

**Can Movement Speed Predict Habitat Preference?  
Assessing the Influence of Topography, Village Proximity,  
and Land Cover on Forest Elephant (*Loxodonta cyclotis*)  
Movement and Preferences in Gabon.**

by

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## 1. ABSTRACT

Understanding animal habitat preference is crucial for the management of animal populations and planning of protected areas. However, current models for estimating habitat preference require arbitrary estimates of habitat availability, which introduce a level of uncertainty and qualitative inference that could affect model accuracy. To overcome this problem, Dickson et al. (2005) suggested that movement speed could be used as a metric of habitat preference, assuming that movement speed would be negatively related to habitat preference. However, this *speed - preference* model ignores potential changes in movement related to behavioral shifts or variations in terrain. To assess the generalizability and practicality of the speed-preference model, I examined the hourly movements of 56 GPS collared forest elephants (*Loxodonta cyclotis*) in Gabon, central Africa between 2015 and 2018 in the context of three relevant environmental covariates (land covers, topography, and village proximity). I analyzed changes in movement speed by attributing a single value for specific environmental characteristics to each movement step and estimated preferences by calculating the density of each individual's GPS points within the covariate of interest from the individual's travel range. I then modeled the relationship between speed and preference with a linear mixed model. Speed failed to predict preferences for different land cover types, and relationships between speed and preference for gradients of topography and village proximity changed in both direction and intensity. Therefore, although using speed to predict habitat preference avoids the limitations of other habitat preference models, this method requires further research to assess the complex interactions between speed and environmental covariates for different animal species.

## 2. EXECUTIVE SUMMARY

Modeling animal habitat preference is important for conservation planning and management. This is especially important for protecting threatened species such as forest elephants. However, many current models of habitat preference require arbitrary estimates of habitat availability. To address this problem, Dickson et al. (2005) suggested that movement speed can be used to predict habitat preference without introducing any arbitrary estimates of habitat availability and demonstrated that mountain lions move slower in favorable land covers and faster in unfavorable land covers.

This *speed-preference* model, however, ignores behavioral shifts and changes in speed associated with topography or obstructions to movement. By introducing these factors, the relationship between speed and preference may not be generalizable to other animal species within different environments. To evaluate the generalizability of the speed-preference model, I used movement data from 56 forest elephants GPS-collared by the Gabon Parks Elephant Collaring Program to ask:

- 1) Can speed predict habitat preference for forest elephants?
- 2) Is the relationship between speed and habitat preference the same as predicted by the original speed-preference model?
- 3) Is this relationship consistent throughout the range of various environmental covariates (land cover, topography, and village proximity)?

I calculated the speed of forest elephants by dividing the linear distance between two consecutive points by their time difference. I then estimated how relevant environmental covariates (land cover, topography, village proximity) affected movement speed by attributing a single value of each covariate to movement steps. Meanwhile, I estimated the preference of collared elephants for specific environmental covariates by determining the density of GPS points within each covariate of interest for each collared individual's travel range. I then analyzed the relationship between speed and fix point densities using linear mixed models.

My study showed that the speed-reference model is not generalizable to forest elephants within the range of land cover, topography, and village proximity in Gabon. Speed failed to predict habitat preference for land cover. Meanwhile, there was a significant positive interaction between speed and topography and village proximity, indicating that the relationship between speed and habitat preference was contextual and not consistent. Topography, in particular, had an especially strong effect in shaping the direction and intensity of the speed-preference relationship in steeper slopes; potentially signifying the important role terrain obstruction plays in determining forest elephant movement speeds.

Therefore, although the speed-preference model avoids the assumptions of most habitat preference models, it requires significant further research before being applied. In particular, it needs to consider the important role that topography has in determining movement speed. Meanwhile, the model should consider the specific environmental context of the animal and conduct preliminary examinations on their movement and preference.

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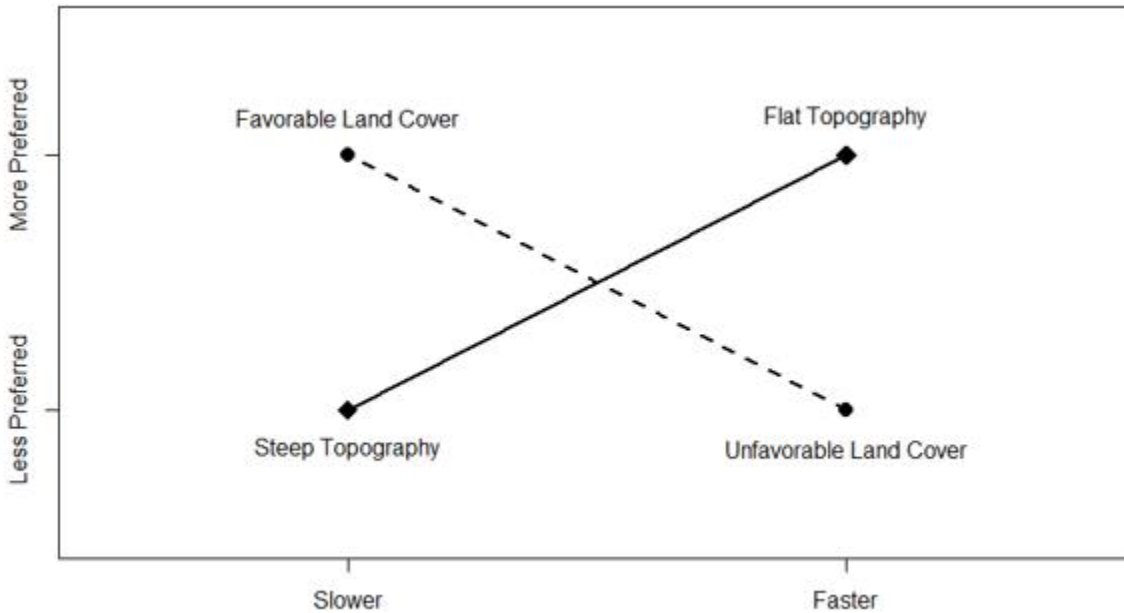
### 3. INTRODUCTION

Conservation planning and management of many, wide ranging terrestrial mammals rely on habitat selection models, such as compositional analyses (Aebischer et al. 1993), to determine the relative importance of specific habitats to animal species. These models have been used to improve habitat accessibility and connect isolated habitats into cohesive units (Schadt et al. 2002), greatly assisting conservation efforts. Most current habitat selection models, however, require arbitrary estimates of habitat availability, which introduce a level of uncertainty and qualitative inference that could affect model accuracy (Dickson et al. 2005). Compositional analyses, for example, estimate habitat availability by considering all areas within buffered vectors as assessable to animals. However, the length of these buffered vectors are completely defined by the user. As a solution to this problem, animal movement speed could potentially be an important metric of habitat preference (Dickson et al. 2005): models using speed to estimate habitat selection do not require arbitrary assumptions about habitat availability and might provide more accurate conclusions than other, traditional methods.

A reasonable assumption of the relationship between movement speed and habitat preference is that animals tend to move faster in areas that offer fewer resources or benefits (Dickson et al. 2005). Under this speed-preference model, we would expect a negative relationship between movement speed and habitat preference, with animals moving slower in more preferred habitats and faster in less preferred areas (Figure 1). Indeed, this model successfully predicted that mountain lions moved slower in preferred habitats such as riparian and chaparral land covers, and moved faster in non-preferred habitats such as urbanized areas (Dickson et al. 2005).

The speed - preference model, however, ignores behavioral shifts and changes in speed associated with topography or obstructions to movement. For example, savanna elephants move significantly slower and tend to avoid steeper areas (Wall et al. 2006); whereas forest elephants tend to avoid areas of human disturbance such as roads and villages (Blake 2002; Blake et al. 2008). Despite the danger of proximity to humans, however, many elephants raid crops (Chiyo et al. 2005). Elephants might move slower than normal in areas of high risk, as most animal species tend to move cryptically in response to human threats (Papworth et al. 2012). In this case, the relationship between movement speed and habitat preference would be the opposite of that

expected if movement speed was determined by habitat preference (Figure 1). With such changes in movement in response to factors such as terrain and threats, speed might not reliably predict habitat preference.



**Figure 1:** The contrast between the theoretical model suggested by Dickson et al. (2005: dotted line) and the predicted relationship between preference and movement speed with varying slope (solid line). Steep slopes require more energy to climb, causing elephants to reduce their speed (Wall et al. 2006). In contrast, elephants move more freely and faster through flatter areas. In such cases, the relationship between speed and habitat preference would be positive — the opposite of that suggested by Dickson et al. (2005).

In this study, I use movement speeds of forest elephants in Gabon derived from GPS telemetry and relate them to the principal land cover types, topography and village proximity to evaluate the generalizability of the speed - preference model by examining three questions: 1) can speed predict habitat preference for forest elephants? 2) is the relationship between speed and habitat preference the same as predicted by the speed-preference model? 3) is this relationship consistent throughout the range of various environmental covariates? I then discuss potential implications of my findings and evaluate the practicality of using movement speed to determine habitat preferences.

## 4. METHODS

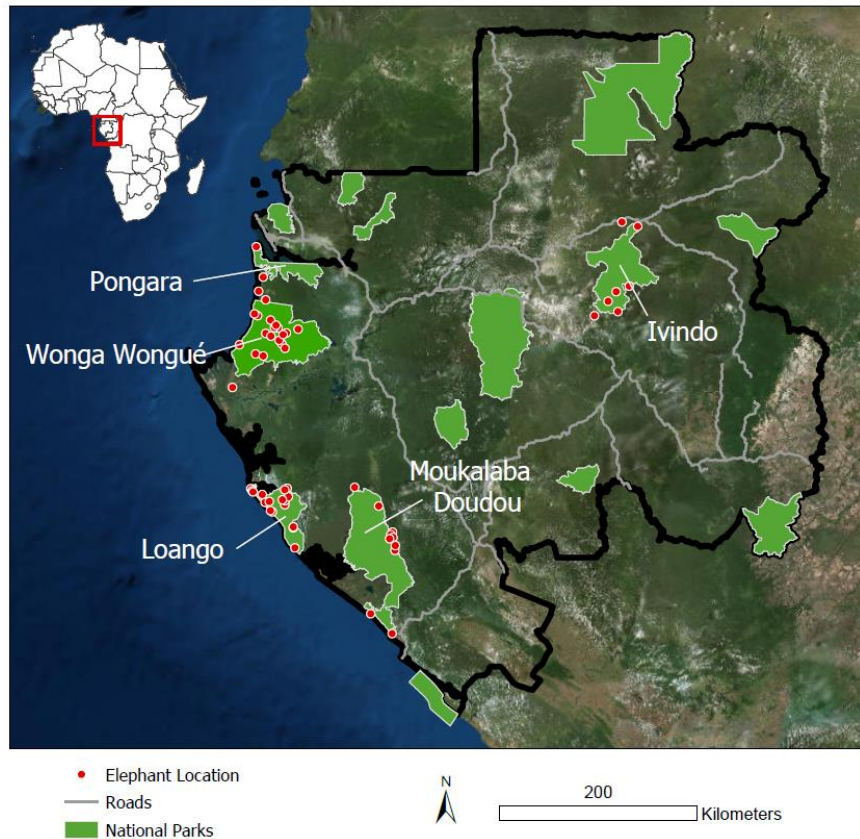
### **Focus Species**

African forest elephants (*Loxodonta cyclotis*) comprise almost a third of the total African elephant population (Maisels et al. 2013), yet remain difficult to study in comparison to their savanna counterparts due to their cryptic nature and preference for forested habitat (Blake 2002). Forest elephants play important ecological roles (Poulsen et al. 2018). As one of the largest frugivores on Earth, forest elephants maintain forest structure through seed dispersal (Campos-Arceiz and Blake 2011). Meanwhile, their movement, browsing, and trampling likely help sustain naturally occurring forest clearings – called “bais” – which often serve as gathering spots for other animals (Turkalo et al. 2013). Given their ecological role and their taxonomic and genetic uniqueness (Ishida et al. 2013), forest elephants are of high conservation interest, especially given their recent population declines from poaching for ivory (Maisels et al. 2013; Poulsen et al. 2017). With deforestation and habitat destruction being major threats to the conservation of forest elephants (Poulsen et al. 2017), understanding and preserving their preferred habitats are key to protecting this species.

### **Study Area**

I obtained all forest elephant tracking data from the Gabon Parks Elephant Collaring Program, funded by the US Fish & Wildlife Service and implemented by the Agence Nationale des Parcs Nationaux (ANPN). Starting in October 2015, this project successfully collared 56 forest elephant individuals (26 male and 30 female) at or around five regions in Gabon – the Ivindo, Loango, Pongara, and Moukalaba Doudou National Parks, and the Wonga Wongué Presidential Reserve (Figure 2).





**Figure 2:** Locations of the 56 collared forest elephants (red circles) in and around five protected areas (labeled) in Gabon. Satellite imagery demonstrates land cover types, and national roads (grey lines) are displayed for context.

### Environmental Covariates

Three environmental covariates are of particular interest to forest elephants and therefore evaluated in this study. 1) Land cover is known to affect movements of terrestrial animals as it is directly related to their preferred habitats (Dickson et al. 2005; Graham et al. 2009). I focused on “forested”, “open habitats”, and “wetlands” land cover types as each has been shown to be important for forest elephant ecology, influencing their feeding and social behaviors (Blake 2002; Mills et al. 2018). 2) Topography affects energy expenditure and ability to move (Wall et al. 2006), which is directly associated with movement speed. 3) Proximity to villages serves as a metric of the relative anthropogenic threat an individual might face, which could affect animal behavior (Koerner et al. 2017).

For land cover, I used a 20m resolution land cover map of Africa (CCI Land cover provided by the European Space Agency), which includes land cover categories of tree cover, shrub cover, grassland, cropland, vegetation aquatic or regularly flooded, sparse vegetation, bare, built up (urbanized), iced, and open water. Within the study area, I reclassified the categories, labeling “tree cover” as “forested”, classifying “vegetation aquatic or regularly flooded” as wetlands, and aggregating all other categories as “open.”

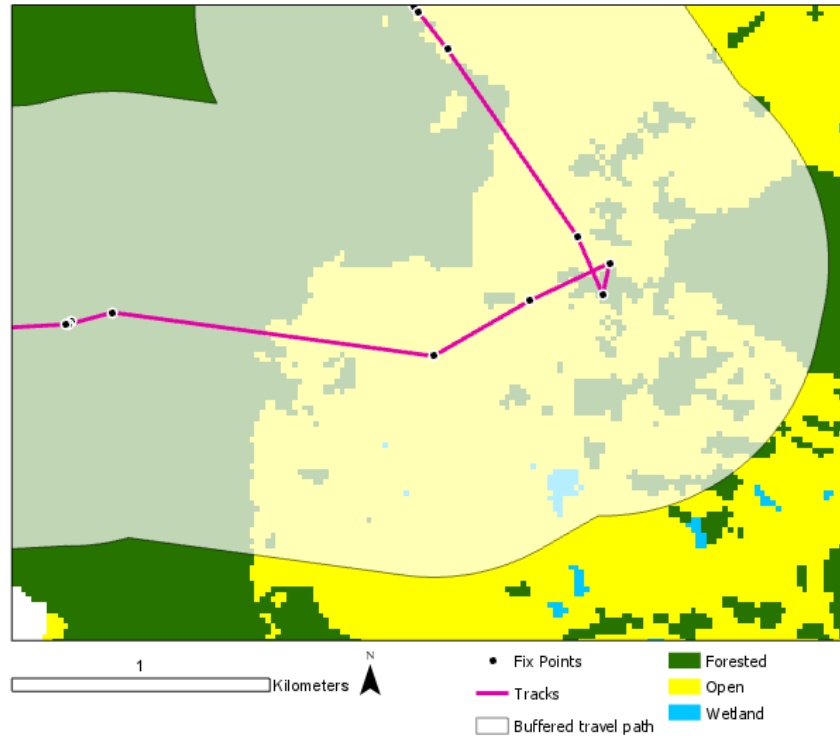
To represent the proximity of elephant locations to a village, I created a raster surface with a resolution of 30m and calculated each pixel’s Euclidean distance from every known village in Gabon. For any analyses regarding village proximity, I ignored any points further than 10km from a village, assuming villages would have little effect on forest elephant movement of behavior beyond that distance (Koerner et al. 2017; Beirne et al. 2019).

I estimated topography with a 30m-resolution raster of slope, which was calculated by the continental Digital Elevation Map. In my analyses, I ignored all pixels with slope greater than 30 degrees as very few elephants traversed them (< 0.1 %).

### **Analysis of Movement**

GPS locations of the collared elephants (henceforth “fix points”) were either recorded every 15 minutes or hourly. Using these fix points, I calculated the speed by dividing the linear distance between two consecutive points by their time difference. This approach assumed a constant rate of movement during each 15 minute or hourly step interval.

To determine the habitat available to an elephant, I created an 850 meter (the 95<sup>th</sup> percentile of distances covered per step length for all collared elephants) buffer around each of the linear step lengths (Figure 3). Unlike other methods of estimating home ranges, such as Kernel Density Estimation or the Minimum Convex Polygon, this method accounted for 100% of the available fix points and considered regions outside of an individual’s core range, allowing for a better representation of habitat preference as all areas available for use are included, whether they are actually used or not.



**Figure 3:** An example of the fix points, tracks, and the 850 meter buffer of a collared individual traveling along the three main land cover classes in this study.

I estimated the preference of collared elephants for a specific environmental covariate by counting all of the fix points within the covariate of interest within the buffered travel range. This count can be thought of as an individual's preference for a particular environment because it measures the extent to which elephants visit and use the area available to them (Wall et al. 2006). However, each travel range does not have equal abundance of habitat for specific environmental covariates. To account for this disparity, I calculated the density of fix points within the available areas for each environmental covariate. Because slope and distances to villages are continuous variables, to calculate fix point densities, I divided them into discrete classes; each degree for slope and every 100 meters for village proximity.

Calculating fix point densities by controlling for the disparity in habitat abundance inflated the importance of fix point densities for rarer habitats. Therefore, I removed the bottom 10% of the areas sampled for each environmental covariate.

I estimated how each environmental covariate affected movement speed by attributing a single value of each covariate to movement steps. For land cover, the step was assigned the category that had the highest proportional representation in the buffered area. For slope and village proximity, the step was assigned the median of slopes and distances encountered throughout that step length. I then evaluated the effect that the selected environmental covariate had on movement speed.

### **Statistical Analysis**

To examine the effect of environmental covariates (land cover, slope, and village proximity) on speed, I used linear mixed models within the R 'lme4' package with sex, hour of day, months, and environmental covariates as fixed effects and elephant, region, and unique days as random effects. Only a single environmental covariate could be included in each model because the fix point densities for each of the covariates were calculated at different unit scales (land cover category, degree of slope, and 100m intervals) across the entire temporal range for each collared individual. Instead, each analysis had to be specific for each covariate and could not include either time as a fixed effect or days as a random effect.

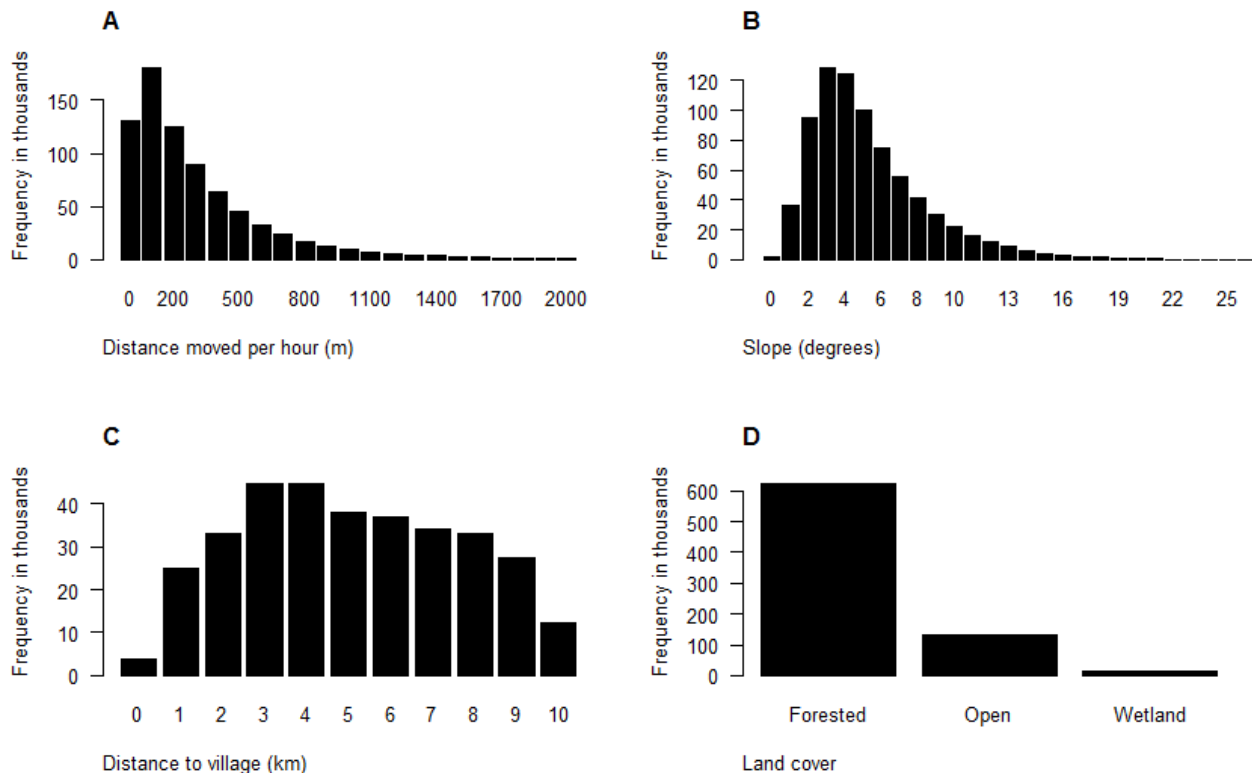
To determine if speed can predict habitat preference, I assessed the relationship between speed and fix point densities for each of the environmental covariates. For each covariate, I conducted a linear mixed model with fix point density as the response variable, speed as a fixed effect, and elephant and region as random effects. I also considered the interaction between speed and the relevant environmental covariate to determine if the relationship between speed and fix point densities remained consistent throughout the range of the relevant environmental covariate. For each of these analyses, I assessed the assumptions of normality and homoscedasticity. I then log-transformed the response variable as necessary to meet the assumptions for conducting linear mixed models.

To select the most parsimonious model for each case, I defined a suite of candidate models including the null model (environmental covariates or fixed effects have no effect on the response variable) and ranked each by their Akaike Information Criterion (AIC). I then defined a top model set as the models  $\Delta AIC \leq 6$  from the best supported model.

## 5. RESULTS

### Movement Statistics

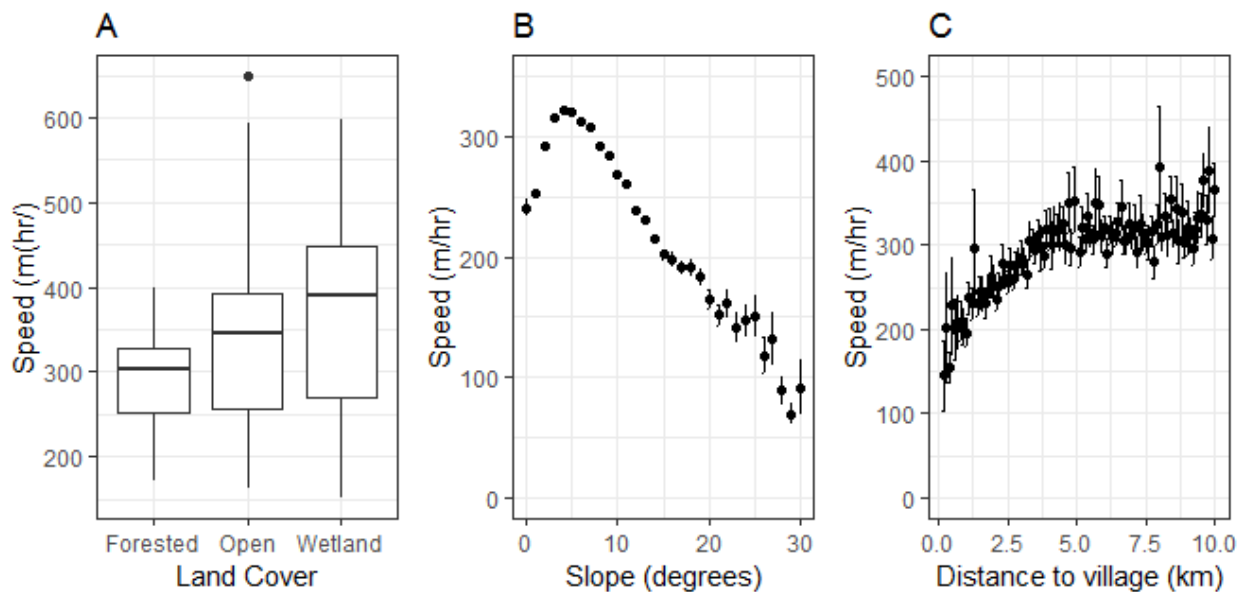
From 56 collared elephants, I obtained 887,601 fix points between October 24, 2015 and January 3, 2019. The buffered ranges calculated from these points encompassed 2686 km<sup>2</sup>, with 2065 km<sup>2</sup> of forest, 590 km<sup>2</sup> of open habitat and 32 km<sup>2</sup> of wetlands, with 81%, 17.2%, and 2% of fix points within forested, open, and wetland habitats respectively. On average, forest elephants traveled 310.1 meters every hour (SD = 396, range: 1.7 to 9781 meters) and ranged on average within areas with 5.3 degrees slope (SD= 3.4, range: 0 to 48.3 degrees) and within 14 km from a village (SD=9.3, range: 0.03 to 37.7km). When limiting distance to village to within 10km —as villages would have little effect on elephant movement beyond that distance (Koerner et al. 2017; Beirne et al. 2019.) — elephants ranged on average 5km from a village (SD=2.6, range: 0.03 to 10km, N=319986) (Figure 4).



**Figure 4:** Frequency distribution of distances moved per hour (A) and distribution of elephant fix points within slope (B), proximity to villages (C), and land cover (D).

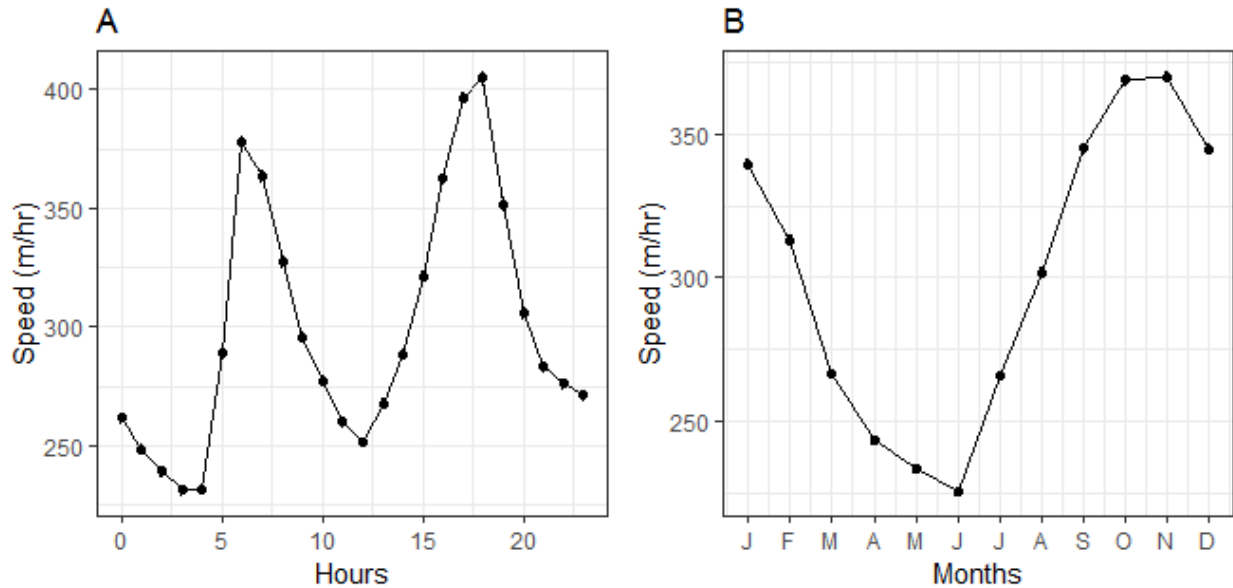
## Speed

The full model, including sex, time, and environmental covariates as fixed effects and elephant, region, and days as random effects was the most parsimonious model (Appendix; Table 1). Of these variables, slope had a significantly negative effect on speed (estimate = -2.9,  $t = -22.1$ ,  $df = 7.7 \times 10^5$ ,  $p < 0.001$ ), with speed decreasing by 2.9 meters per hour for every additional degree of slope. However, this relationship was not strictly linear, with speed tending to increase by about 12.3 meters per hour for every additional degree until 5 degrees of slope (estimate = 12.3,  $t = 27.2$ ,  $df = 4.9 \times 10^5$ ,  $p < 0.001$ ) and decreasing by about 7.3 meters per hour for every additional degree afterwards (estimate = -7.3,  $t = -37.9$ ,  $df = 3.8 \times 10^5$ ,  $p < 0.001$ ). Meanwhile, village distance had a significantly positive effect on speed (estimate =  $7.2 \times 10^{-3}$ ,  $t = 22.3$ ,  $df = 2.5 \times 10^5$ ,  $p < 0.001$ ), with speed increasing by 7.2 meters per hour for every additional kilometer from villages. Finally, speeds were significantly faster in open habitats and wetlands compared to forested areas (open habitats: estimate = 33.4,  $t = 26.3$ ,  $df = 7.7 \times 10^5$ ,  $p < 0.001$ ; wetlands: estimate = 55.2,  $t = 17.6$ ,  $df = 7.7 \times 10^5$ ,  $p < 0.001$ ; Figure 5).



**Figure 5:** Average movement speeds through different land cover types (A), slope (B), and proximity to villages (C). Elephants typically moved faster in open habitats and wetlands than in forested areas. Although slope had a significant effect on speed, the relationship is not strictly linear with speeds increasing until about 5 degrees and decreasing at steeper slopes. Meanwhile, elephants generally moved faster with increased distance from villages.

Although included in the final model, sex did not significantly affect elephant speeds (estimate = 8.6,  $t = 0.5$ ,  $df = 42.7$ ,  $p = 0.6$ ). On a daily basis, forest elephants tended to move faster during dawn and dusk, while on an annual basis, forest elephants moved faster during the months of September to February (Figure 6).



**Figure 6:** Temporal variations in average elephant speed by hour (A) and by month (B).

## Fix point densities

### Land cover

The full model, with sex and land cover as fixed effects and elephant and region as random effects, was the most parsimonious model (Appendix; Table 2). Fix point densities were significantly lower in wetlands (estimate = -35.7,  $df = 84.1$ ,  $t = -2.9$ ,  $p = 0.005$ ) compared to open habitats or forested areas. There were no significant differences in fix point densities between forested and open habitats (estimate = -4.8,  $df = 83.7$ ,  $t = -0.4$ ,  $p = 0.7$ ) (Figure 6).

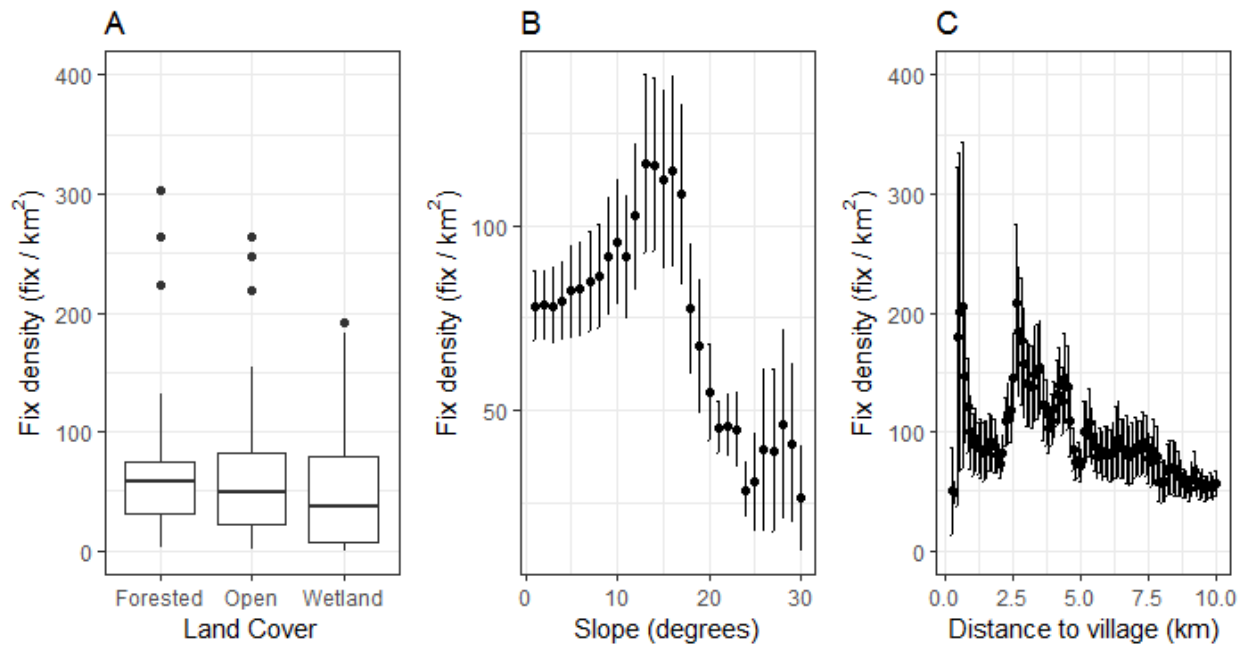
### Topography

The full model, with sex and slope as fixed effects and elephant and region as random effects, was the most parsimonious model (Appendix). Fix point densities increased by 2 fix points / km<sup>2</sup> with every additional degree in flat (< 12 degrees slope) topography (estimate = 2.0,  $t = 3.2$ ,  $df =$

1210.7,  $p = 0.001$ ) and decreased by 4.9 fix points / km<sup>2</sup> with every additional degree in steep (>12 degrees slope) topography (estimate = -4.9,  $t = -5.7$ ,  $df = 1211.4$ ,  $p < 0.001$ ) (Figure 6).

### Village Proximity

The full model, with sex and distance from villages as fixed effects and elephant and region as random effects, was the most parsimonious model (Figure 9). Fix point densities significantly decreased with increased distance from villages overall (estimate = -10.56,  $t = -12.92$ ,  $df = 2887.7$ ,  $p = < 0.001$ ). However, the relationship was complicated, making generalizing a trend difficult. For instance, even though fix point densities were lowest within 200 meters from a village, they tended to be high between 300 and 700 meters. Fix point densities then increased until about 3km before decreasing steadily (Figure 7).



**Figure 7:** Average fix point densities in different land cover types (A), slope (B), and proximity to villages (C). Elephants typically had lower visitation rates in wetlands compared to forested and open habitats. Elephant visitation rates increased with steepness to 12 degrees, and then decreased at steeper slopes. Meanwhile, fix point densities generally decreased with greater distance from villages, although not linearly.



## **Speed and Preference**

### Land Cover

The most parsimonious model only included sex and land cover as fixed effects (Appendix; Table 3). Therefore, speed was not a significant predictor of fix point densities when accounting for different land cover types (estimate = -0.081,  $t = -0.357$ ,  $df = 109.8$ ,  $p = 0.72$ ).

### Topography

The full model, with speed, sex, slope, and the interaction between speed and slope as fixed effects was the most parsimonious model (Appendix; Table 3). The interaction between speed and slope was significant (estimate =  $2.6 \times 10^{-4}$ ,  $t = 12.9$ ,  $df = 1130$ ,  $p < 0.001$ ), with the effect of speed on fix point density increasing with greater slope.

### Village Proximity

The full model, with speed, sex, distance to villages, and the interaction between speed and distance to villages as fixed effects was the most parsimonious model (Appendix; Table 3). The interaction between speed and village distance was significant (estimate =  $1.3 \times 10^{-4}$ ,  $t = 2.4$ ,  $df = 2648$ ,  $p = 0.02$ ), with the effect of speed on fix point density increasing with greater distance from villages.

## 6. DISCUSSION

The speed-preference model predicts that speed can be used to estimate levels of habitat preference (Dickson et al. 2005). Without making assumptions of habitat availability, the model had the potential to more accurately identify habitat preference than traditional methods. Here, I show that the speed-preference model is not generalizable to forest elephants. Speed failed to predict land cover preference for forest elephants and exhibited significant interactions with the environmental covariates of topography and village proximity. These interactions altered both the intensity and direction of the relationship between speed and preference, demonstrating that the relationship may not be consistent throughout the range of environmental covariates.

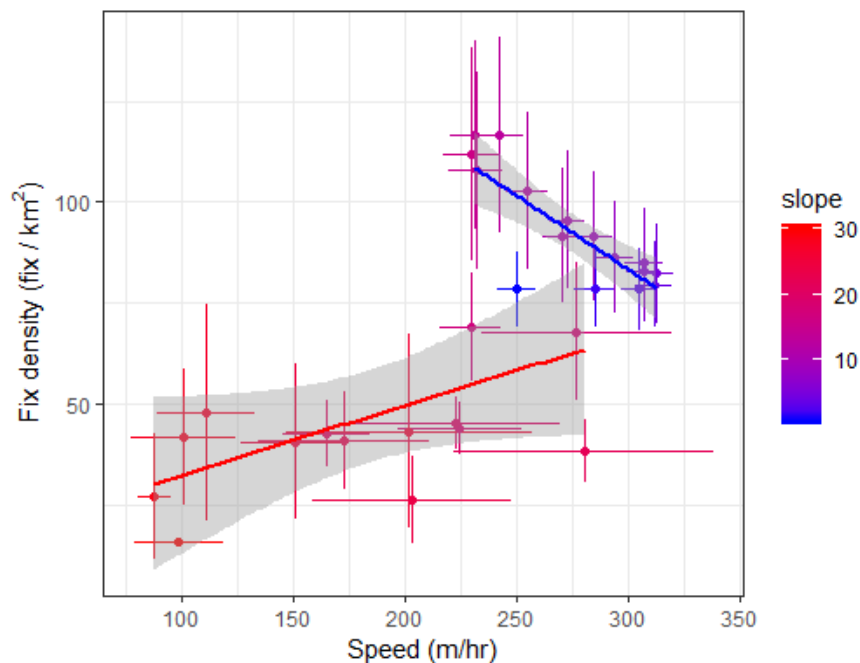
Land cover, topography, and proximity to village significantly influenced the movement speeds of forest elephants. Unlike African savanna elephants (Duffy et al. 2011), forest elephants in this study changed speed with land cover, moving faster in open habitats and wetlands; areas which may have fewer obstruction to movement than forest. Following predictions (Wall et al. 2006; Papworth et al. 2012), collared elephants tended to move slower with increasing slope and proximity to permanent human settlements. These differences in speed are potentially due to the increased energy exertion needed to traverse obstructive terrain (Wall et al. 2006) and changes in behavior as individuals approach sources of potential danger (Papworth et al. 2012).

Levels of habitat preference, as represented in this study by the densities of fix points within certain environmental categories, also differed significantly with varying land cover, topography, and village proximity. Similar to savanna elephants, fix point densities of forest elephants tended to be lower in steeper areas (Wall et al. 2006). Meanwhile, as the principle habitat for forest elephants is forest (Turkalo et al. 2018), fix point densities were predictably highest in forested areas. However, the relationship between fix point densities and distance to village was more complex, with no clear, linear relationship with distance. Even though fix point densities were lowest in areas very close (< 200 m) to villages, there was a spike in fix point densities between 300m and 700m from villages. Many interacting variables could influence the relationship between fix densities and proximity to villages. Even though elephants should consider humans as threats and tend to avoid human settlements accordingly, some individuals might be *attracted* to villages due to greater access to crops (Poulsen et al. 2011). Meanwhile, there is evidence that

some elephants prefer secondary forests that proliferate around disturbed areas (Barnes et al. 1991). Probably due to such complications, previous efforts to assess the relative abundance of elephants with distances to nearest village were also inconclusive (Koerner et al. 2017).

This study detected a significant relationship between fix point density and speed after accounting for topography and proximity to villages. However, these relationships were not as straightforward as that found for cougars (Dickson et al. 2005), for which movement speed was consistently negative and linearly related to habitat preference.

For instance, although the relationship between speed and fix point density was negative with flat topography, in agreement with the speed-preference model, it was negative at the steepest slopes, in contradiction to the model (Figure 8). This matches my expectation that speed is more strongly determined by topography at steeper slopes than habitat and that any predictions of habitat preference using speed should account for this shift.

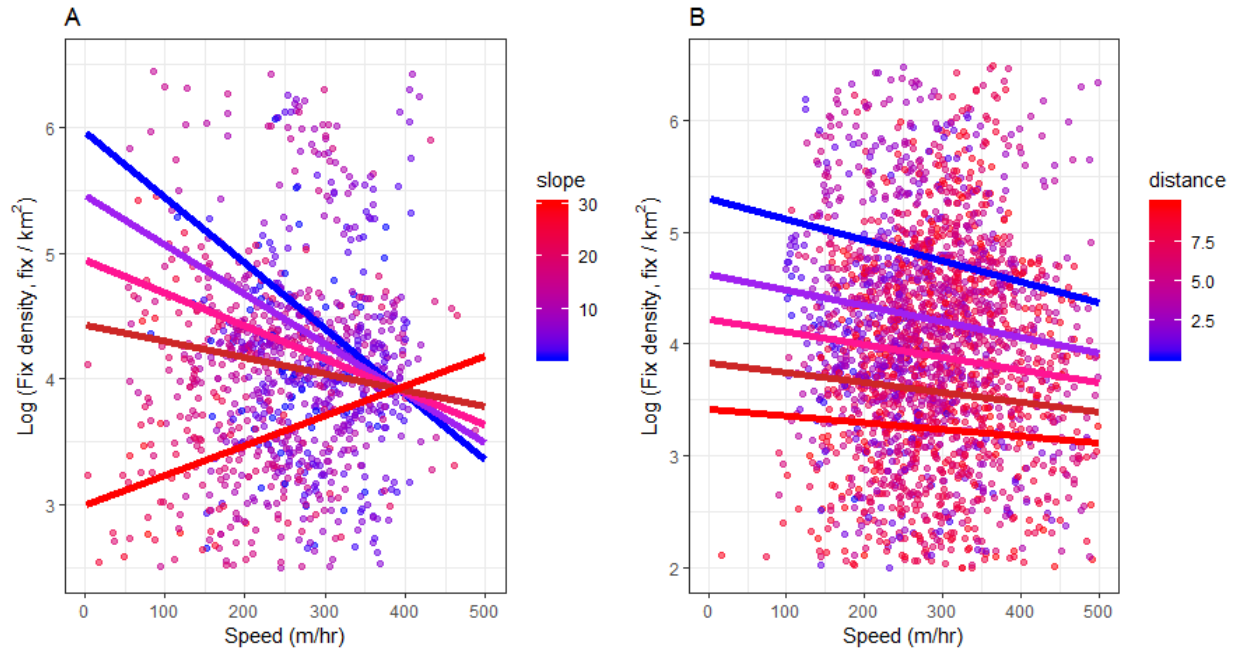


**Figure 8:** A plot of points for each slope category aggregated for all individuals with slope in degrees. This shows the complexity of the relationship between speed and preference for topography, with steeper areas (red) having a significantly positive relationship (estimate = 0.1,  $t = -2.3$ ,  $df = 13$ ,  $p = 0.04$ ) and flatter areas (blue) having a significantly negative relationship (estimate = -0.4,  $t = -4.7$ ,  $df = 13$ ,  $p < 0.001$ ).

I found a similar trend with village proximity, with a negative relationship between speed and fix point densities at close distances to villages and a positive interaction between speed and village proximity at farther distances. However, the negative relationship between fix density and speed contradicted my hypothesis that forest elephants would avoid being very close to human settlements. This result may partially be due to the relatively few fix points (2500 points within 0.5 km from villages) present in areas close to villages and the relatively large range of distances considered in this study.

Compared to the interaction between speed and fix point densities for topography, the positive interaction for village proximity was weaker (Figure 9). The relationship between speed and fix point densities became relatively flat, but never turned positive even at areas farthest from villages. Perhaps the interaction was due more to the decreasing effects of villages on forest elephant behavior with increasing distance. Signs of human activity in northern Gabon dropped significantly after 10 km from a village – the distance at which speed was less useful at predicting fix point densities in my analysis (Koerner et al. 2017). If signs of human activity are directly related to the level of threats that elephants potentially perceive, then at further distances, proximity to villages no longer become important in gauging forest elephant behaviors.

I found that speed could not predict fix point densities for land cover even though there were significant differences in both speed and fix point densities across land cover types. Intuitively, with forested areas (with lower speeds and higher fix point densities) and wetlands (with higher speeds and lower fix point densities), I expected a negative relationship between speed and fix point densities (preference), but these results were not statistically significant. It may be that the relatively coarse land cover map in this study confounds important variables such as more refined land cover types or gradients in canopy cover, disturbance, and precipitation. The land cover map did not accurately distinguish *bais* – naturally occurring clearings that are well-documented hotspots of forest elephant activity (Turkalo et al. 2013). A finer-detail land cover map could serve to identify such areas more consistently while potentially also allowing for an assessment of a greater number of land cover categories and accounting for differing levels of anthropogenic disturbance such as logging.



**Figure 9:** Interactions between speed and fix point densities for topography (A) and village proximity (B), with slope in degrees and distance in kilometers. Both had positive interactions, with negative relationships between speed and fix point densities at flatter and closer areas to villages (blue). However, due to interactions, the relationships became less positive at steeper topography and areas farther from villages (red). With topography, the interaction was strong enough to make the relationship between speeds and fix point densities positive at the steepest areas. In comparison, the interaction with village proximity was weaker, and never became positive even in the farthest areas.

The original speed-preference model was based on rankings of each vegetation type according to preference and speed. This greatly simplified their analyses and aggregated variations associated with individual animals. By ranking the land cover types in this study according to preference and speed, I would also have found a linear relationship between speed and preference, but only by ignoring the complexity inherent in forest elephant movement and habitat preference.

## **Conclusion**

Despite their importance to conservation and management, many methods of modeling habitat depend on arbitrary estimates of habitat availability. Although the speed-preference model avoids this issue, this study found that further research is required as the relationship between speed and preference for mountain lions in the original model was not generalizable to forest elephants. In particular, the model failed to consider the interactions between speed and environmental covariates such as topography and village proximity. These interactions might be due to other factors, such as terrain obstructiveness, playing a more important role in determining speed than habitat preference within certain contexts. Therefore, any attempts to use the speed-preference model should consider the specific environmental context of the animal and conduct preliminary examinations on their movement and preference.

## **7. ACKNOWLEDGEMENTS**

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## 8. APPENDIX

**Table 1: Speed**

Model selection table for movement speed for all models with  $\Delta AIC < 6$  from the best supported model, where 'Int' = Intercept; 'df' = degrees of freedom, and ' $\Delta AIC$ ' = difference in Akaike's Information Criterion score from the best supported model.

Int	Hours	Months	Land Cover	Sex	Slope (degrees)	Village Distance (km)	df	$\Delta AIC$
220.4	+	+	+	+	-2.94	0.0032	44	0
260.9	+	+	+	+	-2.56		43	2.09
224.6	+	+	+		-2.95	0.0032	43	5.75

**Table 2: Habitat Preference**

Model selection table for habitat preference for all models with  $\Delta AIC < 6$  from the best supported model, where 'Int' = Intercept; 'df' = degrees of freedom, and ' $\Delta AIC$ ' = difference in Akaike's Information Criterion score from the best supported model. Cells in grey are not relevant for the analysis of the particular environmental covariate.

Covariate	Int	Sex	Land Cover	Slope (degrees)	Village Distance (km)	df	$\Delta AIC$
Land Cover	99.23	+	+			7	0
Topography	234.9	+		0.87		6	0
Village proximity	173.9	+			-10.56	6	0

**Table 3: Speed and Habitat Preference**

Model selection for the relationship between speed and preference for all models with  $\Delta AIC < 6$  from the best supported model, where 'Int' = Intercept; 'df' = degrees of freedom, and ' $\Delta AIC$ ' = difference in Akaike's Information Criterion score from the best supported model. Cells in grey are not relevant for the analysis of the particular environmental covariate.

Covariate	Int	Sex	Speed (m/hr)	Land Cover	Slope (degrees)	Village Distance (km)	Speed *Slope	Speed *Village distance	df	$\Delta AIC$
Land Cover	4.33	+		+					7	0
Land Cover	4.02			+					8	3.64
Topography	6.07	+	-0.0055		-0.1		0.00026		8	0
Village proximity	5.34	+	-0.0019			-0.19		0.00013	8	0
Village proximity	5.16		-0.0019			-0.19		0.00013	7	0.22

## 9. REFERENCES

- Aebischer, N. Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. *Ecology* **74**, 1313–1325 (1993).
- Barnes, R. F. W., Barnes, K. L., Alers, M. P. T. & Blom, A. Man Determines the Distribution of Elephants in the Rain Forests of Northeastern Gabon. *African Journal of Ecology* **29**, (1991).
- Beirne, C. *et al.* Participatory Monitoring Reveals Village-Centered Gradients of Mammalian Defaunation in Central Africa. *Biological Conservation* **233**, 228–238 (2019).
- Bergman, C. M., Schaefer, J. A. & Luttich, S. N. Caribou Movement as a Correlated Random Walk. *Oecologia* **123**, 364–374 (2000).
- Blake, S. The Ecology of Forest Elephant Distribution and Its Implications for Conservation. (University of Edinburgh, 2002).
- Bunn, A. G., Urban, D. L. & Keitt, T. H. Landscape connectivity: a conservation application of graph theory. *Journal of Environmental Management* **56**, 265–278
- Campos-Arceiz, A. & Blake, S. Megagardeners of the Forest – the Role of Elephants in Seed Dispersal. *Acta Oecologica* **37**, 542–553 (2011).
- Chiyo, P., Cochrane, E., Naughton, L. & Basuta, G. Temporal Patterns of Crop Raiding by Elephants: a Response to Changes in Forage Quality or Crop Availability? *African Journal of Ecology* **43**, 48–55 (2005).
- Dickson, B., Jenness, J. & Beier, P. Influence Of Vegetation, Topography, And Roads On Cougar Movement In Southern California. *Journal of Wildlife Management* **69**, 264–276 (2005).
- Graham, M. D., Douglas-Hamilton, I., Adams, W. M. & Lee, P. C. The Movement of African Elephants in a Human-Dominated Land-Use Mosaic. *Animal Conservation* **12**, 445–455
- Ishida, Y. *et al.* Reconciling Apparent Conflicts between Mitochondrial and Nuclear Phylogenies in African Elephants. *PLoS ONE* **6**, (2011).
- Koerner, S. E., Poulsen, J. R., Blanchard, E. J., Okouyi, J. & Clark, C. J. Vertebrate Community Composition and Diversity Declines along a Defaunation Gradient Radiating from Rural Villages in Gabon. *Journal of Applied Ecology* **54**, 805–814 (2016).
- Loarie, S. R., Van Aarde, R. J. & Pimm, S. L. Fences and Artificial Water Affect African Savannah Elephant Movement Patterns. *Biological Conservation* **142**, 3086–3098 (2009).
- Maisels, F. *et al.* Devastating Decline of Forest Elephants in Central Africa. *PLoS One* **8**, (2018).



Mills, E. C. *et al.* Forest elephant movement and habitat use in a tropical forest-grassland mosaic in Gabon. *PLoS One* **8**, (2018).

Papworth, S., Milner-Gulland, E. J. & Slocombe, K. Hunted Woolly Monkeys (*Lagothrix Poepigii*) Show Threat-Sensitive Responses to Human Presence. *PLoS One* **8**, (2013).

Roever, C. L., van Aarde, R. J. & Leggett, K. Functional Connectivity within Conservation Networks: Delineating Corridors for African Elephants. *Biological Conservation* **157**, 128–135 (2013).

Schadt, S. *et al.* Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecological Applications* **12**, 1469–1483 (2002).

Turkalo, A. K., Wrege, P. H. & Wittemyer, G. Long-Term Monitoring of Dzanga Bai Forest Elephants: Forest Clearing Use Patterns. *PLoS One* **8**, (2013).

Turkalo, A., Wrege, P. H. & Wittemyer, G. Demography of a Forest Elephant Population. *PLoS One* **13**, (2018).

Wall, J., Douglas-Hamilton, I. & Vollrath, F. Elephants Avoid Costly Mountaineering. *Current Biology* **16**, (2006).