperature and maximum temperature and for season and the moving average of the maximum temperature ($r^2 = 0.83$ and $r^2 = 0.82$). The tracked males remained near the Lango Lodge (see Figure 1 in the main text). Therefore, sex and distance to lodge presented a relevant correlation ($|r^2| = 0.82$). The latter also correlated with distance to road ($r^2 = 0.90$). Correlations were obtained with the *R* package *polycor* (Fox, 2010), which is specially designed to handle continuous and categorical data and the force-directed graph was developed using the functions included in the *R* package *qgraph* (Epskamp, Cramer, Waldorp, Schmittmann, & Borsboom, 2012).

[Figure B1 Here]

APPENDIX C – LINEAR DISPLACEMENT PER ELEPHANT

The mean distance performed by the tracked elephants was 1.87 km per day. Female displacements were longer (2.05±1.82), although they presented higher variability than that of males (1.65±1.25). The smallest displacement for both sexes was close to zero. Female 4 performed the longest displacement per day, which correspond to the three outliers depicted in Figure C1. Additional details about these displacements can be found in the main text.

[Figure C1 Here]

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APPENDIX TABLES AND FIGURES:

Table A 1. Sex, estimated age in years, trapping and collar-fitting data (Start), last fix data (End), total number of fixes obtained (NFixes) and total number of days tracked (NDays) per individual.

Indivdual	Sex	Age	Start	End	NFixes	NDays
M1	Male	30-35	20/11/2014	11/3/2016	5685	477
F2	Female	10-15	21/11/2014	11/3/2016	112	476
M3	Male	20-25	22/11/2014	14/3/2016	2597	478
F4	Female	40+	25/11/2014	28/3/2016	1155	489
F5	Female	10-12	28/11/2014	11/3/2016	1439	469
F7	Female	10-15	29/11/2014	1/4/2016	1166	489
F8	Female	20+	4/12/2014	14/3/2016	2612	466

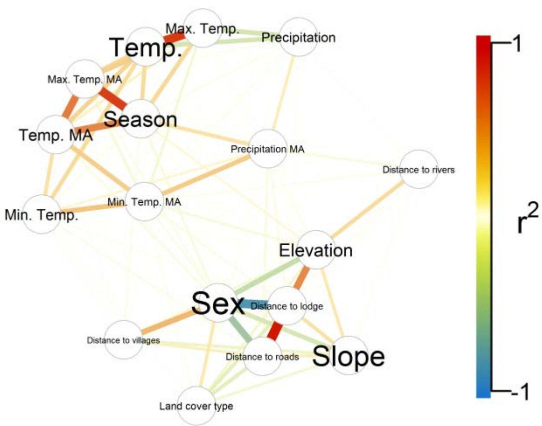

Figure B 1. Force-directed graph based on the correlation (Pearson r^2) between the geographical, meteorological and anthropogenic variables obtained with the *R* package *qgraph* (Epskamp et al., 2012). MA corresponds to moving average, Min. to minimum and Max. to maximum.

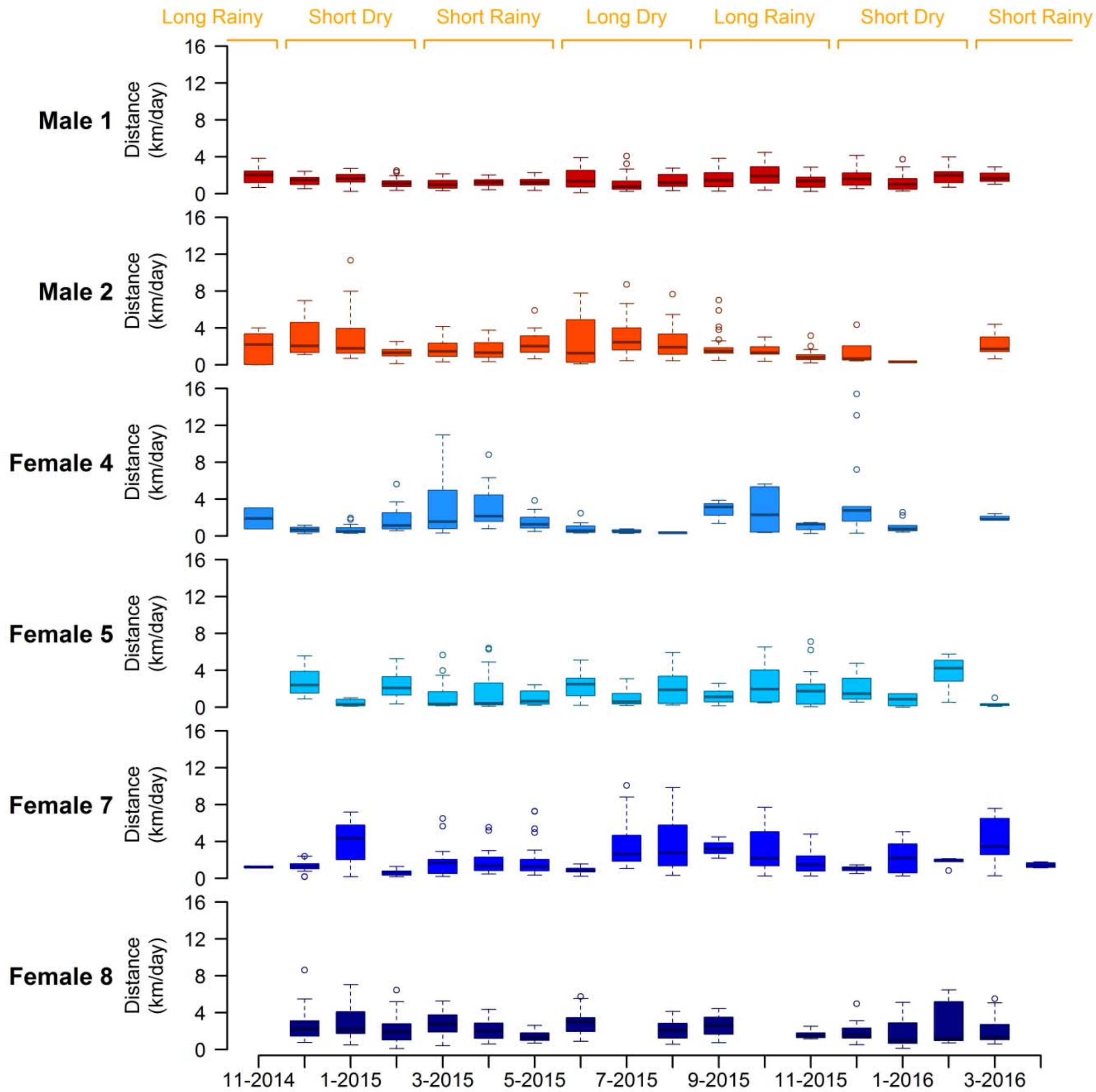

Figure C 1. Box plots of the linear displacement (km) per month by each individual considered in the analysis (i.e., excluding collar #9 and collar #2). The mean tracking days per individual was 382 (374–388), and the mean number of fixes per individual was 1931 (1069–5034).