

DISSERTATION

IMPLICATIONS OF MOVEMENT BEHAVIOR RESPONSES OF BOTH ASIAN AND  
AFRICAN ELEPHANTS IN CHANGING LANDSCAPES OF THE 21<sup>ST</sup> CENTURY

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Aung Nyein Chan

Department of Fish, Wildlife, and Conservation Biology

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Doctoral Committee:

Advisor: George Wittemyer

Peter Leimgruber  
Barry Noon  
Cameron Aldridge

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## ABSTRACT

### IMPLICATIONS OF MOVEMENT BEHAVIOR RESPONSES OF BOTH ASIAN AND AFRICAN ELEPHANTS IN CHANGING LANDSCAPES OF THE 21<sup>ST</sup> CENTURY

An organism moves to fulfil its most fundamental survival and reproductive needs. Studying movement behavior can provide insights into both inter- and intra-specific interactions, how a species interacts with its environment and accesses resources, species distribution, etc. Given human presence affects mammalian movement across the globe, animal movement studies are increasingly important to assess and understand the impacts of humans on wildlife. Movement behavior response to human presence is particularly relevant and important to understand in the 21<sup>st</sup> century since global human population is projected to reach 9.7 billion by the year 2050. The unprecedented level of human presence and associated land use changes will impact all living organisms on the planet, particularly megaherbivores such as Asian and African elephants which have some of the largest space use requirements among terrestrial mammals. My dissertation research focuses on studying and understanding the movement behavior responses of Asian and African elephants to human-related landscape changes.

The Asian elephant (*Elephas maximus*) which is currently listed as endangered under the IUCN red list of threatened species. The population status of the species is unclear but declining. The species is facing habitat loss and fragmentation due to agricultural expansion, heightened human-elephant conflicts related to human encroachment in previous wilderness areas, and illegal killings, including but not limited to, poaching for skin, ivory, and meat. The largest remaining tracts of wildland (i.e., habitat suitable for wild elephant to exist) among the current

extant range countries/states occurs in the country of Myanmar. However, the struggling economy and unstable political climate put unusual amount of stress on the remaining elephant populations across the country. Asian elephant numbers are declining across much of their range in Myanmar, driven largely by serious threats from land use change resulting in habitat loss and fragmentation. To effectively manage and conserve the remaining populations of endangered elephants in the country, it is crucial to understand their movement behavior across the country's agricultural gradient.

Chapter 1 provided baseline information on elephant spatial requirements and the factors affecting them in Myanmar. This information is important for advancing future land-use planning that considers space-use requirements for elephants. Failing to do so may further endanger already declining elephant populations in Myanmar and across the species' range. We used autocorrelated kernel density estimator (AKDE) based on a continuous-time movement modeling (ctmm) framework to estimate dry season (26 ranges from 22 different individuals), wet season (12 ranges from 10 different individuals), and annual range sizes (8 individuals), and reported the 95%, 50% AKDE, and 95% Minimum Convex Polygon (MCP) range sizes. We assessed how landscape characteristics influenced range size based on a broad array of 48 landscape metrics characterizing aspects of vegetation, water, and human features and their juxtaposition in the study areas. To identify the most relevant landscape metrics and simplify our candidate set of informative metrics, we relied on exploratory factor analysis and Spearman's rank correlation coefficients. Based on this analysis we adopted a final set of metrics into our regression analysis. In a multiple regression framework, we developed candidate models to explain the variation in AKDE dry season range sizes based on the previously identified, salient metrics of landscape composition. Our objectives were to (1) estimate the sizes of dry, wet, and annual ranges of wild

elephants in Myanmar; and quantify the relationship between dry season (the period when human-elephant interactions are the most likely to occur) range size and configurations of agriculture and natural vegetation within the range, and (2) evaluate how percentage of agriculture within dry core range (50% AKDE range) of elephants relates to their daily distance traveled. Elephant dry season ranges were highly variable, averaging 792.0 km<sup>2</sup> and 184.2 km<sup>2</sup> for the 95% and 50% AKDE home ranges, respectively. We found both the shape and spatial configuration of agriculture and natural vegetation patches within an individual elephant's range play a significant role in determining the size of its range. We also found that elephants are moving more (larger energy expenditure) in ranges with higher percentages of agricultural area.

Chapter 2 reveals how elephants interact with agriculture and other important environmental variables such as natural vegetation, roads, and water, etc. Habitat loss and fragmentation due to accelerated agriculture expansion is a major threat to existing wildlife populations across Asia. Although it had been shown that Asian elephant space use was correlated with the level of fragmentation on the landscape in Chapter 1, the mechanism underlying this process is not well documented and can serve to help focus conservation efforts. We analyzed selection behavior of wild elephants across three study sites with different levels of agriculture use patterns in Myanmar, assessing the impact of structure in the agriculture-wildlands interface on habitat selection by elephants. Given elephants exhibit heterogeneous spatial behavior, we fitted two types of selection models to gain insight into the diversity of strategies employed at the local- and home-range scale. We used variance partitioning analysis to quantify the explanatory contribution of individual, study site, and sex. We found that the variation in the resource selection behavior was mainly due to individual differences, and the level of agriculture present in an individual's range was the most influential to its selection

behavior. Gaining a deeper understanding of habitat selection behavior by elephants across the changing landscapes of Asia can help inform management decisions and conservation actions.

As the military coup in 2021 in Myanmar affected my ability to continue working in Myanmar, we decided to transition into assessing the connectivity between Etosha National Park and an adjacent Kunene multi-use conservancies area in Namibia for African elephant (*Loxodonta africana*) as Chapter 3. This region is of particular importance in African elephant conservation since the population is doing relatively well in the area and could serve as one of the remaining strongholds for the species. The loss of habitat and fragmentation of landscapes could lead to declines in wildlife populations, highlighting the need to identify and preserve critical habitats. Connectivity between populations plays a crucial role in mitigating the risks faced by small populations and ensuring their long-term persistence. As a result, the identification of corridors has become a key objective in wildlife conservation. Various methods have been developed to identify high connectivity locations, including resistance surface modeling and empirical-based approaches using GPS tracking data. We used GPS telemetry data from 66 elephants to empirically quantify connectivity using a graph-theoretic approach and assessed landscape features influencing connectivity. We applied the 'movescape' approach to define and locate different types of corridors and examined how landscape features differed across these corridors. Our results revealed strong variation in connectivity across the landscape, with paths of high connectivity near water sources between the study areas. We found that factors related to water sources and human presence primarily influenced connectivity. The findings of this study provide valuable insights into the connectivity patterns and landscape features influencing connectivity for African elephants in northwestern Namibia. We discussed this findings in the context of future conservation management scenarios.

Finally, Chapter 4 assessed the current knowledge on population status of Asian elephants across all 13 range countries or states. We conducted a literature search on Google Scholar using keywords, “Asian elephants”, “Population size”, “Abundance”, and “Density”. We found 26 articles and 9 governmental and non-governmental reports from 2000 to 2022 to evaluate the extent of population assessments using statistically robust methods. Our findings indicate that only 4.39% of the current known distribution of Asian elephants had been assessed using robust sampling and statistical approaches. Out of the 13 range states, only 7 had conducted assessments, with only 3 countries performing robust population assessments in the last 5 years. We highlight the urgent need for more comprehensive and up-to-date studies to accurately estimate the population size of Asian elephants. We recommend investing in spatial capture-recapture approaches using fecal-DNA and photographic capture-recapture methods where feasible to improve abundance estimation. The results of this review emphasize the critical role of accurate population knowledge for effective conservation and management actions for endangered species like the Asian elephant.

This dissertation provides critical pieces of information regarding movement ecology and conservation of both Asian elephant and African elephant. We present analyses on space use requirements, resource selection behavior and the quantification of sources of variation in the movement behavior for Asian elephant in Myanmar. Chapter 1 and chapter 2 were the first two studies to assess movement behavior in Myanmar using empirical data. Since identifying and conserving corridors is one of the key objectives for African elephant’s conservation, chapter 3 provides crucial information for managers on the ground in Etosha National Park and surrounding areas. Finally, we highlighted the research gap in Asian elephant conservation by reviewing studies and reports on population status across the species’ range.

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“If I have seen further than others, it is by standing upon the shoulders of the Giants.”

~ Isaac Newton (1675)

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# **CHAPTER 1: Landscape characteristics influence ranging behavior of Asian elephants at the human-wildlands interface in Myanmar<sup>1</sup>**

## **Introduction**

The ability to understand how range size and movement patterns of a species vary in changing landscapes is important for informing decision processes and landscape planning efforts by resource managers and conservation agencies (Morato et al., 2016; Wadey et al., 2018). Information on space requirements across different levels of human presence on a landscape can guide planning efforts and ensure success of management objectives. The advent of GPS technology in wildlife telemetry has revolutionized how movement data are collected in the field of wildlife science (Wall et al., 2014; Kays et al., 2015). The ability to collect large volumes of location data with high temporal resolution allows robust inference on spatial requirements, including home range size, range shifts by season, and movement patterns within the home range. When paired with a powerful open-source technology, such as Google Earth Engine and R, understanding of the spatial context of the movement and space use patterns can be determined with relative ease. Such information allows scientists to address key conservation challenges, advancing ecological knowledge of a species and serving to answer applied questions (Gorelick et al., 2017; Seidel et al., 2018; Wittemyer et al., 2019).

To understand the drivers of an animal's movements, it is critical to appropriately understand the landscape context influencing its movement decisions (Nathan et al., 2008). Traditionally,

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<sup>1</sup> Adapted from Chan, A.N., Wittemyer, G., McEvoy, J., Williams, A.C., Cox, N., Soe, P., Grindley, M., Shwe, N.M., Chit, A.M., Oo, Z.M., and Leimgruber, P. 2022. Landscape characteristics influence ranging behavior of Asian elephants at the human-wildlands interface in Myanmar. *Movement Ecology* (2022) 10:6. <https://doi.org/10.1186/s40462-022-00304-x>

ecologists have used software, such as FRAGSTATS, to quantify landscape metrics (Lamine et al., 2018) and address related ecological questions of interest (Midha and Mathur, 2010). However, new analytical approaches are providing ecologists with more flexibility and unified workflow within one programming environment such as R (Hesselbarth et al., 2019). Easy extraction and quantification of landscape conditions using such platforms allow ecologists to carry out further analysis, such as data visualization, exploratory factor analysis, and generalized linear regression, to make inference on the ecological influence of landscape variables (Seidel et al., 2018) with greater ease. Coupling such information with data on animal space use can allow deeper insight to how landscape characteristics shape space-use relationships, such as home range behavior.

The endangered Asian elephant (*Elephas maximus*) is particularly susceptible to habitat loss being the largest terrestrial mammal with large and heterogeneous habitat requirements (Owen-Smith, 1988; Sukumar, 1989; Fernando et al., 2008). The species is facing serious anthropogenic pressure across its geographic range (Santiapillai and Jackson, 1990; Leimgruber et al., 2003; Choudhury et al., 2008; Calabrese et al., 2017). Agricultural expansion is driving habitat fragmentation and loss and is resulting in significant increase in human-elephant conflicts (often the killings of people and elephants). The combined effects of habitat loss and increased conflict represent a major threat to remaining elephant populations across Asia. This is exacerbated by the persistent threat of poaching to the survival of remaining elephant populations (Leimgruber et al., 2003; Calabrese et al., 2017; Sampson et al., 2018).

Myanmar, home to approximately 1,400 wild elephants (Leimgruber and Wemmer, 2004), has the largest amount of remaining wildlands among the species' range countries (37.86 %) although the landscape is changing rapidly (Leimgruber et al., 2003, 2011). The status of

Myanmar's elephants is unclear, but likely elephants are declining as they continue to face threats in the wild (Leimgruber et al., 2011; Songer et al., 2016). Recent evidence of increased poaching is a serious concern (Sampson et al., 2018). At the same time, range loss, driven by rapid development across the country due to recent changes in the political system and an increased development focus (Prescott et al., 2017), is thought to be the primary driver of elephant decline in the country. One study suggested that the geographic distribution of elephants in Myanmar declined by 5% (~15,000 km<sup>2</sup>) between 1992 and 2006 (Songer et al., 2016). Even within a proposed national park in Myanmar, forest cover is declining (Connette et al., 2017). There are only a few studies that have assessed the space use of wild Asian elephants (Fernando et al., 2008; Kumar et al., 2010; Alfred et al., 2012; Moßbrucker et al., 2016), and only one study assessing ranging behavior of wild elephants in Myanmar in relation to seed dispersal (Campos-Arceiz et al., 2008) to our knowledge. Therefore, it is crucial to obtain information relating space use and ranging behavior of elephants to their landscape context in the country.

Developing tools for assessing elephant space use and ranging requirements becomes even more critical with continued habitat loss. As human populations continue to increase, human encroachment into the remaining "wildlands" within the elephant's range countries is likely to accelerate. This encroachment will inevitably lead to increased human-elephant encounters and conflicts. Additionally, increased fragmentation due to habitat loss could result in increased range size as elephants are forced to move further to meet the resource requirements (Fernando et al., 2005; Alfred et al., 2012). Elephants are likely to change their ranging pattern (area used and movement rates) in response to fragmentation and resource availability, and this is particularly relevant in the dry season in Southeast Asia when the configuration of resources varies across the

landscape and availability of high-value food items (and resulting conflict) increases during the harvesting period (Sukumar, 1989; Campos-Arceiz et al., 2008).

We looked at the relationship between animal space use and landscape context, by deriving metrics describing shape and configuration of land cover types (agriculture, water, and natural vegetation) within individual ranges. Our two main objectives of this study were to (1) quantify dry season range sizes in Myanmar and assess how ranging behavior during the dry season varies based on different configurations of available agriculture and natural vegetation (including testing for range size thresholds relative to percentage of agriculture); and (2) evaluate how percentage of agriculture within dry core range (50% AKDE range) of elephants relates to their daily distance traveled. In addition, we examined wet season ranging and annual ranging behaviors where data allowed.

## **Methods**

### *Study areas*

Our study was conducted in three areas of conservation interest in central, western, and southern Myanmar (Figure. 1.1). Site 1 (Latitude: 17.1013 – 18.1960, Longitude: 95.7043 – 96.4787) is in the central part of Myanmar in the foothills of Bago Yoma mountain ranges. Historical unsustainable teak extraction in this site created a highly disturbed forest mosaic that is increasingly being invaded by other human land uses, including the construction of hydroelectric reservoirs, settlements, as well as commercial teak, sugarcane, rice, and rubber plantations. Site 2 (Latitude: 16.0554 – 17.0842, Longitude: 94.1860 – 94.6838) is a mountainous area along the west coast of the Ayeyarwaddy state that stretches from north to south creating an elongated forest with hard boundaries on east and west. Rice plantations dominate the matrix between forest patches in this site, where rubber and peppercorn agricultural

use is also prevalent. Site 3 (Latitude: 10.7141 – 12.0981, Longitude: 98.3356 – 99.4626) is part of the larger Dawna Tanintharyi Landscape which extends from mountain ridges along the border with Thailand to the coastal plain. Land use at site 3 is primarily composed of oil palm and betel nut plantations, surrounded by lowland deciduous forests. Threats of human encroachment, road development, and agricultural expansion into the remaining forest are rising in the area.

The study areas are strongly seasonal, with rainfall records demonstrating the extended dry season occurs between early December and late March, and the wet season between early June and mid-September (Biswas et al., 2015). During the dry season, human-elephant conflicts (HECs) peak in relation to the harvest of rice, sugarcane, and other agricultural products (Sukumar, 2003; Fernando et al., 2005). Rainfall is significantly higher at site 3, resulting in markedly different forest composition. Forests at site 3 are predominantly lowland evergreen forests, while at site 1 and 2, they are mostly mixed deciduous forests with strong seasonal leaf-fall patterns.

#### *Elephant capture for GPS collaring*

All capture and animal sedation were performed by veterinarians from Myanmar Timber Enterprise (MTE). MTE is the Myanmar government agency responsible for the management of logging elephants, and their staff have extensive experience in veterinary care of captive and wild Asian elephants, including sedation. Individuals were independently captured during the collaring period, and no collared elephants were found in the same social unit. All capture and handling procedures followed or exceeded the guidelines provided by the American Society of Mammalogists (Sikes, 2016). Elephants were immobilized using Etorphine and Xylaxine for sedation and Naltrexone for reversal. The immobilization and collaring process took

approximately 30 minutes per individual on average and was carried out early in the morning or late in the afternoon when air temperature was relatively lower ( $<35^{\circ}$  C). All the collars are set to record a GPS fix every hour. Due to high collar failure and poaching soon after collar deployments (Sampson et al., 2018), telemetry datasets were often patchy and covered relatively short periods. Consequently, we only included individuals with 1)  $> 60$  days of tracking data and/or 2) that had an established range (based on a semi-variogram analysis of range stability described below). To assess whether animals established ranges during the tracking periods, we used methods described by (Calabrese et al., 2016) in their continuous-time movement modeling package (ctmm) in R. When the semi-variogram function for the relocation data of an elephant approached an asymptote, we classified that dataset as capturing an established range (Calabrese et al., 2016), which occurred within 60 days each season for the elephants in this study.

For dry season range analysis, we analyzed data from eight individuals from site 1 (4 females: 4 males), six from the site 2 (1 female: 5 males), and eight from site 3 (2 females: 6 males) – totaling 22 different individuals. We performed data analysis on data collected from December 2016 through March 2020. Therefore, our analysis covers four dry seasons. There were four individuals whose tracking periods covered two dry seasons. To avoid problems with pseudo-replication when developing our regression model set, we excluded the year with fewer data points for each of these four individuals such that each only supplied one season to the analysis.

For the wet season ranges estimation, we utilized data from five individuals from site 1 (1 female: 4 males), three from the site 2 (3 males), and two from site 3 (2 males). There were two individuals who had data spanning two wet seasons, allowing estimation of 12 wet-season

ranges. Because of the relatively small sample size, we did not run a regression analysis on wet season data.

For annual home range estimation, we included individuals with  $> 365$  days tracked, which amounted to 8 individuals: five individuals from site 1 (1 female: 4 males), one from the site 2 (1 male), and two from site 3 (2 males).

### *Range estimation*

We employed a ctmm framework (Calabrese et al., 2016) to estimate seasonal (dry and wet) and annual range sizes among individuals. We compared the fit to our data of independent and identically distributed (IID), Ornstein-Uhlenbeck (OU), and Ornstein-Uhlenbeck Foraging (OUF) movement models using an autocorrelation estimation method. We picked the best fitting model and applied it to fit the autocorrelated density estimator (AKDE) function to estimate range size. We calculated 95% and 50% AKDE percentile level ranges for all individuals. We assumed 50% AKDE level as core areas within the respective ranges where animals spent 50 percent of their time. To enable comparison with other studies, we calculated and presented 95 percentile Minimum Convex Polygon (MCP) ranges.

### *Predictor variables and candidate models*

To assess which landscape conditions were related to dry season range size, we applied gamma regression models with estimated AKDE range sizes as a response variable based on the assumption that our response variable can only be a non-zero positive number. Our covariate dataset of landscape properties was developed by classifying Landsat 8 imageries to develop land cover maps for each of our study areas (Chan et al. unpublished data). We used the ‘landscapemetrics’ package in R to derive different measures for characterizing landscape metrics from our land cover map (Hesselbarth et al., 2019). To describe the landscape of each

individual range, we calculated several different shape, area, edge, and aggregation metrics for water, agriculture, and natural vegetation classes (Table 1.1). In addition, we quantified landscape-level metrics, including Shannon's diversity index, relative patch richness, and relative patch density (Table 1.1). We computed 48 landscape metrics in total.

To simplify these 48 metrics for our regression analysis, we relied on exploratory factor analysis with oblique minimal rotation of principal factor axes to reduce the data dimensionality. This approach relaxes the assumption of normality (Costello and Osborne, 2005) and allowed us to identify the variables that best characterized variations in our landscapes (Table 1.1). Specifically, we included the highest positive and negative loading variables from the first five principal factor axes to reduce the metrics to the primary explanatory variables while explaining sufficient variance in the data. Afterwards, we compared single variable models among metrics belonging to the same land cover class. We kept the variables if the AIC corrected for small sample size (AICc) score was within 8 of the top model and excluded variables that did not meet the criteria in our candidate model set. AICc is the metric used to rank the models in your candidate model set in such a way that the most parsimonious model will have the lowest AICc value among the model set. This allowed us to eliminate variables with relatively low explanatory power. We also assessed the Spearman's rank correlation coefficients between all the variables before including them in the final candidate model sets (all the variables included in the model set were less than 0.6).

From the retained variables (Table 1.1), we then developed different biologically meaningful combinations of agriculture and natural vegetation indices in the model set for both the 95% and 50% AKDE level for dry season ranges. We included a model with a quadratic term for percentage of agriculture to determine whether we could assess the threshold relationship

between agriculture and range size. We also assessed the effect of sex, site, and year by adding these covariates to our best performing model and ranked the models using AICc for both 95% and 50% AKDE top models. We investigated these effects further in 50% AKDE range sizes analysis by dropping uninformative parameters in our model sets based on model weights and parameter estimates and presented the most parsimonious and biologically meaningful model since the effect of site/region came out stronger in our model set (Arnold, 2010).

In addition to our range size models, we developed a candidate model set to assess the correlation between landscape metrics and average daily distance moved by the elephants. We calculated average daily distance moved by calculating the sum of hourly distance moved (straight-line distance between the two consecutive points) and dividing by the total number of days tracked for each individual. We did not include days where fix success rate was below 80% in our daily distance traveled calculation. For this candidate model set, we tested several hypotheses using the most informative variables from the 50% AKDE dry season analysis. We tested whether sex, site/region, and/or two agriculture metrics (percentage of agriculture presence and perimeter-area ratio of agriculture patches within the range) influenced average daily distance moved by elephants by fitting gamma regression model as described above. We set female and study site 2 as a reference category for sex and region categorical predictor variables, respectively, in the model.

We used AICc to rank models in the candidate model set (Burnham and Anderson, 2002). We selected the model with the lowest AICc as the best/top model in respective candidate model set. To account for variation in range sizes driven by sampling differences, we included the number of days tracked as an additional variable in the top model. We retained the number of days tracked variable if it was included in a model within 2 AICc scores of the top model. All

variables were standardized to a mean of 0 and a standard deviation of 1 before fitting the model for easier interpretation of the results and standardize the effect size of all covariates. All analyses were conducted in R version 3.6.3 using ‘ggplot2’ (version 3.3.0), ‘dplyr’ (version 0.8.5), ‘ctmm’ (version 0.5.9), ‘landscapemetrics’ (version 1.4.3), and ‘AICcmodavg’ (version 2.2.2) (Wickham, 2016; Mazerolle, 2019; Fleming and Calabrese, 2020; R Core Team, 2020; Wickham et al., 2020).

## **Results**

### *Determinants of seasonal home range size*

Home range size estimates varied across seasons and individuals (Table 1.2). Elephant dry season ranges were highly variable averaging 792 km<sup>2</sup> (+/- 867.6 km<sup>2</sup>; range from 38.4 km<sup>2</sup> to 3,166.4 km<sup>2</sup>) for the 95% AKDE ranges while the 50% AKDE range sizes averaging 184.2 km<sup>2</sup> (+/- 201.5 km<sup>2</sup>; range: 7.4 km<sup>2</sup> to 728.5 km<sup>2</sup>). Despite more limited sample sizes ( $n_{\text{wet}} = 12$ ,  $n_{\text{annual}} = 8$ ), analysis of wet season range indicated the average 95% AKDE ranges was 1,520 km<sup>2</sup> (range: 43.5 – 5,362.2 km<sup>2</sup>), and the average AKDE 50% ranges was 356.1 km<sup>2</sup> (range: 12.8 – 1,277.5 km<sup>2</sup>). Considering only full annual ranges, the average range covered 1,093.1 km<sup>2</sup> (range: 89.6 – 3,057.4 km<sup>2</sup>) and 252.9 km<sup>2</sup> (range: 20.3 - 777.2 km<sup>2</sup>) for 95 % and 50% AKDE home ranges respectively. We did not find differences in range sizes between males and females, probably because of the overall large variation in range size (average and standard deviation of female 50% AKDE = 153 km<sup>2</sup> +/- 221 km<sup>2</sup>; average and standard deviation of male 50% range: 196 km<sup>2</sup> +/- 199 km<sup>2</sup>). The variation between the sites was greater for the 50% AKDE range size (including site as a covariate improved the explanatory power), but the effect of the site did not add much to the explanatory power of the best performing model of our 95% AKDE range

analysis (Site 1:  $\bar{x} = 750.3 \pm 892.5 \text{ km}^2$ ; Site 2:  $\bar{x} = 947.4 \pm 945.6 \text{ km}^2$ ; Site 3:  $\bar{x} = 713.3 \pm 865.9 \text{ km}^2$ ).

The variation in 95% AKDE level dry season ranges was best explained by metrics characterizing agricultural land use rather than those of natural areas (Table 1.3); whereas metrics describing landscape configuration of natural vegetation classes explained the difference in 50% AKDE range sizes (core range area) (Table 1.4.1). The top models contained four statistically significant variables with three agriculture and one natural vegetation metrics in the top model for 95% AKDE ranges; and one metric for each agriculture and natural vegetation and site variable for 50% AKDE ranges (Figure 1.2 and 1.3). To assess the effects of sex, site, year on ranging behavior, we ran a secondary model including these variables in the top model of 95% AKDE range sizes. These variables did not add any significant explanatory power to our top model ( $\delta\text{AICc}$  is greater than 4).

The top model for 95% AKDE range included significant coefficient estimates for percentage of agriculture on the landscape, fractal dimension mean and edge density of agriculture, and the coefficient of variation of patch area for natural vegetation (Figure 1.2 and Table 1.3). In general, elephants tend to have larger 95% AKDE range when the shape of agriculture patches were irregular (higher mean fractal dimension) and agriculture land use percentage on a landscape increased (Figure 1.2). On the other hand, more patchy agriculture on a landscape (higher edge density) corresponded to smaller 95 % AKDE range (Figure 1.4). On average, one unit increase in the metric describing variation in natural vegetation patches (1 standard deviation from the mean) resulted in a  $3.17 \text{ km}^2$  increase in potential range size while holding the rest of the variables in the model at their mean value (Figure 1.4). The likelihood ratio-based r-squared for our top model was 0.9533.

The top model for 50% AKDE of the estimated dry season range included significant coefficient estimates for disjunct natural vegetation area density, landscape shape index of agriculture, and the site variable as a factor (reference site: site 2) (Fig. 3, Table 4.2). Smaller core range areas corresponded to more complex natural vegetation patches (i.e., increase in perimeter-area ratio, Figure 1.5). In contrast, larger core range sizes corresponded with less compact patches of agriculture (i.e., higher landscape shape index, Figure 1.5). On average, an increase in 1 unit of landscape shape index score of agriculture (1 standard deviation from the mean) corresponded to an increase of 3.13 km<sup>2</sup> in core range area. Estimated 50% AKDE ranges were smaller in Tanintharyi (Site 3) than in the reference site Ayeyarwaddy delta (Site 2) (Figure 1.3). The likelihood ratio-based R-squared for our top model was 0.929.

#### *Daily travel distance*

The average daily distance traveled by the elephants in the dry season was 3.9 km (range: 1.3 – 7.3 km), with males moving 3.8 km (+/- 1.6 km; n = 19) and females 4.1 km (+/- 1.6 km; n = 7) per day. According to our top model, the average daily distance moved was 3.8 km at 13.9 percent agriculture within their home range (Table 1.5). Percentage of agriculture on a landscape (pland\_ag) was the only covariate in our most parsimonious model (top model) to explain variation in average daily travel distance by elephants. An approximate increase of 15 percent in agriculture on the landscape resulted in an increase of 1.2 km in the daily distance traveled by the elephants. Study sites and sex of the individual were not included in the top model in our sample (Table 1.5).

## Discussion

This is the first study to report different seasonal ranges (primarily dry season) of Asian elephants in Myanmar. The results show high variation in ranges sizes and demonstrated that some of this variation can be explained by differences in landscape metrics describing the relationship between natural vegetation and agriculture. We note there was greater variation in 95% AKDE range size within relative to between the three study sites across the country, suggesting strong variability between individual space use strategies. We also showed that elephants in Site 3 (Tanintharyi) had smaller core ranges. This could be the result of a high presence of palm oil plantations and the higher degree of fragmentation in natural vegetation throughout the southern landscape of Myanmar. Percentage of agriculture within the range positively correlated with average daily distance traveled by the elephants (i.e., elephants traveled further and faster in areas with higher percentage of agriculture). These findings demonstrate that elephants' ranging behavior in Myanmar is influenced by different configurations of agriculture and natural vegetation on the landscape.

We identified percentage of agriculture, mean fractal dimension and edge density of agriculture (i.e., patchiness), and coefficient of variation in natural vegetation patches (i.e., differentiation between patch sizes) within an elephant's range as the variables of importance in quantifying the level of fragmentation within an individual's potential range (i.e., 95% AKDE range). Within the elephant's core range (i.e., 50% AKDE range), we showed that landscape shape index for agriculture (i.e., the patch becomes less compact as the index increases) is the most important variable in explaining the variation in range sizes. We also showed that increase in agriculture resulting in loss of natural vegetation within elephants' ranges corresponded to an increase in range sizes. We did not detect a relationship between range size thresholds relative to

percentage of agriculture (our top model did not include the quadratic variable allowing such inference). However, further investigation on a larger data set would be valuable to determine the nature of this relationship. Sampling across a broader gradient of human agricultural use could provide more specific inference on this relationship, though it may be difficult to determine such thresholds if it is a gradual process and the number of elephants living near this theoretical threshold are small.

It is inevitable that Asian elephants will face increasing fragmentation and habitat loss due to agricultural expansion and urbanization across the range countries (Leimgruber et al., 2003; Sodhi et al., 2004; Songer et al., 2016). The level of human footprint on a landscape can affect movement of animals (Tucker et al., 2018). Therefore, it is crucial to quantify the structure and magnitude of fragmentation within the species' core range and understand the impact on animal movement behavior as a first step in any science-based management and conservation program. Previous research indicated that Asian elephants benefit from a mixture of natural vegetation and agriculture on a landscape (Fernando and Leimgruber, 2011; Songer et al., 2016; Calabrese et al., 2017). Our results agree with the existing literature on Asian elephant's movement behavior in fragmented landscape, where elephants in more fragmented habitat are likely to move further (increased energy expenditure) to meet their survival and fitness requirements (Fernando et al., 2005; Campos-Arceiz et al., 2008; Alfred et al., 2012). Increased movement may chiefly be a strategy whereby elephants reduce the inherent risk of being near humans. For example, Asian elephants on the island of Borneo moved faster in landscapes with increased human modification, presumably to avoid encounters with humans (Evans et al., 2020). However, elevated movement rates across human-modified landscapes may also be important to reduce poaching risks (Sukumar, 1990; Webber et al., 2011). This may be

particularly true in Myanmar, where poaching for elephant skin has recently increased sharply across the agriculture-wildland interface (Sampson et al., 2018).

Asian elephant range sizes are thought to be strongly determined by availability of water on a given landscape (Sukumar, 1989; Fernando et al., 2008); however, the variables capturing water land cover class were not included in top models of neither 95% AKDE range nor core range sizes of elephants in our analysis for the dry season. This may indicate that water is not a limiting factor within these landscapes, possibly because elephants have already adjusted their range to meet their water requirement for the dry season, or because water is relatively widely available. Alternatively, it is possible that the land cover map used in this study did not adequately capture all aspects of water availability on the landscape, or that the grain of our satellite imageries used to produce our land cover maps (30 x 30 meters) was too coarse to capture the seasonal variation of smaller water sources within our study sites.

To facilitate direct comparison between the results from this study and that of others, we reported MCP range sizes as well as AKDE. We found that dry season 95% AKDE range sizes ranged from 38.4 km<sup>2</sup> to 3,166.4 km<sup>2</sup> in Myanmar, which is similar to ranges reported in Sumatra, Indonesia using the same estimator (ranges from 275 – 5,179 km<sup>2</sup>) (Moßbrucker et al., 2016). We estimated MCP annual ranges in Myanmar at 65.8 to 1,152 km<sup>2</sup> which shows more variation in range sizes than other studies using the same range estimation method – Sri Lanka: 51.2 – 179.2 km<sup>2</sup> (Fernando et al., 2008), Malaysia: 122 – 114 km<sup>2</sup> (Kumar et al., 2010), and India: 105 – 320 km<sup>2</sup> (Sukumar, 1989). All the compared studies were conducted either within protected areas or surrounded by protected areas, whereas our study sites were primarily outside of the protected areas. In general, our study reported a lot more variations in range sizes since we included individuals from three different study sites across the country with different landscape

configurations. This highlights further that ranging behavior of elephants are affected by land use types and their spatial configurations.

Our relatively small sample size of individuals and variable fix success across collars influenced our results to some extent. We relied on AKDE range estimates given they are relatively robust to differential sampling and fix success issues (average fix success rate ~75% during the wet season in this study). Notably, our AKDE analysis yielded larger range sizes for wet season than annual ranges, despite the annual range estimates including all data used to estimate the wet season range (in addition to data from the dry season) for some individuals. The larger AKDE wet season estimate was likely a result of the small sample size and temporally dispersed relocation points in the dataset that may result from dispersal behavior or a function of poor collar performance during the wet season causing more uncertainty in the estimates (Fleming and Calabrese, 2017). We calculated 95% minimum convex polygon and found annual ranges were larger than wet season ranges (Table 1.2). This is not intended as a comparison between the two estimators, but an exploration of the seasonal and total differences. We also estimated large ranges in the dry season for some individuals (particularly individual 1997) that had relatively lower fix success (~70 percent fix success rate during the dry season). While it is probable that fix success played a role in the estimates, these large ranges are likely biologically driven. For instance, individual 19971 was a young male (15-25 estimated age) navigating the human-dominated landscape of Bago Yoma, and the large range size may be driven by physiological demands and reproductive strategies in the highly fragmented landscape (Taylor et al., 2020).

Elephants continue to face habitat loss and fragmentation across their range due to development (Leimgruber et al., 2003; Calabrese et al., 2017). This will in turn increase human-

elephant encounters (Fernando et al., 2005). Although there are several ways to mitigate human-elephant conflicts particularly at the agriculture-wildland interface, such as electric fencing, bee fencing, and chili fencing, it is important to identify if we are mitigating the problem or simply moving it elsewhere (Barua et al., 2013; Shaffer et al., 2019). When deploying temporary or permanent fencing on a landscape, we are fragmenting the landscape, which can drive behavioral responses from the elephants. For instance, increased fragmentation in the study system is related to larger ranges. Mitigation approaches could cause the elephants to move more broadly, potentially spreading conflict areas across a broader area. Therefore, it is important to consider the impact of mitigation methods on elephants' ranging behavior in a larger landscape scale although these mitigation methods could prove to be useful for given locations or when implemented strategically as part of a broader landscape planning effort. Our study provides a useful model to predict the degree to which ranging behavior of elephant in Myanmar could change based on changes in fragmentation on the landscape. For example, in Site 2 (Ayeyarwaddy Delta), an increase in 1 unit of landscape shape index score of agriculture (1 standard deviation from the mean, i.e., patchier) corresponded to an increase of 3.13 km<sup>2</sup> of core dry-range area. Elephants may be able to persist in these heterogeneous agriculture-natural-vegetation landscape mosaics for the long term if human-elephant conflicts can be managed appropriately by targeting actions that keep human and elephant casualties low and reduce economic impacts on local farmers. To reach this goal, managers and policy makers must pay attention to changes in elephant space use in relation to land-use development and human-elephant conflict mitigation actions to help ensure ecologically sustainable policy and decisions by managers and conservationists. It is also important to ensure the remaining wildlands for elephants are protected, which will provide refuge habitat and could reduce the overall area use

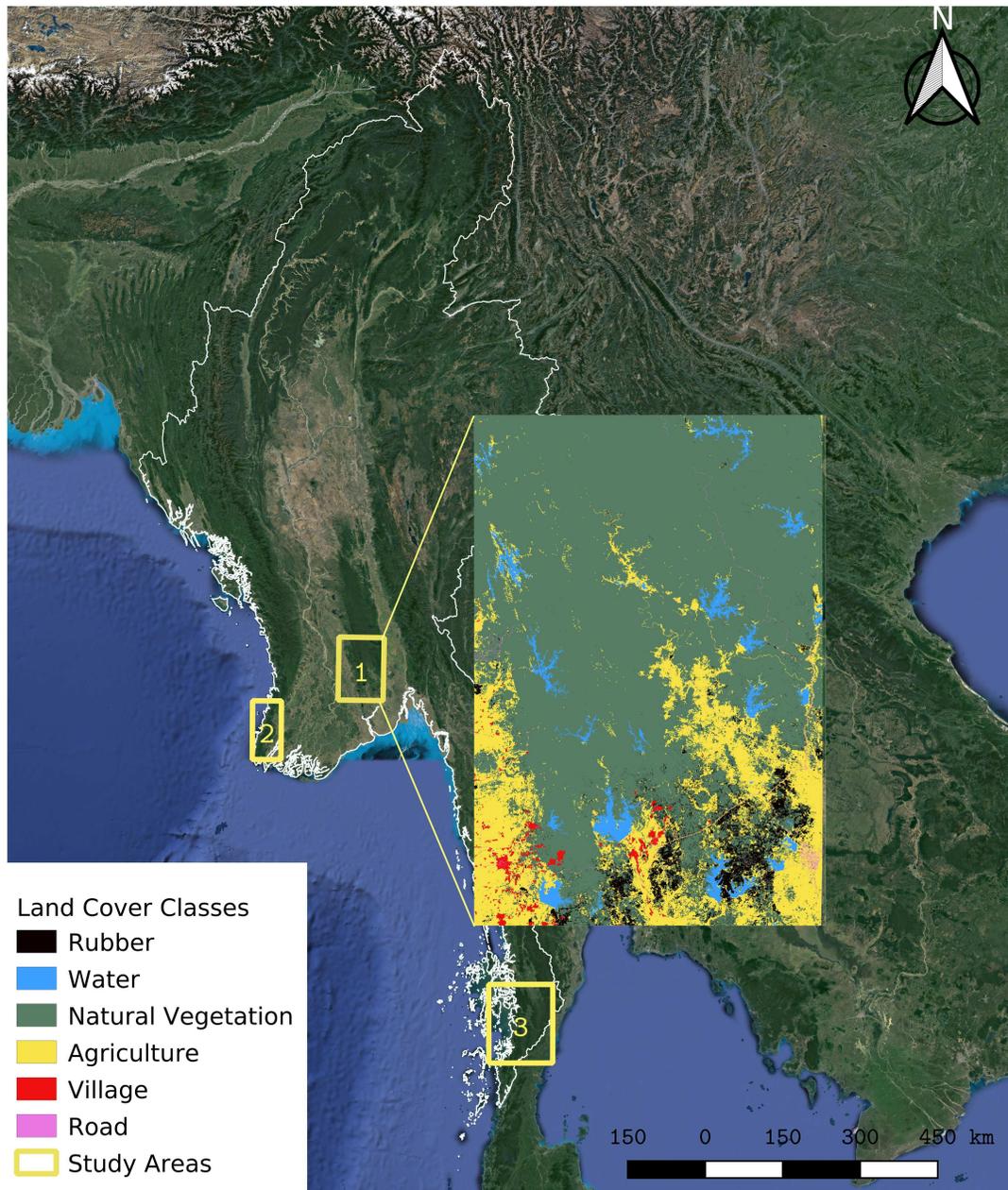
by elephants – range use increased with less natural area (Figure 1.5). The degradation of remaining natural areas should be prevented at all costs to reduce negative interaction between human and elephants in the country.

Our models were evaluated for three study sites in Myanmar. We encourage managers and policy makers to re-evaluate the parameters and their effect sizes by following the same approach when making management decisions in respective study/management areas. Increasing human footprint as a result of land use changes on a landscape will impact ranging and other movement behavior of the elephants (Tucker et al., 2018; Evans et al., 2020). Therefore, if information regarding the potential effect size of change on those behaviors is taken into account during the decision-making process, it should help to ensure elephants continue to exist in the area of concern.

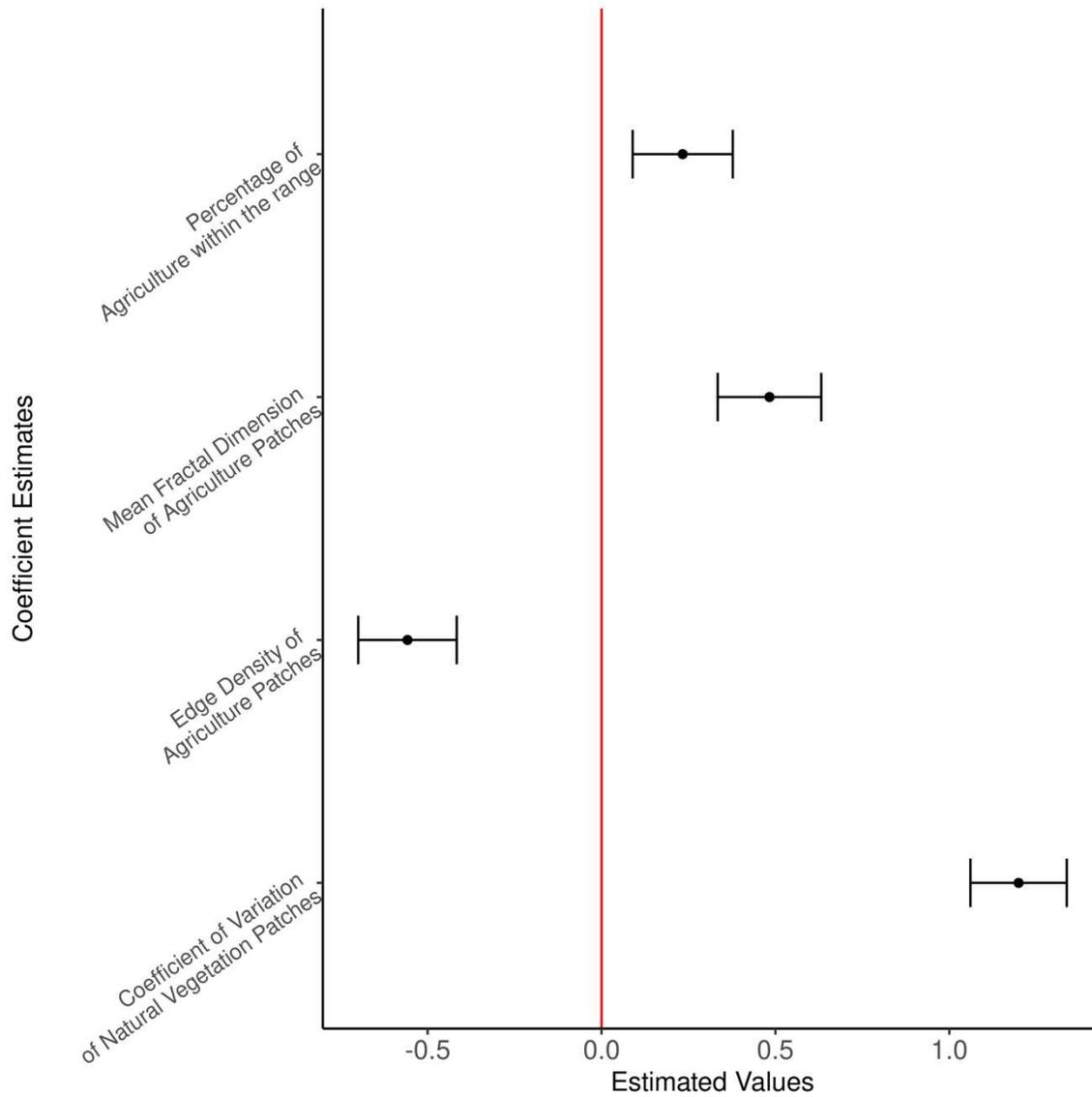
This study provides foundational information on the movement ecology and ranging behavior of the Asian elephant in Myanmar. Although Myanmar has lower elephant numbers than countries such as Sri Lanka and India, it has large tracts of suitable habitat for Asian elephants, making it a key range country for the species (Leimgruber et al., 2003). Determining habitat requirements through studies of habitat selection and space use, can serve the country by providing managers and policy makers with concrete information on habitat requirements of this endangered species. This study provides such baseline information, while also providing insight to how landscape structures influence elephant space use. It also highlights the importance of assessing elephant use of areas outside of protected areas, which have been traditionally overlooked. Since it was predicted that 41.8 % of the 256,518 km<sup>2</sup> of the available habitat for Asian elephants will be lost by the end of century (Kanagaraj et al., 2019), we expect more fragmentation and land-use changes within elephant's core ranges which could potentially lead to

larger ranging behavior increasing both the number of and distribution of human-elephant conflicts. We showed that increasing agriculture will lead to detrimental consequences on elephants, but determining the threshold will be difficult and could be the point of no return once a population gets there. Therefore, monitoring with the help of GPS tracking and high-resolution satellite imageries, we can provide empirically sound information on how elephants are navigating in human-dominated landscapes and effectiveness of potential mitigation methods for HEC. We believe the species could benefit from us applying science-based management decisions for future land-use planning.

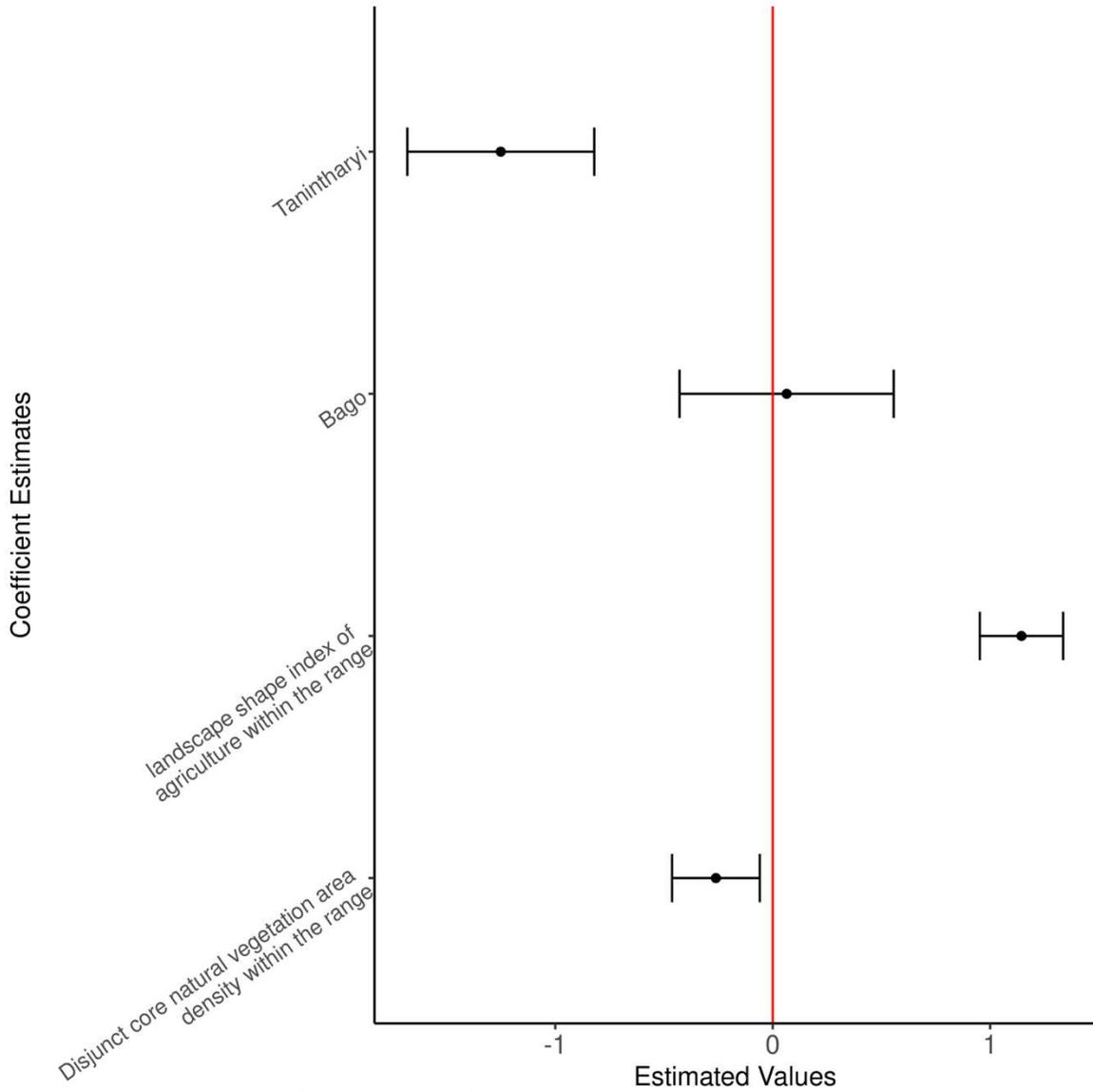
## Tables and Figures



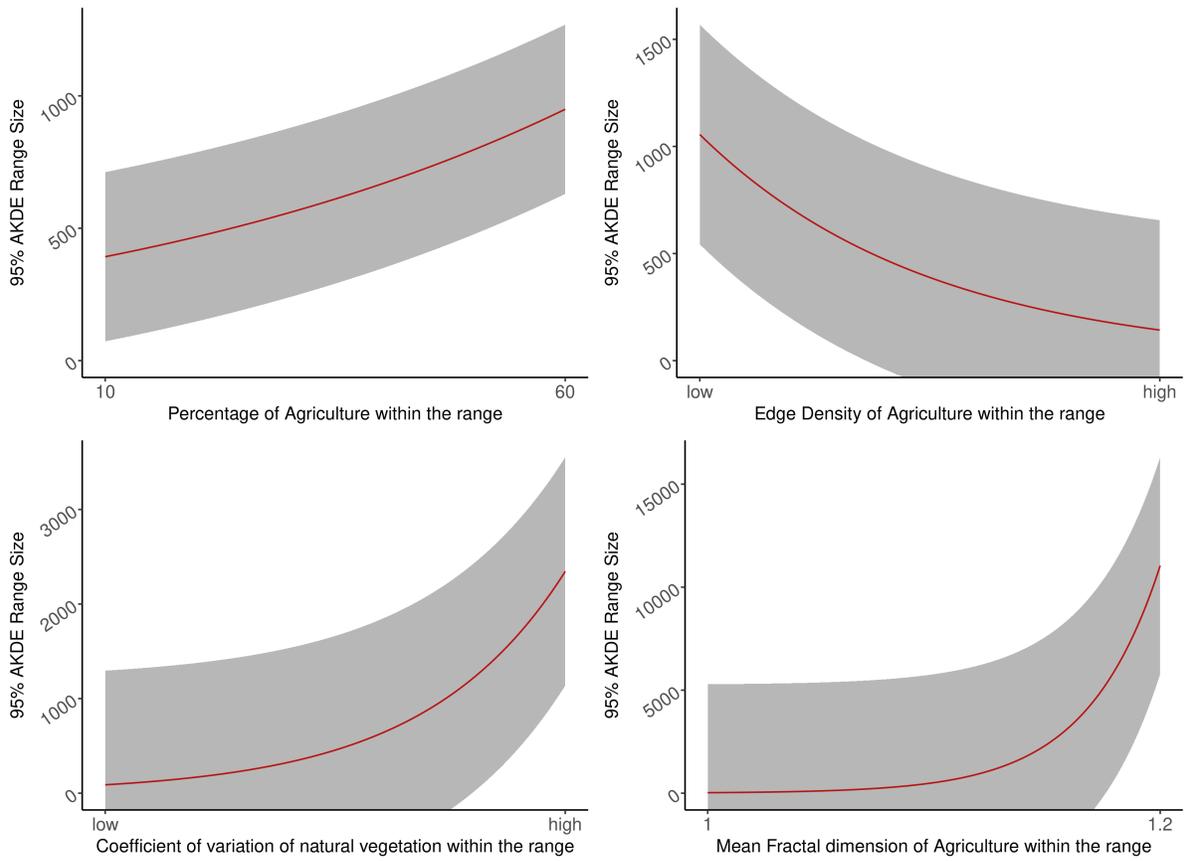
**Figure 1.1:** The location of the three study areas in Myanmar: Site 1 located in the foothills of Bago Yoma Mountain Range, site 2 located within the Ayeyarwaddy Delta region, and site 3 which is part of Dawna Tanintharyi Mountain Range. The insert shows the land cover map for site 1 from which various landscape metrics were derived for analysis of range conditions.



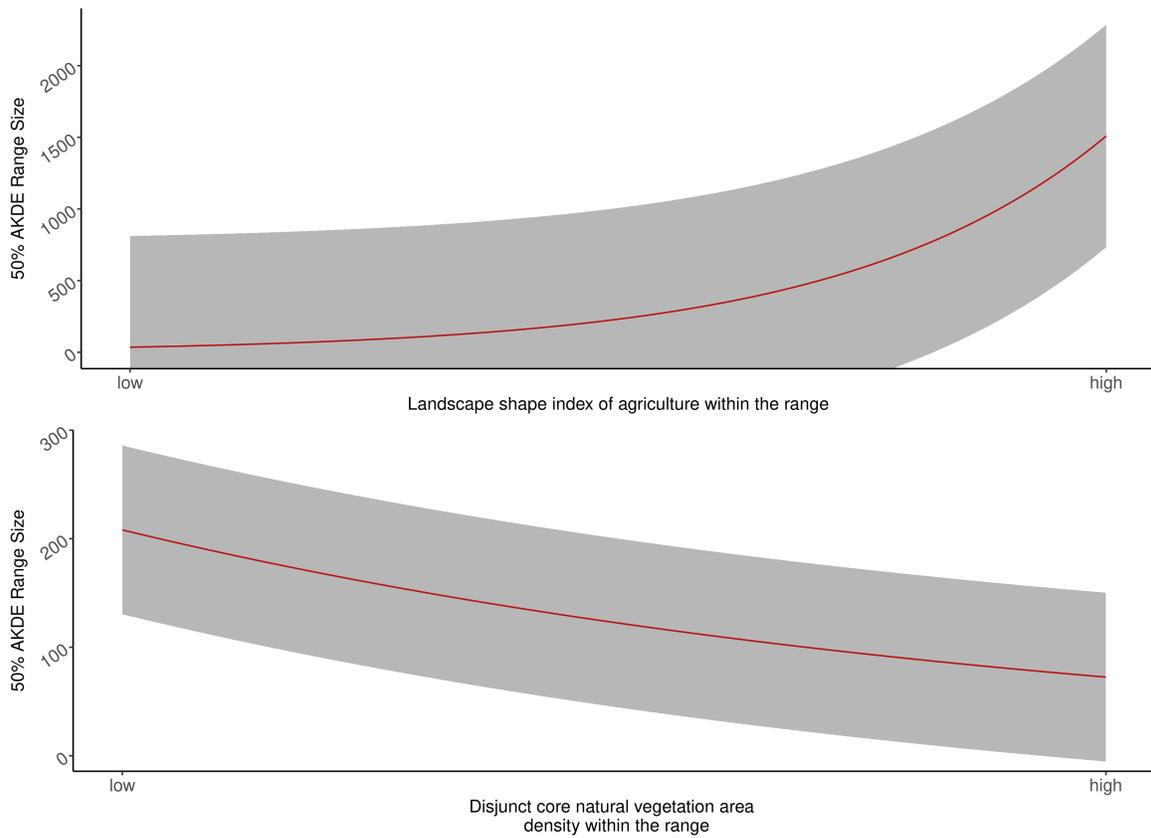
**Figure 1.2:** Estimated coefficient values from the model explaining the relationship between dry season 95% AKDE range of Asian elephant and landscape metrics describing the patterns of agriculture and variability in natural vegetation cover were the important independent variables in explaining variation in range size.



**Figure 1.3:** Estimated coefficient values from the model explaining the relationship between dry season 50% AKDE range of Asian elephant and landscape shape index for agriculture and several metrics representing natural vegetative constitution were the covariates explaining variation in range size. Site 2 (Ayeyarwaddy Delta region) is set as the reference site when fitting the model.



**Figure 1.4:** Functional relationship between the estimated regression coefficients of the top predictive landscape metrics and the dry season 95% AKDE range size of Asian elephant. Predicted range size for elephants during the dry season increased as the landscape becomes more irregular and dominated with agriculture.



**Figure 1.5:** Functional relationship between the estimated regression coefficients of the top predictive landscape metrics of the dry season 50% AKDE range size. Predicted 50% AKDE range size for elephants during the dry season increased as the index of agriculture shape (i.e., agricultural boundary length) increased and decreased where more intact natural vegetation was found.

**Table 1.1:** Description of landscape metrics used in this study (Hesselbarth et al., 2019).

<b>Abbreviations</b>	<b>Full name</b>	<b>Metric Type</b>	<b>Description</b>
frac_mn_*	mean fractal dimension index	Shape	Fractal dimension based on the patch perimeter and patch area: value (x) approaches 1 if all patches are squared and 2 if all patches are irregular
frac_sd_*	standard deviation of fractal dimension index	Shape	Standard deviation of the fractal dimension index, where $x = 0$ if the fractal dimension index is identical for all patches and increases without limit as the variation of the fractal dimension indices increases.
para_mn_*	mean perimeter to area ratio	Shape	A patch complexity metric that approaches 0 if the perimeter-to-area ratio for each patch approaches 0 (i.e., the form approaches a rather small square) and increases without limit, as perimeter-to-area ratio increases (patches become more complex).
para_cv_*	coefficient of variation of perimeter to area ratio	Shape	Coefficient of variation of perimeter-area ratio where $x = 0$ if the perimeter-area ratio is identical for all patches and increases without limit as the variation of the perimeter-area ratio increases.
para_sd_*	standard deviation of perimeter to area ratio	Shape	Standard deviation of perimeter-area ratio where $x=0$ if perimeter-to-area ratio is identical for all patches and increases without limit as the variation of the perimeter-area ratio increases. This is scale dependent.
area_cv_*	coefficient of variation of patch area	Area and Edge	Summarizes variation in patch area where $x = 0$ if all the patches are identical in size and increases without limit as the variation of patch area increases in the landscape.
area_mn_*	mean patch area	Area and Edge	This is the simplest metrics – mean patch area of a given class. If all patches are small, $x = 0$ and increases without limit as the patch areas increases.
pland_*	percentage of landscape	Area and Edge	Characterizes the composition of the landscape as percentage of class *. When the proportional class area is decreasing, the value approaches 0. The metric is equal to 100 when only one patch is present on the landscape.
pd_*	patch density	Aggregation	Describes the fragmentation of the class as patch density where x approaches 0 as the proportional class area decreases. It is equal to 100 when only one patch is present. It is standardized to 100 hectares area.

dcore_mn_*	mean number of disjunct core area	Core area	This counts the disjunct core areas, whereby a core area is a patch within the patch containing only core cells. If ncore = 0 for all patches, x = 0 and increases without limit as the number of disjunct core area increases.
dcad_*	disjunct core area density	Core area	This is the number of disjunct core areas per ha relative to the total area. When no patch of class * contains a disjunct core area, x = 0, and increases without limit as disjunct core areas become more present (i.e. patches becoming larger and less complex).
ed_*	edge density	Area and Edge	Describes the configuration of the landscape as the sum of all edges of class * in relation to the landscape area. If only one patch is present, x = 0, and increases without limit as the landscape becomes more patchy.
lsi_*	landscape shape index	Aggregation	Metric based on actual edges and minimum hypothetical edges. When only one squared patch is present or all patches are maximally aggregated, x = 1, and increases without limit as the length of the actual edges increases (i.e. the patches become less compact).

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**Table 1.2:** Estimated 95 and 50 percentile AKDE ranges, and 95 percentile minimum convex polygon area in squared kilometers for dry season, wet season and annual range.

ID	Year	Site	Dry MCP 95%	Wet MCP 95%	Annual MCP 95%	Dry AKDE 95 %	Dry AKDE 50%	Wet AKDE 95%	Wet AKDE 50%	Annual AKDE 95%	Annual AKDE 50%
17104	2017	Site 3	244.8	243.1	302.7	703.6	185.2	697.1	175.0	513.9	142.1
17104	2018	Site 3	NA	164.7	NA	NA	NA	795.5	166.4	NA	NA
17105	2017	Site 3	109.3	100.9	284.1	975.5	213.1	454.5	92.6	600.0	152.5
19970	2016	Site 1	105.9	200.2	340.2	248.3	63.5	412.0	86.8	529.3	98.5
19971	2016	Site 1	201.7	240.9	1153.0	1509	355.7	3662.2	875.2	2780.4	635.8
22912	2016	Site 1	229.2	113.4	575.1	223.8	51.8	3977.2	914.0	775.6	121.5
22912	2017	Site 1	91.3	128.7	NA	502.2	89.6	230.9	56.9	NA	NA
IRI2016- 3121	2019	Site 3	57.3	NA	NA	65.7	11.7	NA	NA	NA	NA
IRI2016- 3122	2019	Site 3	50.8	NA	NA	72.7	17.1	NA	NA	NA	NA
IRI2016- 3123	2019	Site 3	184.3	NA	NA	2543.7	584.6	NA	NA	NA	NA
IRI2016- 3124	2019	Site 3	292.1	NA	NA	1170.5	257.9	NA	NA	NA	NA
IRI2016- 3125	2019	Site 3	89.2	NA	NA	146.5	35.7	NA	NA	NA	NA
ST2010- 2594	2017	Site 3	14.3	NA	NA	28.4	7.4	NA	NA	NA	NA
ST2010- 2707	2017	Site 2	132.4	141.1	NA	1545.4	381.6	2059.2	477.7	NA	NA
ST2010- 2710	2017	Site 2	191.2	NA	NA	2790.9	644.7	NA	NA	NA	NA
ST2010- 2710- REDEPLOY	2018	Site 1	150.6	NA	NA	591.9	143.8	NA	NA	NA	NA
ST2010- 2711	2017	Site 3	139.9	NA	NA	530.6	132.0	NA	NA	NA	NA
ST2010- 2713	2017	Site 1	61.7	NA	NA	388.5	87.2	NA	NA	NA	NA
ST2010- 2714- REDEPLOY	2018	Site 1	180.9	NA	NA	433.7	85.6	NA	NA	NA	NA
ST2010- 2716	2018	Site 1	74.1	27.9	65.8	171.3	40.7	43.5	12.8	89.6	20.3
ST2010- 2716	2019	Site 1	77.4	NA	NA	151.6	29.5	43.5	NA	NA	NA
ST2010- 2853	2018	Site 2	82.3	NA	NA	638.6	148	NA	NA	NA	NA

ST2010-2854	2018	Site 2	31.3	26.8	NA	64	15.9	54.9	14.3	NA	NA
ST2010-2855	2018	Site 2	113.6	160.3	262.4	857.6	214.4	486.1	124.2	398.3	74.9
ST2010-2855	2019	Site 2	78.9	NA	NA	204.6	42.4	NA	NA	NA	NA
ST2010-2856	2018	Site 1	188.4	239.6	678.8	867	222.2	5362.2	1277.5	3057.4	777.2
ST2010-2856	2019	Site 1	184.8	NA	NA	3166	728.5	NA	NA	NA	NA
<b>Average</b>			129.14	170.27	492.97	791.9	184.2	1519.5	356.1	1093.1	252.8

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**Table 1.3:** Candidate model set for 95% AKDE dry season range showing the performance of the top model relative to others in the model set. The top model is composed of three landscape metrics describing configuration and composition of agriculture and one regarding natural vegetation composition within the range.

<b>Model</b>	<b>Variables</b>	<b>AICc</b>	<b>K</b>	<b>dAICc</b>	<b>AICc Weights</b>
M_Ag_Nv_1	(Intercept) + pland_ag + frac_mn_ag + ed_ag + area_cv_natveg	284.93	5	0.00	0.89
M_Ag_Nv_2	(Intercept) + pland_ag + I(pland_ag^2) + frac_mn_ag + ed_ag + area_cv_natveg	289.18	6	4.26	0.11
M_Global	(Intercept) + area_cv_natveg + ed_ag + pland_ag + I(pland_ag^2) + dcore_mn_water + frac_mn_ag + para_mn_natveg + para_mn_water	299.78	9	14.85	0.00
M_Ag_Nv_3	(Intercept) + ed_ag + pland_ag + area_cv_natveg	306.08	4	21.16	0.00
M_Nv_W_2	(Intercept) + area_cv_natveg + para_mn_water	312.09	3	27.17	0.00
M_Nv_W_1	(Intercept) + area_cv_natveg + para_mn_water + dcore_mn_water	315.38	4	30.45	0.00
M_Ag_W_1	(Intercept) + pland_ag + frac_mn_ag + ed_ag + para_mn_water + dcore_mn_water	322.88	6	37.96	0.00
M_Water	(Intercept) + para_mn_water + dcore_mn_water	338.71	3	53.79	0.00
M_Null	(Intercept)	339.37	1	54.44	0.00
M_Ag_W_2	(Intercept) + pland_ag + frac_mn_ag + ed_ag + para_mn_water	343.15	5	58.23	0.00
M_Ag_1	(Intercept) + pland_ag + frac_mn_ag + ed_ag	346.12	4	61.20	0.00
M_Ag_2	(Intercept) + pland_ag + I(pland_ag^2) + frac_mn_ag + ed_ag	347.80	5	62.87	0.00

**Table 1.4.1:** Candidate model set for 50% AKDE dry season showing the top model carrying the majority of the model set weight (85.28%) composed of one metric describing the shape of the agriculture patches and three metrics describing shape and configuration of natural vegetation patches within the range.

<b>Model</b>	<b>Variables</b>	<b>AICc</b>	<b>K</b>	<b>dAICc</b>	<b>AICc weights</b>
M_Ag_Nv_2	(Intercept) + lsi_ag + dcad_natveg + dcore_mn_natveg + para_mn_natveg	238.98	5	0	0.88
M_Global	(Intercept) + dcad_natveg + dcore_mn_natveg + para_mn_natveg + area_mn_natveg + lsi_ag	243.38	6	4.4	0.10
M_Ag_Nv_3	(Intercept) + lsi_ag + dcore_mn_natveg + dcad_natveg	247.04	4	8.06	0.02
M_Ag_Nv_1	(Intercept) + lsi_ag + dcore_mn_natveg	251.5	3	12.52	0.00
M_Ag	(Intercept) + lsi_ag	253.47	2	14.48	0
M_Nv_4	(Intercept) + dcad_natveg	273.91	2	34.92	0
M_Null	(Intercept)	275.17	1	36.19	0
M_Nv_3	(Intercept) + dcad_natveg + dcore_mn_natveg	276.32	3	37.33	0
M_Nv_2	(Intercept) + dcad_natveg + dcore_mn_natveg + para_mn_natveg	278.97	4	39.98	0
M_Nv_1	(Intercept) + dcad_natveg + dcore_mn_natveg + para_mn_natveg + area_mn_natveg	281.11	5	42.13	0

**Table 1.4.2:** Evaluating the effect of sex, site, and year on the differences in core range sizes on the best performing model of Table 1.3.

<b>Model</b>	<b>Variables</b>	<b>AICc</b>	<b>K</b>	<b>dAICc</b>	<b>AICc Weights</b>
M_Site_1	(Intercept) + lsi_ag + dcad_natveg + regionBago + regionTanintharyi	229.98	5	0.00	0.85
M_Sex_Site	(Intercept) + lsi_ag + dcad_natveg + Sexmale + regionBago + regionTanintharyi	234.16	6	4.18	0.11
M_Site_2	(Intercept) + lsi_ag + dcad_natveg + dcore_mn_natveg + para_mn_natveg + regionBago + regionTanintharyi	237.14	7	7.16	0.02
M_Sex	(Intercept) + lsi_ag + dcad_natveg + dcore_mn_natveg + para_mn_natveg + Sexmale	238.53	6	8.54	0.01
M_Ag_Nv_2	(Intercept) + lsi_ag + dcad_natveg + dcore_mn_natveg + para_mn_natveg	238.98	5	9.00	0.01
M_year	(Intercept) + lsi_ag + dcad_natveg + dcore_mn_natveg + para_mn_natveg + season2017_2018 + season2018_2019 + season2019_2020	251.77	8	21.79	0

**Table 1.5:** Candidate model set for average daily distance moved showing percentage of agriculture present within the 50% AKDE dry season range was the best variable examined at explaining the variation in mean average daily distance moved by the elephants during the dry season.

<b>Model</b>	<b>Variables</b>	<b>AICc</b>	<b>K</b>	<b>dAICc</b>	<b>AICc Weights</b>
M_3	(Intercept) + pland_ag	93.6200	2	0.00	0.48
M_Null	(Intercept)	96.07	1	2.45	0.19
M_4	(Intercept) + pland_ag + Sexmale	96.20	3	2.58	0.16
M_1	(Intercept) + pland_ag + para_mn_ag	96.43	3	2.81	0.14
M_2	(Intercept) + pland_ag + site1 + site3	98.31	4	4.69	0.02
M_Global	(Intercept) + pland_ag + site1 + site3 + para_mn_ag	98.88	5	5.26	0.01

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## **CHAPTER 2: Can Asian elephants persist just by eating crops?<sup>2</sup>**

### **Introduction**

Global cropland is projected to rise by 26 percent with the majority of the increase occurring throughout Africa and Southeast Asia by 2050 (Williams et al., 2021). As human-driven landscape alterations expand, it is likely that human-wildlife interactions will concomitantly increase (Calabrese et al., 2017; Leimgruber et al., 2003; Liu et al., 2017). A surge in human-wildlife interactions, as a result of such landscape change, is emerging as a major threat to mega-herbivores, such as the Asian elephant, whose habitat preferences often overlap with arable lands (Branco et al., 2019; Songer et al., 2016). The available range for these large mammals is being constricted rapidly, significantly increasing the threats to elephants. Understanding this process and its longer-term implications requires the study of how these animals respond to growing human pressure, and how we might alleviate such effects.

The ecological niche is one of the most fundamental concepts in ecology which can provide us with a theoretical underpinning to study how species interact with their biotic and abiotic environment to maximize their survival and reproductive fitness (Hutchinson, 1957). Although niche theory primarily applies at the population- or species- level, it can also serve as a foundational theory for studying variation in individual behavior. The term behavioral hypervolume (Bastille-Rousseau and Wittemyer, 2019) was coined as an adaptation of Hutchinson's n-dimensional hypervolume theory (originally used to describe a niche space of a species) to the study of individual behavior ecology. This is particularly relevant for management

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<sup>2</sup> Adapted from: Chan, A.N., Leimgruber, P., Williams, A.C., Shwe, N.M., Aung, S.S., Lwin, N., Oo, Z.M., Chit, A.M., Wittemyer, G. 2023. Can Asian elephants persist just by eating crops? *Biological Conservation*. In Review.

and policy decisions for an endangered species, such as the Asian elephant, where there is wide variation in individual behavior (Evans et al., 2020). The behavioral hypervolume (Bastille-Rousseau and Wittemyer, 2019) can be defined by assessing resource selection behavior – the quantification of a species' interaction with its environment (Northrup et al., 2022) across multiple scales of interest; i.e., within a home range (Boyce, 2006) and at an individual step-level (Thurfjell et al., 2014). Studying individual heterogeneity in resource selection behavior can shed light on the magnitude of individual variation present in the population of interest across a heterogeneous landscape, with implications for management.

Myanmar is one of the last remaining strongholds for biodiversity in the region but is under immense pressure (Reddy et al., 2019). Conservation in Myanmar is critical because of its biodiversity status (Prescott et al., 2017), but can be challenging given the current political and military situation, as well as the fact that different parts of the country are disputed by different ethnic groups and the military junta. Recent civil unrest in response to the Coup in 2021 has severely limited the technical and institutional capacity for wildlife management and conservation in these areas by the Ministry of Natural Resources and Environmental Conservation and conservation-focused non-governmental organizations due to an increase in arm-conflicts and political tension between the Burmese military and armed ethnic groups. Consequently, the degree of wildlife management capacity is highly variable across the country. Additionally, most of the rural populations are being displaced into the remaining wildlands of Myanmar where the last strongholds of diverse and unique biodiversity (such as *Elephas maximus*, *Panthera tigris*, *Manis* spp., *Buceros bicornis*, and *Ophiophagus hannah*) remain. Among these, Asian elephants are considered to have some of the largest space-use requirements (Chan et al., 2022) and, as such, are at high risk given the changes occurring throughout the

country. Moreover, poaching, human encroachment, agriculture expansion, and human-elephant conflicts act as stressors on the already at-risk remaining elephant population (Leimgruber et al., 2003; Sampson et al., 2019; Songer et al., 2016). Understanding how the species is adapting to the rapidly changing landscapes of Myanmar can provide needed information to effectively manage the remaining populations in Myanmar. The lessons learned could also apply or provide an analytical framework in tackling this challenging issue to other parts of the species' geographic range that face rapid landscape conversions and often are also politically unstable (e.g., Cambodia, Laos, Vietnam, Sumatra).

Understanding how conflict-prone species, such as Asian elephants interact with landscape features, such as agriculture, is key to effectively managing conflict (Fernando et al., 2005). This is especially true in countries and regions where most of the livelihood is based around farming, as is the case for much of the Asian elephant geographic range. Determining whether a specific behavior, such as crop raiding is fluid (i.e., every individual in the population will crop raid given a specific landscape configuration and pattern within its range) or not can greatly benefit consequent management decisions (Darlington et al., 2022; Haus et al., 2020; Lewis et al., 2015). Previously, we have shown that elephants tend to have larger range sizes when the landscape is more fragmented with agriculture (Chan et al., 2022). However, the underlying mechanism was not clear. The relationship between resource selection behavior and the level of human disturbance (i.e., fragmentation) within the home range has not been assessed. In addition, human-elephant conflict is emerging as a serious threat to elephants across Asia (Fernando et al., 2008) and in Myanmar (Sampson et al., 2019, 2018; Williams et al., 2020). As such, it is critical to understand how agricultural fragmentation influences resource selection

behavior and movement which will in turn inform us in developing science-based holistic management plans for the species across its range.

In this study, we assessed how elephants interact with agriculture and other habitat features during the dry season when human-elephant conflict is the most common (Sukumar, 2003, 1990). We used relocation data from GPS collars across three study sites with varying degrees and patterns of fragmentation. Our objectives were (1) to evaluate resource selection of elephants across fine and broad scales, (2) to develop and apply a framework to quantify if variation in selection behavior is driven by individual, regional, and/or sex differences, and (3) to evaluate whether the pattern and percentage coverage of agriculture (i.e., fragmentation) within an individual's dry season range affects the selection of agriculture by the elephants. We discuss our results in relation to the conservation challenges facing elephants in Myanmar and across the species range.

## **Method**

### *Study Sites*

Our study was conducted in three human-elephant conflict areas – central (site 1), western (site 2), and southern Myanmar (site 3) (Chan et al 2022). Site 1, located at the edge of the Bago Yoma (Latitude: 17.1013 – 18.1960, Longitude: 95.7043 – 96.4787), consists of a mosaic of agriculture and natural vegetation, primarily bamboo thickets. Decades of legal and illegal timber extraction in this site created a highly disturbed forest mosaic that is increasingly being invaded by other human land uses, including the construction of hydroelectric reservoirs, settlements, sugarcane, paddy, and rubber plantations. The site also has a hard edge between natural vegetation in the east and human-dominated landscape features in the west. Site 2 is a mountainous area along the west coast of the Ayeyarwaddy delta region (Latitude: 16.0554 –

17.0842, Longitude: 94.1860 – 94.6838) and stretches approximately 100 km from north to south, creating an elongated forest with hard boundaries on both its east and west side. Rice plantations dominate the matrix between forest patches in this site, where rubber and peppercorn agricultural use is also prevalent primarily in NgaPu Taw Township. Site 3 is part of the larger Dawna Tanintharyi Landscape (Latitude: 10.7141 – 12.0981, Longitude: 98.3356 – 99.4626) which extends from mountain ridges along the border with Thailand to the coastal plain. Land use at site 3 is primarily composed of large-scale oil palm and betel nut plantations, surrounded by lowland evergreen forests. The region is experiencing increased threats from human encroachment, road development, and agricultural expansion. Our analyses focused on the dry season — the time of year when the majority of the crop raiding by elephants occurred (Sukumar, 1990; Webber et al., 2011). Therefore, we focused on understanding the selection behavior of the elephants during this season while dissecting the variation in this behavior to inform land use planning and management decisions.

#### *Elephant capture and relocation data*

We used hourly GPS tracking data from Asian elephants (as described in Chan et al. 2022) but excluded individuals with less than an 80% fix-success over the individual tracking period within the dry season (December – March). There were four dry season ranges derived from three individuals in site 1; seven dry season ranges from six different individuals in site 2; and five dry season ranges from five individuals in site 3 – totaling sixteen dry season ranges from fourteen individual elephants. There was only one female in our sample at each study site with a total of 3 females in the study. The average number of relocations was 2138 (SD = 516) points per individual.

### *Environmental layers*

We derived agriculture, surface water, road, village, and natural vegetation raster layers from land cover maps (as described in Chan et al. 2022). Distance to nearest land use features was calculated using the proximity function in QGIS (GDAL 2022). For integrating topographical information into our analysis, we obtained a digital elevation layer from SRTM in Google Earth Engine and calculated a roughness index in QGIS (Wilson et al., 2007). For assessing how the landscape-level prevalence of agriculture v. natural elevation influenced elephant habitat selection, we computed the percentage of agriculture and natural vegetation within a 175-m x 175-m moving window in R using the focal function (Hijmans, 2017). The size of the window (i.e., 175 meters) is roughly equivalent to the average hourly distance moved by elephants in our study.

### *Selection Analysis*

Resource selection behavior occurs at different scales (Boyce, 2006) – understanding how certain landscape features influence this behavior at a particular scale is key to understanding the movement ecology of the species. We assessed wild elephant habitat selection at two different scales. We conducted both integrated step selection analysis (Avgar et al., 2016) and third-order resource selection analysis (i.e., within-home-range resource selection functions; Johnson, 1980). We fit both model types at the individual elephant level allowing assessment at the individual (e.g., sex-specific) and aggregated study area scale (Bastille-Rousseau et al., 2018; Murtaugh, 2007). Given strong diurnality in movement, we set daytime (sunrise–sunset) as a reference category in contrast to crepuscular and night-time movement in all models. We also set non-agriculture and non-natural vegetation as reference layers in models where agriculture or natural vegetation were included as categorical variables. All continuous variables were

standardized to a mean of 0 and a standard deviation of 1 for easier interpretation and model convergence before model fitting.

For integrated step selection analysis, we generated availability samples by randomly drawing 15 points for every used point (1:15 use-available ratio) from Gamma (for step length) and Von Mises (for turning angles) distributions fitted to empirical data. Every point from the realized trajectory was defined as used (1) and compared to the corresponding 15 randomly generated, available points (0) from the simulated trajectory. We fitted 6 conditional logistic candidate models to data for each of the 16 dry season GPS datasets from 14 individual elephants and estimated the step selection function. We then used the Akaike Information Criterion, corrected for small sample sizes (Burnham and Anderson, 2002) to evaluate the best-fitting model. In all these models, our model structure was aimed to capture two primary processes—the movement and the selection process—and their interactions. To account for the movement process, we included step length and cosine of the turning angle as covariates in all 6 candidate models. To investigate factors influencing the selection process, we included distance to village, distance to surface water, and terrain roughness index. Additionally, we evaluated the explanatory power of percent agriculture, distance to native vegetation, and agriculture (as a categorical variable) using AICc. Finally, we examined interactions between step length and day- and nighttime, step length and percent agriculture, step length and agriculture, or step length and distance to village to provide a better understanding of the interaction between movement and selection of these features. We selected the model with the lowest AICc as the most parsimonious model for each individual dry period and presented estimated beta coefficients and model explanatory power ( $R^2$ ) from the best-performing model.

For third-order resource selection analysis, we generated 30 random, available points for each used point (1:30 use-available ratio) within the 95 percentile Minimum Convex Polygon (Northrup et al. 2013). As with the step selection function models, we fitted 16 dry ranges separately. We hypothesized agriculture, natural vegetation, terrain roughness, and distance to the nearest village would influence resource selection of elephants at the range (3rd order) scale. We defined all the observed relocation data as used points (1) and randomly generated points as available points (0) under a use-available framework using logistic regression. We fitted different combinations of agriculture, natural vegetation, terrain roughness, and distance to the nearest village and conducted a model comparison using AICc as described above. We also included a model with no covariate (null model) in the candidate model set to represent the hypothesis that the resource selection process is random at the range scale.

#### *Variance Partitioning of Selection Coefficients*

We used variance partitioning analysis (Oksanen et al., 2022) to quantify the explanatory contribution of individual, study site, and sex in both step selection and resource selection functions. In addition, we evaluated the overlap of explanatory variables (i.e., ID, region, and sex). For each selection coefficient, we drew 1000 random samples from a normal distribution defined by the coefficient mean and standard deviation estimated from the most parsimonious model (the lowest AICc score) out of the candidate model set for each elephant. We then regressed our bootstrapped selection coefficients with individual ID, region, and sex using a linear regression framework and calculated the adjusted r-squared to evaluate the variables explaining the most variance (i.e., highest adjusted r-squared value).

### *Functional Response*

Using RSF outputs, we assessed the functional response (Myerud and Ims, 1998) of agriculture selection to percent agriculture, edge density, mean fractal dimension of agriculture, and coefficient of variation of natural vegetation within the range – metrics identified to affect the dry season range size (Chan et al., 2022). To assess which landscape metrics were most strongly related to agricultural selection, we used AICc model selection (Burnham and Anderson 2002) to identify the best-performing model (i.e., lowest AICc score). We also reported the adjusted r-squared of the models.

All the selection and functional response analyses were carried out in R version 4.1.3. using packages ‘amt’, ‘AICcmodavg’, ‘ggplot2’, ‘dplyr’, ‘lubridate’, ‘raster’, and ‘vegan’ (Wickham, 2016; Hijmans, 2017; Mazerolle, 2019; Signer et al., 2019; R Core Team, 2020; Wickham et al., 2020; Oksanen et al., 2022).

### **Results**

Crepuscular and night movements (defined as happening between sunset – sunrise) were greater than those in the day (positive selection coefficient estimates for step length and day/night interaction term in the best model) across all three study sites (Figure 2.1). For elephants at sites 2 and 3, night movements were significantly linked to movement in agriculture (+ selection coefficient estimates for step length and agriculture interaction term in the model; Figure 2.2), suggesting elephants avoided humans by reducing activity during the day while exploiting agriculture for food during the night.

In our integrated step selection analysis, the most parsimonious model (i.e., the lowest AICc score) for all individuals included agriculture, step length, cosine of the turning angle, distance to native vegetation, distance to village, distance to road, distance to surface water, and

roughness. Interaction terms between agriculture and step length, distance to village and step length, and day/night and step length were also retained as covariates in the best model.

Individual elephants exhibited marked differentiation in the degree of selection for agriculture and distance from villages but generally tended to select areas closer to natural vegetation at the step scale (Appendix 1: Figure S1.1-1.2). Most of the study elephants (all except one) preferred areas with less rugged terrain (negative selection coefficient for roughness index) (Appendix 1: Figure S1.3). Distance to road and distance to surface water were not in the top models (Appendix 1: Figure S1.4-1.5).

The most parsimonious model for third-order resource selection analysis (RSF) included agriculture and native vegetation as categorical variables, terrain roughness index, and distance to village. Selection for agriculture and distance to village demonstrated marked variability across individuals (Figure 2.1; Appendix 1: Figure S1.6). As found with step selection analysis, all elephants in sites 1 and 3 avoided rugged areas within their respective dry season ranges (Appendix 1: Figure S1.7). However, selection for terrain ruggedness in site 2 demonstrated high inter-individual variability (i.e., individual elephants selected, avoided, or showed no preference for ruggedness).

Variance partitioning analysis, structured to determine if individual, site, or sex-specific differences explained the variability in selection coefficient estimates, indicating the selection responses can primarily be attributed to individual differences, although the degree to which individual explains variation in estimates differed among different environmental features (Table 2.1). Although differences in sex and study sites explained a small amount of variation in the selection process, they did not add additional explanatory power during the variance partitioning

analysis when fitted to the same model with individual IDs as covariates. Study sites explained more variation in the selection process than sex when comparing them individually.

Selection for agriculture by an elephant was positively correlated to the edge density of agriculture patches in its dry season range (i.e., the measure of fragmentation of agriculture within a given range; Figure 2.3). The more patches of agriculture within the individual range, the more likely an elephant was to select for agriculture regardless of sex and study site. The adjusted r-squared for the model was 0.4991.

## **Discussion**

The selection behavior of the study elephants, at both the range-level (RSF) and step-level scale (iSSF), was influenced primarily by the juxtaposition of agriculture, natural vegetation, and human features (e.g., villages; Appendix 1). This implies that as land is converted from natural vegetation to agriculture, elephant selection behavior and use of agricultural areas in the landscape will change. In general, we found a strong positive correlation between dry season range fragmentation and agriculture selection (Figure 2.3), indicating landscape conversion is a key driver of agricultural use by elephants. Despite the dominance of this key driver, we found a large degree of variation in the selection behavior of individual elephants at both steps- and dry-season range-level scales. Most of the variation was driven by individual differences as opposed to study site- or sex-specific patterns (Table 2.1). A previous range-wide analysis of the African elephant movement also revealed large individual variations in the elephant's response to a key environmental factor, with water access being the limiting factor for the elephant movement in the dry land study system (Bastille-Rousseau et al., 2020). We did not find water to be a limiting factor in our study, likely given the general wide water availability in the study.

At the population level, we found that elephants display neither a strong preference nor avoidance of agriculture in sites 1 and 2; whereas we found a positive selection in site 3 (Figure 2.1). Elephants appear to be highly adaptable to a broad range of habitat characteristics, including landscapes dominated by human land use such as agriculture. However, the long-term effect of this adaption, particularly on survival and fitness, to rapidly changing local conditions is unclear and could potentially harm the remaining population in the country. Some elephants across our three study sites were actively selecting for agricultural patches in increasingly fragmented mosaics of agriculture and forest, leading to increased human-elephant conflicts (Figure 2.3). Current strategies for reducing human-elephant conflict in Myanmar, such as managing specific demographic groups (i.e., relocating bulls) may not be effective since the resource selection behavior is primarily driven by individual preferences rather than sex, age, or region (Table 2.1; i.e., not all males are exhibiting crop-raiding behavior). This is also the case for other species with frequent contact with humans and heterogeneity in individual behavioral responses, such as white-tailed deer (Haus et al., 2020) and American black bear (Duquette et al., 2017). Funds used for active management targeted at the population level, such as culling and translocation, might be better spent on alternative programs focusing on subsidizing non-palatable crop production, crop compensation, education, and seasonal fencing.

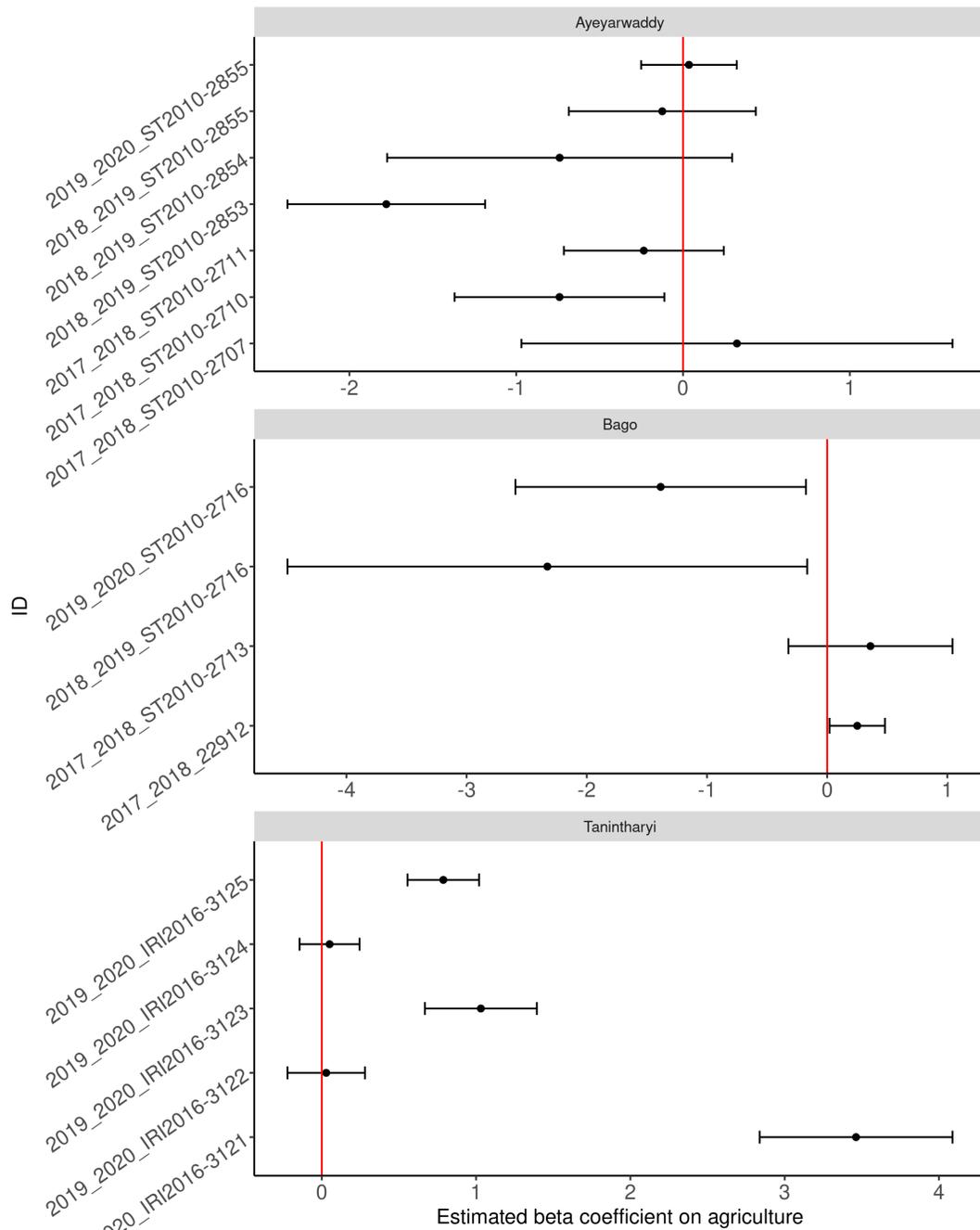
Human-elephant conflict (HEC) is one of the main threats to the remaining elephant population in the country in addition to poaching for illegal trade (Sampson et al., 2019, 2018). HEC disproportionately impacts lower-income communities (Barua et al. 2013). Increased agriculture selection by elephants can facilitate human-elephant conflicts, and this study demonstrates landscape configuration is a key driver of this selection behavior (Figure 2.3). Although common HEC mitigation methods such as electric fencing could address the symptoms

of HEC (Shaffer et al., 2019), consideration of ecological aspects at larger scales that relate to conflict can better address the fundamental drivers of this problem. Our study highlights the importance of agricultural fragmentation in driving conflict, indicating attempts to reduce conflict must consider the composition and juxtaposition of the wildland-agricultural interface.

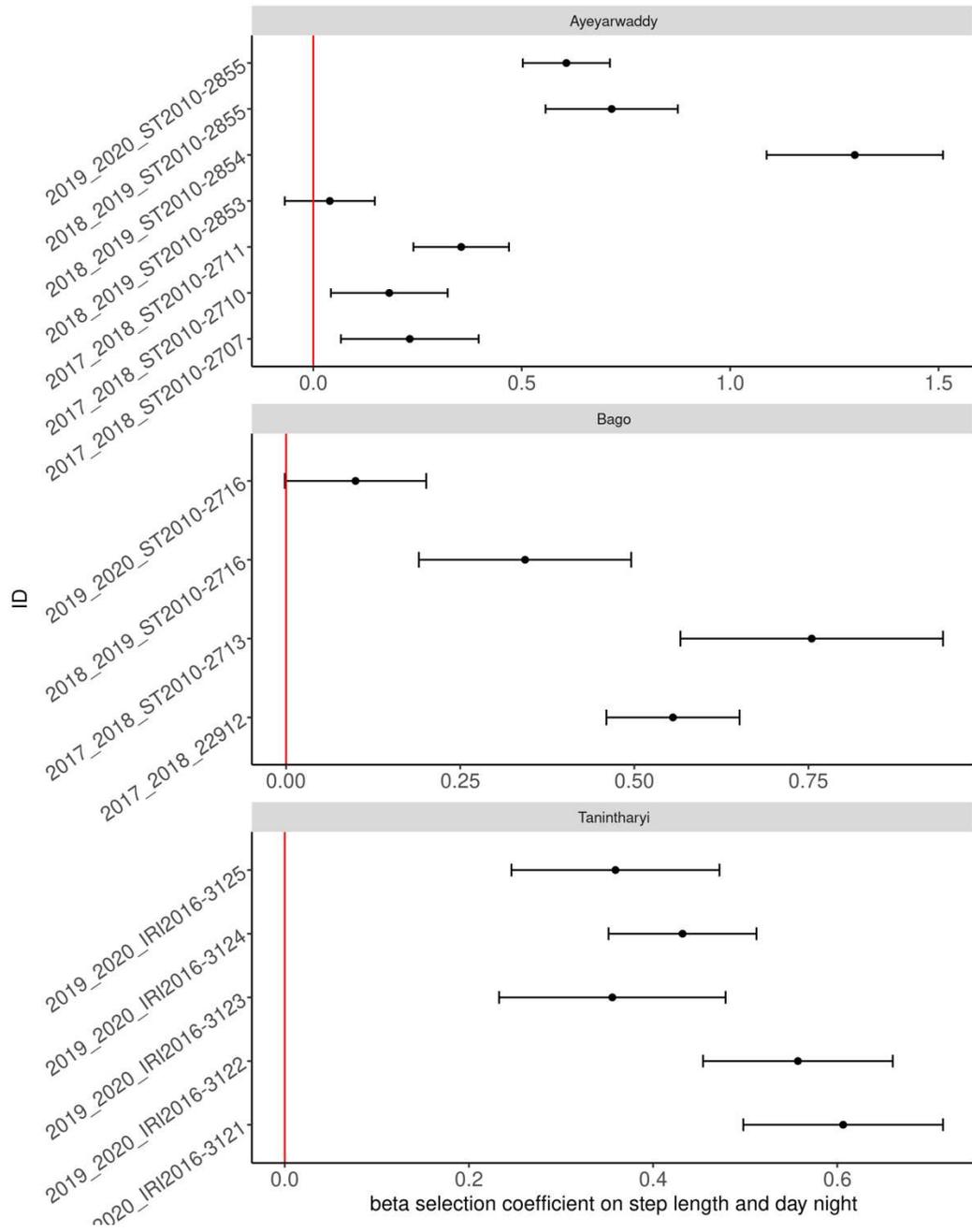
This is the first movement-based report of elephants' selection behavior in a subsistence agricultural landscape in Myanmar. Therefore, this lays the foundational work for studying elephants' selection responses to the different configurations of land use and cover types in similar landscapes across Asia. Although the relationship presented here between the selection behavior of elephants and landscape features is from Myanmar, the correlations we found occurred across 3 strongly differentiated study sites which represent common scenarios Asian elephants are facing throughout their range – particularly in areas outside of formal government protections. For example, results from site 3 might be particularly relevant to areas where large-scale oil palm plantations are present, such as in Indonesia and Malaysia (Aini et al., 2015; Suba et al., 2017). We are likely to see different selection responses to varying levels of fragmentation across the Asian elephant distribution range. Therefore, testing if elephants demonstrate stronger selection for agriculture in more agriculturally fragmented landscapes across the species' geographic range is important for understanding how the species responds to the changing landscape. It is likely there is differentiation in conflict relative to different degrees of fragmentation, and it may be that a threshold level of fragmentation is predictive of the presence or absence of conflict, given forest cover positively affects the presence of elephants (Songer et al., 2016). Therefore, managers should be cognizant of the fact that the correlation between the probability of agriculture selection and increasing fragmentation suggests elephants may not be able to adapt and coexist in highly modified landscapes.

Another key component in determining the cost of this adaptive behavior in the changing landscape is to quantify fitness in terms of mortality risk and/or reproductive success. It is documented that other conflict-prone species, such as the American black bear, show stronger selection for human-related food sources in areas with relatively lower human density (Duquette et al., 2017). Additionally, black bears in Colorado were found foraging extensively on urban food sources when natural forage quality is low (Lewis et al., 2015). This could be the case in Myanmar where elephants face the continuation of major threats, such as poaching and range loss, habitat degradation, and fragmentation due to agriculture expansion (Kanagaraj et al., 2019; Kumar et al., 2018; Sampson et al., 2018; Songer et al., 2016), which may encourage the use of anthropogenic resources when comp. Consequently, elephants presented with more fragmented ranges selected for agriculture in Myanmar. This work provides additional evidence that reducing human-elephant conflict requires carefully managing land-use in areas where humans and elephants coexist.

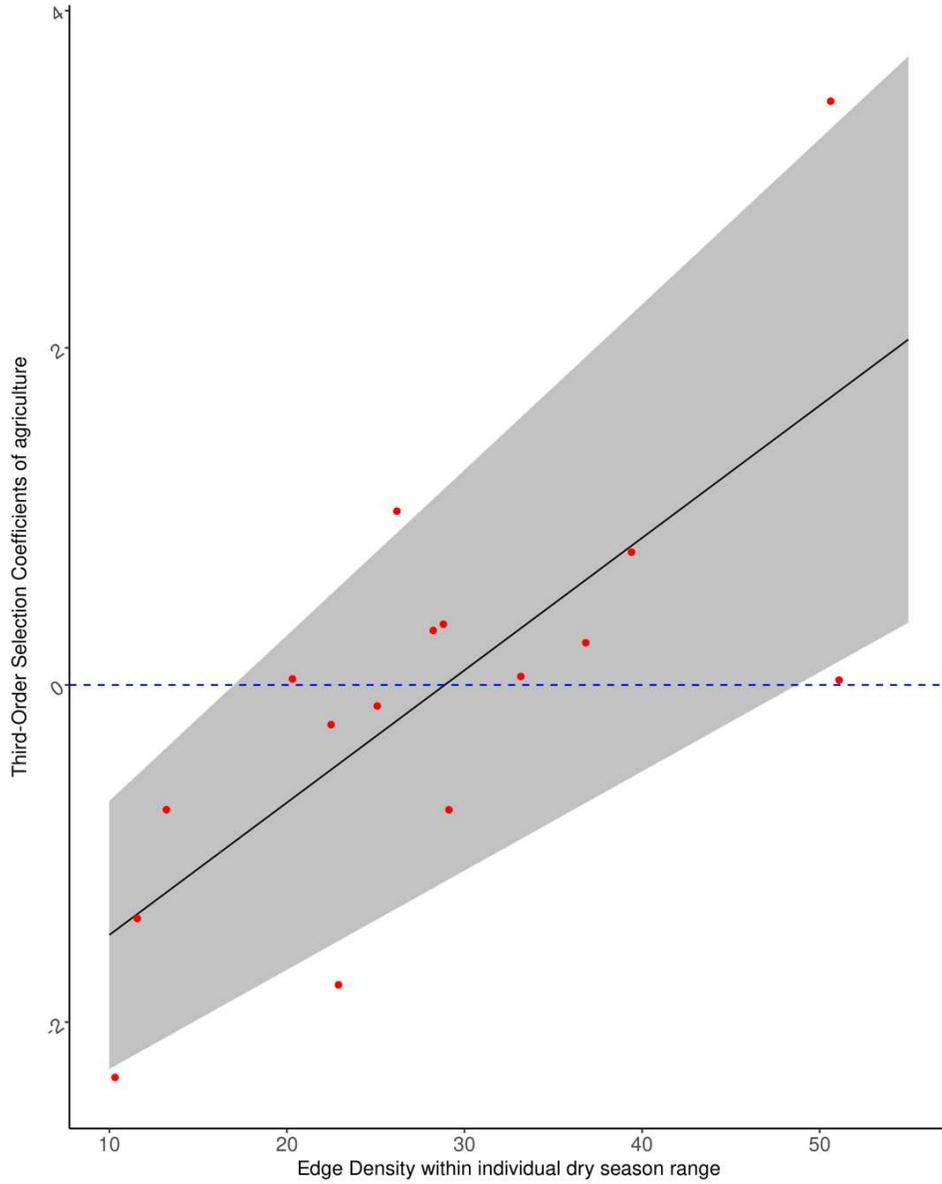
## Tables and Figures



**Figure 2.1:** Individual selection coefficients for agriculture from the 3rd order RSF analysis indicated strong heterogeneity in agricultural selection within individuals at a site and between sites. At this scale, some elephants in site 3 (Tanintharyi) select strongly for agriculture.



**Figure 2.2:** Individual selection coefficients for the interaction between step length and day/night from the integrated step selection analysis indicating more movement occurred at night for the majority of individual elephants.



**Figure 2.3:** Functional response in habitat selection for agriculture (estimated from RSF model) by Asian elephants across Myanmar relative to the edge density of agriculture within each individual dry season range

**Table 2.1:** Showing the result from variance partitioning analysis of selection coefficients from the best performing model of iSSF analysis. The variation in the selection coefficients of all covariates examined was predominantly explained by differences in individuals, rather than study site or sex.

<b>Selection Coefficients</b>	<b>Variable explaining the most variance</b>	<b>Variance explained (Adjusted R<sup>2</sup>)</b>
Agriculture	Individual	0.6656
Distance to natural vegetation	Individual	0.6395
Distance to village	Individual	0.9325
Distance to road	Individual	0.6799
Distance to surface water	Individual	0.6764
Roughness	Individual	0.8497
Agriculture x Step Length	Individual	0.7289
Distance to village x Step Length	Individual	0.9852
Step Length x Day Night	Individual	0.9489

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## **CHAPTER 3: Landscape features structuring connectivity of desert elephants**

### **Introduction**

Human modification of landscapes is a primary threat to wildlife (Kennedy et al., 2019). Given global human population is projected to reach 9.7 billion by 2050, with more than half of population growth expected to occur in Africa (United Nations, 2022), landscape modification is expected to increase across Africa. For instance, global cropland will increase by 26%, mainly in Africa and Asia (Williams et al., 2021a). The associated land conversion and habitat loss are likely to exacerbate ongoing declines in wildlife populations and will be detrimental to the long-term persistence of species (Brook et al., 2008). Thus, identifying and preserving critical wildlife habitats is crucial for ensuring the persistence of species, particularly in the face of rapid landscape changes (Fahrig, 2003; Hanski, 1999).

Small populations are especially at risk of extinction due to being more vulnerable to inbreeding depression, demographic stochasticity, environmental catastrophes, and genetic drift (Caughley, 1994). Connectivity between populations has been identified as the critical mechanism to alleviate such demographic stressors and reduce the risk of extirpation (Caughley, 1994; Hanski, 1999). Ensuring connectivity is an important mechanism for the long-term persistence of populations as it enables demographic rescue, genetic exchange between different populations, and mobility across landscapes to avoid or minimize negative consequences in the face of climate dynamics. In recognition of the importance of connectivity, the identification of corridors has become a core objective in wildlife conservation and management globally (Jennings et al., 2020; Kaszta et al., 2020; Osipova et al., 2019).

Numerous methods have been developed to identify and predict high-connectivity locations. Among the most widely used approaches are resistance surface modeling based on circuit theory or least-cost path analysis (Etherington, 2016; McRae et al., 2008). In the case of least-cost paths, model misspecification or the animal not knowing the least-cost path in the environment can result in inaccurate prediction (Kumar et al., 2022). Some researchers advocate for an alternative but related approaches, such as instituting correlated random walks on a resistance surface with the inclusion of mortality layers (Fletcher et al., 2019). However, obtaining mortality risk information may be challenging and misspecification issues remain. More recently, empirical-based approaches have been developed to identify and quantify connectivity from GPS tracking data without modeling (Bastille-Rousseau and Wittemyer, 2021). Namely, the application of graph theoretic approaches allows straightforward calculation of the importance of a given GPS position or path to the broader landscape connectivity (Bastille-Rousseau et al., 2018). Since these methods rely on empirical data, such graph-theoretic approaches need large sample sizes to appropriately capture and characterize connectivity across the landscape. Nonetheless, due to their empirical basis, these approaches provide an accurate representation of the observed elephant movement on the landscape (Bastille-Rousseau et al., 2018; Bastille-Rousseau and Wittemyer, 2021).

The African elephant (*Loxodonta africana*) is the largest extant terrestrial mammalian species and is listed as endangered by the IUCN (Gobush et al., 2022). The remaining populations of African elephants face several primary threats, including illegal killing, human-elephant conflict, and changes in land use that result in habitat loss and fragmentation (Gobush et al., 2022; Tucker et al., 2018; Wittemyer et al., 2014). Due to its significant body size, this species requires more space compared to other species on the landscape (Peters, 1986). As a

result of increased human encroachment, elephant range is increasingly restricted, with many historically viable areas no longer able to support elephants (Wall et al., 2021). Land conversion for agriculture (Williams et al., 2021) and accelerated human population growth around protected area edges (Wittemyer et al., 2008) combine to threaten both core populations and their connectivity. To address these common challenges, major efforts have been undertaken to track African elephants across their range to better understand the spatial needs of the species (Wall et al., 2021).

The arid lands of northwestern Namibia harbor important elephant habitat that contains both nationally protected areas and community lands that support elephant populations (Leggett, 2006). A key objective for elephant management in this area is to maintain connectivity between Etosha National Park and the surrounding community conservation areas in the Kunene region. To fulfill this goal, it is important to identify key connectivity areas and the factors predictive of connectivity. We used GPS telemetry data from elephants in the region to address the following objectives: 1) empirically quantify connectivity across the landscape using a graph theoretic approach (namely the betweenness metric) applied to the tracking data, 2) assess the landscape features (i.e., geologic, biotic and human-made) influencing connectivity in the study area, 3) apply the ‘movescape’ approach (Bastille-Rousseau and Wittemyer 2021) to define and locate different types of corridors, and (4) assess how/if landscape features (i.e., geologic, biotic and human-made) differ across these corridor types. We discuss these results in light of the conservation challenges facing elephants.

## **Methods**

### *Study Area*

The study area lies in northwestern Namibia, encompassing both the Kunene community-owned lands and Etosha National Park (ETS; Figure 3.1). This semi-arid region exhibits a strong rainfall gradient receiving up to 500 mm in the eastern section of Etosha to less than 150 mm in the western portion of Kunene (Funk et al., 2015). Etosha National Park is a 22,270 km<sup>2</sup> largely fenced protected area (with porous sections in the northwest near Kunene), estimated to support an elephant population of approximately 2,900 animals (Kilian, 2015). The Kunene area consists of a patchwork of community conservancies and hunting concessions that support approximately 1,100 elephants (Craig and Gibson, 2016), with low human population density. The elephant populations are known to be dispersing between the two areas (Kilian, 2015). Land cover types in the area include semi-arid savannah and arid desert.

### *Data Collection*

We analyzed GPS relocation data collected from 66 African elephants (37 females, 29 males) across our study site (37 from ETS; 29 from Kunene) collected between 2008 and 2015. All capture and collaring procedures were performed by veterinarians from the Namibian Ministry of Environment and Tourism, following South African National Standards for animal welfare and care (SABS, 2000). The fix-interval for the collars varied – there were 41 individuals with 30-minute collars, 15 individuals with 20-minute collars, and 10 individuals with 15-minute collars. To remove spatial errors in the dataset, we applied a filter excluding any consecutive relocation points greater than or equal to 10km/hour. We used ‘adehabitatLT’ to create the type II trajectory objects from relocation data and used the cleaned trajectory objects when calculating movement metrics in the next section (Calenge, 2015).

### *Movement Metrics and Types*

To empirically quantify connectivity across the landscape derived from the tracking data (Objective 1), we employed graph theoretic approaches to calculate attributes of connectivity defined by elephant movements across the ecosystem (Bastille-Rousseau and Wittemyer, 2021). Graph metrics were calculated on a 150-m x 150-m grid overlaying the study area, where the 150 meters spatial resolution was chosen because it was the average 30-minute inter-step distance traveled by the study elephants. Connectivity was defined using betweenness – the measure of the number of shortest paths connecting all nodes on a graph that pass through a given node (Objective 1). We used the 'movescape' framework to delineate spatial structuring in areas with high connectivity that can serve to define the type of corridor (objective 3; Bastille-Rousseau and Wittemyer, 2021). To do this, we analyzed the relationships between three metrics from network theory, namely degree, betweenness, and weight, and two metrics from the animal trajectory (i.e., speed and the dot product of the turning angle). We performed two-step Gaussian mixture modeling to cluster movement types at both the individual and population levels, by setting the maximum number of clusters to be 8. The latter is the greatest number of biologically meaningful clusters (2 movement speeds and 3 levels of intensity of use) likely to exist (Bastille-Rousseau and Wittemyer, 2021). We then evaluated the optimal number of clusters using the Bayesian Information Criterion (BIC) to achieve a more conservative evaluation given the large dataset (number of relocations = 2,437,675; (Aho et al., 2014).

### *Environmental Variables and Modeling Approach*

To address our second objective to characterize landscape features associated with connectivity, we built candidate models to evaluate factors influencing the global centrality measure (betweenness) of any given pixel in our study area. We log-transformed the response

variable (betweenness) and applied random-effects linear regression to quantify factors influencing the connectivity of a given pixel on the landscape. Our model included an auto-covariate term based on an inverse weighting scheme, a symmetric neighborhood metric, and a search radius that was defined dynamically for each elephant to select the lowest value at which all points have neighbors to account for spatial autocorrelation (Bardos et al., 2015).

Environmental covariates explored were elevation, slope, roughness index, global human modification index, distance from waterholes, distance from perennial rivers, distance from seasonal rivers, distance from roads, distance from towns and settlements, distance from wetlands, and normalized difference vegetation index (Table 3.2). Elevation and global human modification index were directly downloaded from Google Earth Engine (Gorelick et al., 2017; Jarvis et al., 2008; Kennedy et al., 2019). The roughness index was calculated in QGIS (QGIS Development Team, 2019; Wilson et al., 2007). We computed the yearly maximum and coefficient of variation (i.e., standard deviation/mean) of the normalized difference vegetation index (NDVI) for every pixel in our study area across our study period (2008 – 2015) using Landsat 7 and 8 imageries on Google Earth Engine. We developed five candidate models, to assess the influence of geologic, environmental, anthropogenic, and combined landscape features on betweenness values. Our candidate model set includes the geologic model (slope, distance from waterholes, distance from perennial rivers, distance from wetlands), anthropogenic model (global human modification index, distance from roads, distance from settlements), environmental model (maxNDVI, cvNDVI, distance from waterholes, distance from perennial rivers, and distance from wetlands), water model (distance from waterholes, distance from perennial rivers, distance from wetlands), and global model (combination of all the variables in the models above) (Appendix 2: Table S2.1).

To address our fourth objective of determining landscape conditions related to different types of corridors, we used a similar spatial regression structure, including the incorporation of an auto-covariate term and contrasting different covariate sets in each model. We used generalized linear models with a logit-link function to assess landscape features associated with the different movement clusters related to high connectivity areas. Additional covariates explored included percent settlement within an average step (150 meters) moving window and cattle abundance in addition to all the environmental covariates described above. Both variables were included in the human model and global model while the rest of the models remain the same in the candidate model set. We applied this spatial logistic regression to quantify landscape differences between high connectivity areas with fast and slow speeds (fast and slow corridors) according to mean speed values of a particular cluster (Table 3.1) and differences between the corridor and non-corridor pixels, and separately for males and females. We only included pixels with greater than or equal to 95% confidence assigned to a particular movement cluster for this analysis.

Before including variables in the models, we checked for multicollinearity by examining the variance inflation factor (VIF). VIF values for all the variables were less than 2 which is well below the recommended criteria to be included in the same model (Dormann et al., 2013). We evaluated the models in the candidate model sets using BIC and made inferences from the best-performing model (i.e., the model with the lowest BIC score). To visualize the connectivity of our study area, we applied linear interpolation of the max betweenness values onto the steps in between (Bastille-Rousseau and Wittemyer, 2021; Figure 3.1). All covariates were centered to their mean and scaled by dividing by their standard deviation (Gelman and Hill, 2006). All analyses were conducted in R using ‘car’, ‘dplyr’, ‘ggplot2’, ‘lubridate’, ‘lme4’, ‘moveNT’,

‘ROCR’, and ‘spdep’ (Bastille-Rousseau, 2023; Fox et al., 2016; Grolemond and Wickham, 2011; Roger Bivand, 2022; Sing et al., 2005; Wickham, 2016; Wickham et al., 2020; Zwisser et al., 2011). Model selection tables for every regression analysis can be found in the accompanied Appendix 2. Additionally, we included a comparison between different intensities of use in the Appendix 2: supplementary materials for Chapter 3.

## **Results**

We found connectivity (measured as betweenness values) varied strongly across the landscape, with well-defined paths of high connectivity near natural water sources and in the area between Kunene region and Etosha National Park (Objective 1; Figure 3.1). We also found that all the covariates assessed contributed to the explanatory power of the most parsimonious model of betweenness values (i.e., connectivity) (Objective 2). Maximum and coefficient of variation of NDVI (productivity) values of a given year, distance from waterholes, and distance from roads and settlements were positively correlated with betweenness (i.e., higher values, higher connectivity). On the other hand, natural water sources, such as distance from perennial rivers and distance from wetlands, as well as slope were negatively correlated with betweenness (i.e., closer to water and less slope had higher connectivity; Figure 3.2).

We identified 7 unique population-level movement types (clusters) with different levels of use intensity, directionality, betweenness, and movement speed following the ‘movescape’ analytical approach (Objective 3; Table 3.1). No individual was found to have more than 7 clusters indicating that the chosen maximum number of clusters (8) was sufficient for this dataset. Four of these clusters were related to areas of high connectivity (i.e., clusters 1, 3, 6, and 7). However, clusters 1 and 6 were associated with low and medium speed (extended use), whereas clusters 3 and 7 were associated with faster speed (Table 3.1).

To address objective 4, we contrasted the environmental covariates associated with corridor (clusters 1, 3, 6, and 7) and non-corridor (clusters 2 and 4) pixels. We found that the global model was the most parsimonious model for both males and females with AUC values of 0.781 and 0.683, respectively. For both males and females, cattle abundance, distance from wetlands, distance from perennial rivers, and slope were negatively correlated with corridor pixels, indicating corridors were near water, in flatter areas, and away from livestock. Distance from towns and global human modification index were positively correlated with corridor pixels, indicating corridors were further from towns but in areas of higher human modification. Interestingly, corridor pixels are positively correlated with distance from waterholes for males while they are negatively correlated for females. Our measure of productivity had a positive effect on corridors for females only (Figure 3.3).

The top model of differences between highly directional, fast-corridor (cluster 3), and slow-corridor (cluster 6) was the global (AUC = 0.8954) and water (AUC = 0.8667) models for males and females, respectively. However, it was clear that water proximity was key for structuring the location of these two types of corridors for both sexes (Table 3.1). For females, fast corridors tended to be away from water resources, while males displayed the opposite (Table 3.1). Both males and females were using locations on the landscape near waterholes with much slower speeds and higher weight (Table 3.1; Figure 3.4).

## **Discussion**

As human population and landscape modification accelerate, proactive conservation of key areas for landscape connectivity are critical to the long-term protection of wildlife populations. This study provides insight into important corridors and associated environmental features within and between two regions of conservation importance for African elephant

conservation in Namibia using 8 years of GPS tracking data. We found areas of high connectivity were relatively ubiquitous, highlighting that the landscape remains open to elephant movements within each region (Figure 3.1). Connectivity within our study site was primarily influenced by proximity to natural water sources and anthropogenic features, similar to many other African elephant populations and large ungulates across the continent (Bastille-Rousseau et al., 2018; Crego et al., 2021; Osipova et al., 2019).

We identified 4 different corridor types in the ecosystem, whereby each was identified by differing levels of use intensity, speed, and directionality. Although the majority of individuals (at least 75%) contributed to the classification of 3 corridor types (high-use slow, low-use fast, and medium-use slow corridors), only 13.6 % of individuals in our sample exhibited the highest-use fastest corridor movement (Table 3.1). This illustrates that individuals differed in their movement behaviors and responses to landscape features as documented in other elephant movement studies (Bastille-Rousseau and Wittemyer, 2019; Chan et al., 2022). Such diversity in movement and space use strategies is important to take into consideration when making management decisions.

Water structured the landscape connectivity in our study system (Figure 3.2), similar to what has been found in Samburu, Kenya (Bastille-Rousseau and Wittemyer, 2021), another water-limited system. In this semi-arid environment, where water limitation is extreme, perhaps it was not surprising elephant connectivity was strongly structured with respect to this resource. When we mapped the resulting 7 different movement clusters spatially (Figure 3.5), we found that elephants in Etosha National Park use high-speed, directed walks when approaching waterholes. This aligned with the results from Polansky et al. 2015, which identified such behavior using behavioral change point analysis (Polansky et al., 2015). This high-speed directed

movement corresponded to cluster 7 in this analysis (Table 3.1; Figure 3.5). Furthermore, Polansky et al. documented a switch in movement types near waterholes (Polansky et al., 2015). Similarly, the movescape approach identified a shift to slower more stationary use at water holes, identified as clusters 1 and 6 (slow, high/medium intensity of use). With a reduction in precipitation projected in the region due to climate change (Bucchignani et al., 2018), the importance of access to water for meeting the survival and reproductive needs of these elephants will only increase. These model outputs could be invaluable in identifying and conserving critical areas and corridors to help meet those needs.

Notably, we found that elephants avoided using areas with high cattle abundance that were close to human settlements and towns, passing through such areas using higher-speed corridors as defined by the movescape technique. Other studies have also reported that covariates related to human presence affect the connectivity of African elephants (Bastille-Rousseau and Wittemyer, 2021; Epps et al., 2011; Osipova et al., 2019; Songhurst et al., 2016). Furthermore, the movements of other large herbivores, such as reticulated giraffes and plains zebra, were impeded by cattle ranching on the landscape (Crego et al., 2021). Balancing the livelihood needs of local people with connectivity required by large wild herbivores remains challenging (Donaldson et al., 2017; Rudnick et al., 2012).

Across several representations of connectivity, we found that human-related features were highly influential, as documented across numerous mammalian species (Morrison and Bolger, 2014; Stabach et al., 2016; Tucker et al., 2018). Because the mobility of the remaining populations of African elephants is threatened by human presence (Bastille-Rousseau and Wittemyer, 2021; Lohay et al., 2022), the projected population growth and associated economic development (United Nations, 2022; Williams et al., 2021a) are a threat to the integrity of

African elephant populations and other highly mobile species across Africa. With the reported disproportionate growth around the protected areas where the majority of elephant populations find refuge (Wittemyer et al., 2008), carefully managing incoming infrastructure development will be one of the key components to ensure remaining corridors are protected in the region.

Differences in movement behaviors and factors structuring the locations of different corridors were found between males and females, which also has been documented in other populations (Beirne et al., 2021; Roever et al., 2013; Vogel et al., 2020). When evaluating environmental features associated with different corridor types (i.e., fast v. slow) between the sexes, covariates related to water sources primarily structured the different corridor usage types for females while both water and human-related covariates determined different corridor types for males (Appendix 2: Table S2.2.1-2.2.2; Figure 3.4). Similarly, in Samburu, Kenya, water sources were one of the important variables in explaining corridor type, but also human presence and productivity-related variables played an important role for both sexes (Bastille-Rousseau and Wittemyer, 2021).

Connective movements between the Kunene community-managed area and Etosha National Park were relatively rare. About 4 individuals in our sample of 66 used the corridors between the western part of Etosha National Park and an adjacent Kunene multi-use community area (Figure 3.1). The relatively low connectivity may be due to our sample (lack of individuals using both areas); alternatively, it may reflect the historic separation of the area using electric fences. Ensuring the connectivity between the two can benefit both elephant populations (Bulman et al., 2007; Caughley, 1994; Hanski, 1999). The bottleneck in this connective movement could have negative impacts similar to those documented for wildebeest (Morrison and Bolger, 2014) and other large mammals with similar space requirements (Crego et al., 2021;

Lohay et al., 2022). Areas with higher wildlife protection efforts and lower anthropogenic impacts, such as Etosha National Park, could act as a source population on the landscape (Lee and Bolger, 2017). Finally, identifying wildlife corridors and infrastructure crossings (Bastille-Rousseau et al., 2018) can facilitate protection and land use planning efforts to promote connectivity and ensure long-term population persistence (Lohay et al., 2022; Morrison and Bolger, 2014).

This study highlights how the structure of the landscape can influence connectivity adding valuable pieces of information to understanding the movement behavior of this species (Wittemyer et al., 2019). Given the reproductive biology and relatively low population size, ensuring the connectivity between protected areas, such as Etosha National Park, and surrounding, buffer areas (Kunene region) could be key in ensuring long-term population persistence for the elephant populations in the region and could be a case study for other areas across Africa amidst the threats facing the species over the next century (Bucchignani et al., 2018; Gobush et al., 2022; Williams et al., 2021b).

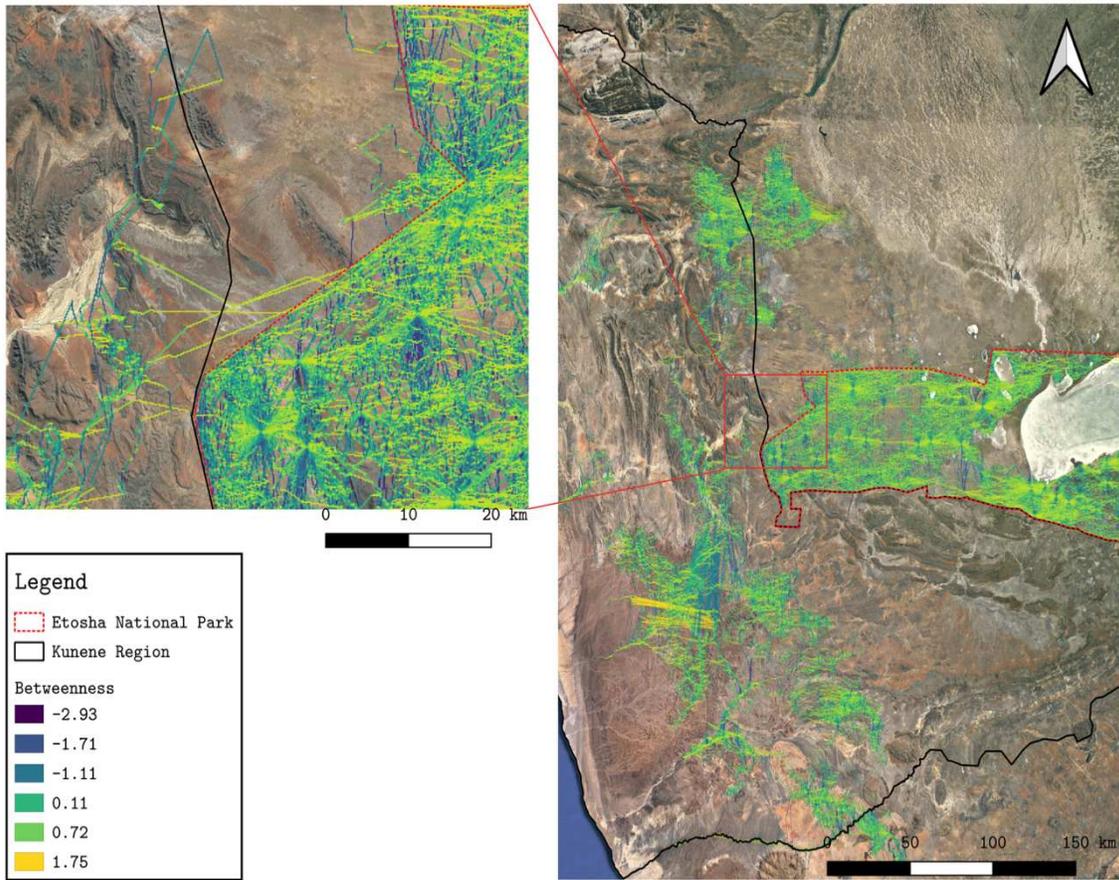
## Tables and Figures

**Table 3.1:** Summary of the unsupervised classification applied to 5 movement metrics of 66 African elephants inhabiting Etosha National Park and the Kunene multi-use conservancies area in Northwestern Namibia.

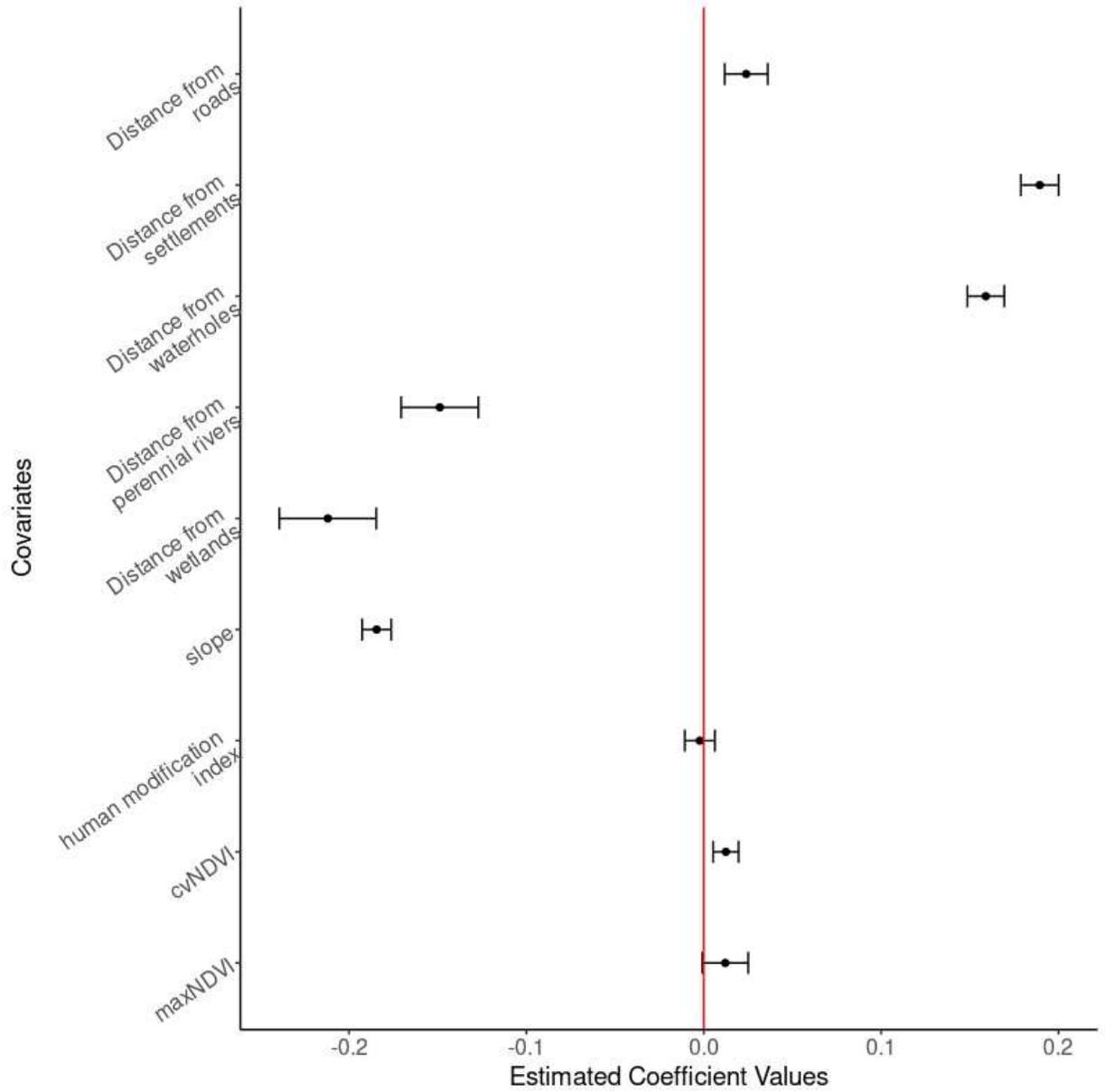
Metrics	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7	
Weight	1.9658	1.1028	-0.2394	-0.2762	-0.374	0.0761	19.3168	
Degree	2.0242	0.9491	-0.2309	-0.2301	-0.5927	0.3681	2.4292	
Betweenness	1.304	-0.1948	1.9268	-0.1969	-0.0745	1.2165	5.7943	
Speed	-0.3027	-0.4018	2.3684	-0.0986	0.6917	0.0987	1.9898	
DotP	-0.2971	-0.3189	0.0424	-0.0274	0.5599	0.1499	0.0069	
Proportion of pixels	0.1529	0.1804	0.1345	0.1886	0.0705	0.256	0.0172	
Proportion of Individuals	0.8636	0.9697	0.7576	0.9848	0.5455	1	0.1364	
Intensity of Use	high-use	high-use	low-use	low-use	low-use	medium-use	highest-use	
Corridor Type	slow	NC	fast	NC	NC	slow	fast	
	NC	Non-corridor pixels with average negative Betweenness values						

**Table 3.2:** Covariate layers used in the modeling framework and associated data sources.

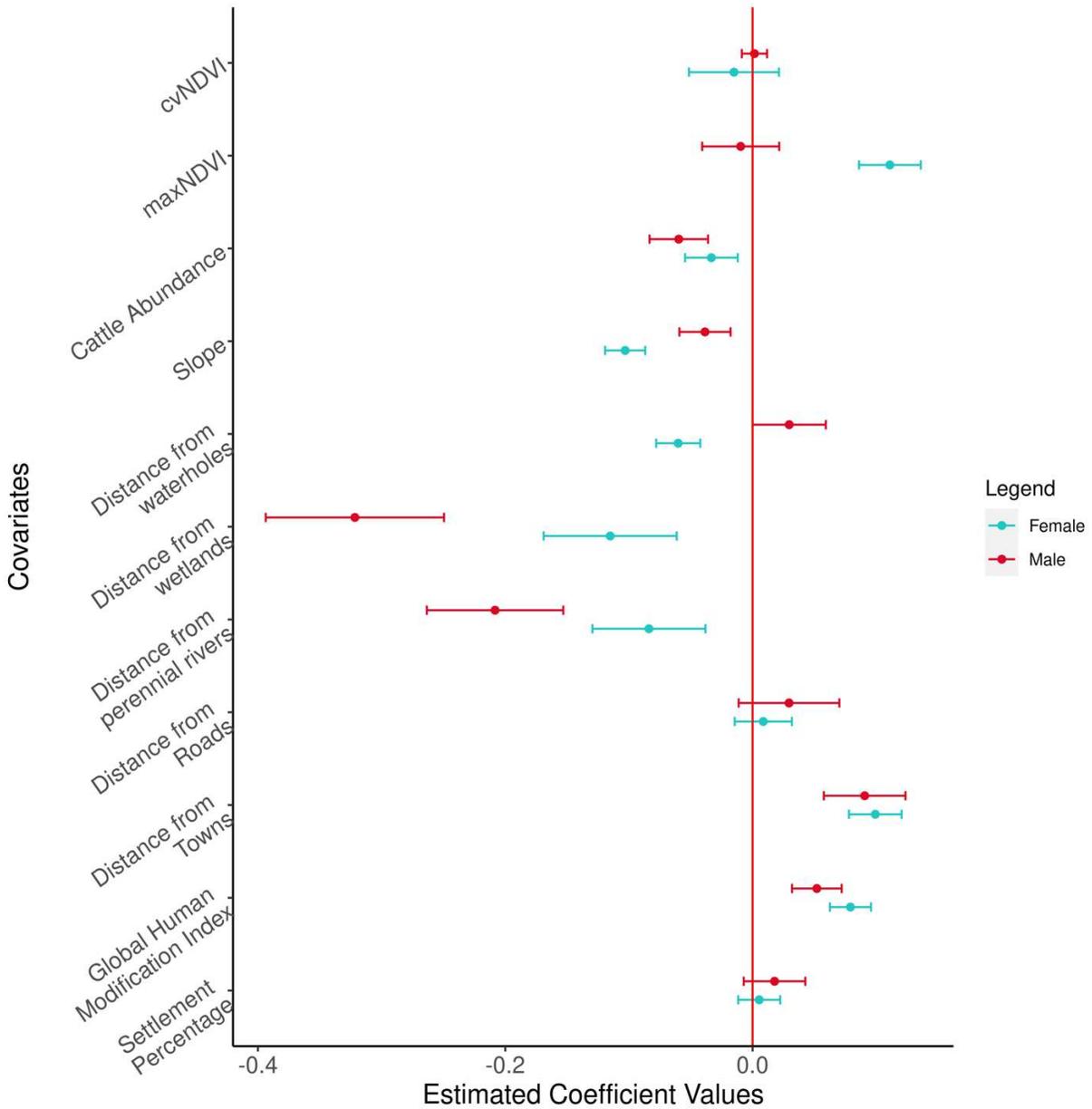
<b>Layer Names</b>	<b>Source</b>
Elevation and slope	SRTM image collection in Google Earth Engine (Jarvis et al., 2008)
Roughness index	Calculated using roughness algorithm in QGIS using elevation layer as an input
Global Human Modification Index	gHM layer in Google Earth Engine (Kennedy et al., 2019)
Percent settlement	Derived from (Sirko et al., 2021)
Distance from water holes	Etosha Ecological Institute
Distance from perennial rivers	Etosha Ecological Institute
Distance from roads	Etosha Ecological Institute
Distance from towns and settlements	Etosha Ecological Institute
Distance from wetlands	Etosha Ecological Institute
Normalized difference vegetation index	Landsat 7 and 8 image collection from Google Earth Engine
Cattle abundance	Etosha Ecological Institute



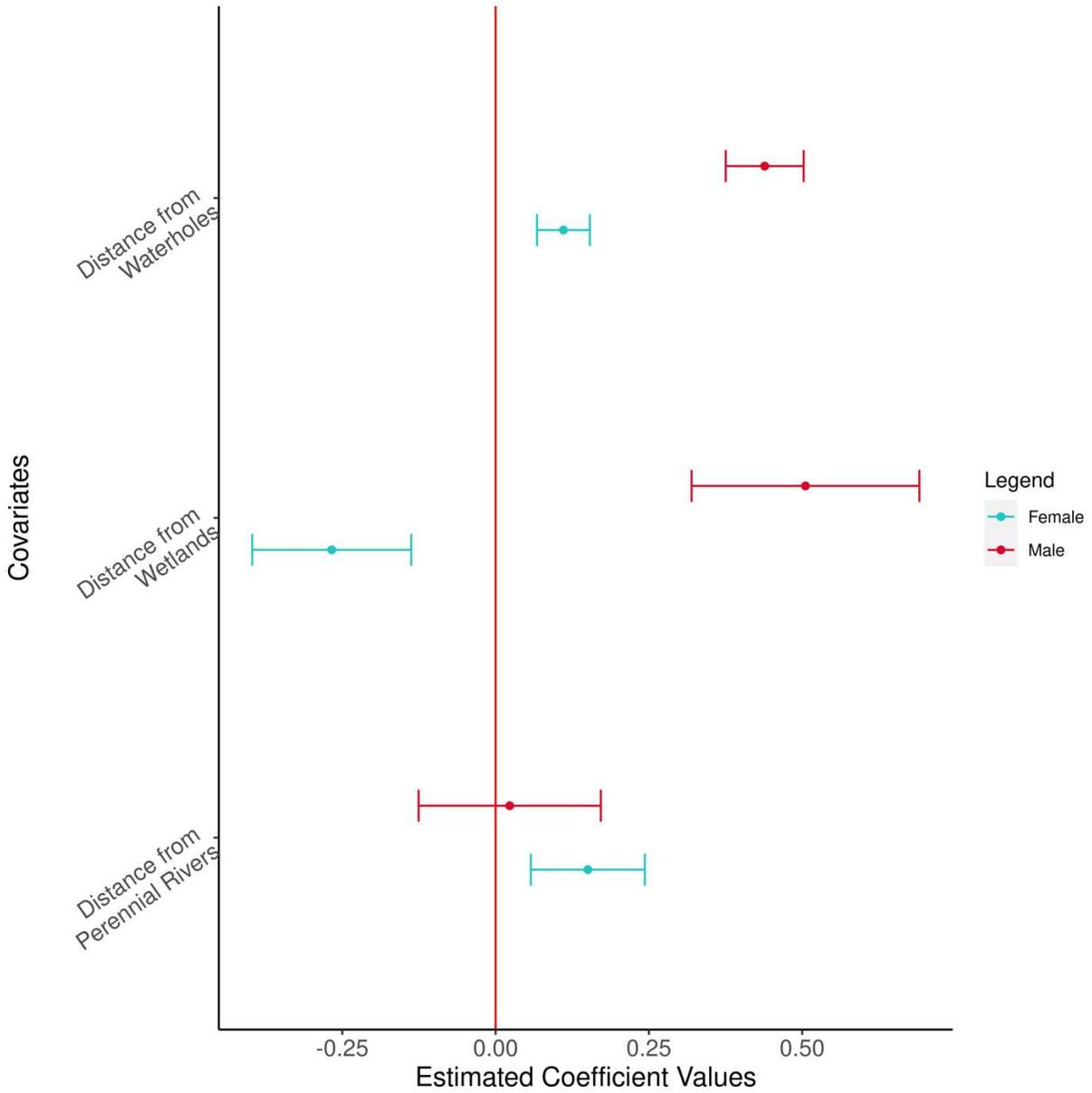
**Figure 3.1:** The study area including Etosha National Park (red outline) and Kunene multi-use conservancies area (black outline). Elephant paths from GPS tracking data of 66 wild African elephants are color scaled by their betweenness values. High betweenness values (yellow) indicate areas with strong connectivity (corridors). The expanded panel shows the area of connective movements between Etosha and Kunene. The background is satellite imagery provided by Google Satellites.



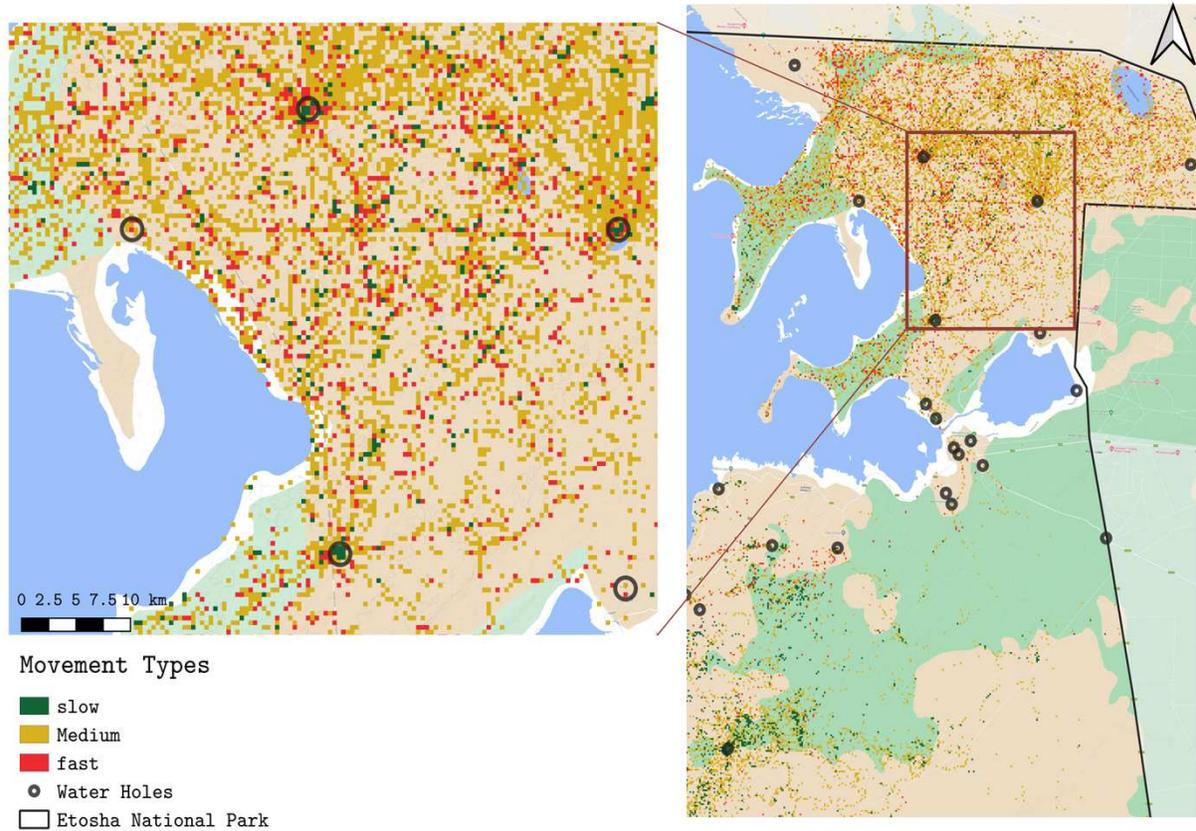
**Figure 3.2:** Coefficient estimates from the most parsimonious model explaining the variation in betweenness (connectivity) on the landscape. The covariates with the highest coefficient values tended to be related to water on the landscape.



**Figure 3.3:** The subset of coefficient estimates and associated confidence intervals included in the most parsimonious model for males (red) and females (females) evaluating differences between the corridor and non-corridor. Landscape features related to water distribution and human modification were the strongest predictors of differentiation between the corridor and non-corridor areas for both sexes.



**Figure 3.4:** Coefficient estimates and associated confidence intervals included in the most parsimonious model for both males and females evaluating differences between fast and slow corridors.



**Figure 3.5:** Fastest corridors (red, cluster 7) were unique routes used by elephants with high intensity between the waterholes inside Etosha National Park. Once the elephants reached the waterholes, movement types switched from fast to slow (green, cluster 1). The background imagery is from the Stamen terrain map.

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## **Chapter 4: Uncertainty of Asian elephant populations across the range states**

### **Introduction**

Understanding the state and trend of individual populations is crucial for effective species management and conservation efforts for any species of conservation concern (Caughley, 1994; Colyvan et al., 2009). The status of Asian elephant populations across their range has been a topic of concern and interest for years given the general lack of information on the species. Currently, the Asian elephant is classified as an endangered species due to various anthropogenic issues that have led to population declines across its range (Williams et al., 2020). It is estimated that the global population of wild Asian elephants has plummeted over the past few decades with 48,323–51,680 individuals speculated to remain in the wild across 13 different range countries/states (Menon and Tiwari, 2019). However, the number of extant individuals of Asian elephants is highly uncertain, as survey effort, coverage and approaches vary broadly across range states, and estimated numbers were not obtained from a robust sampling design and statistical framework in many cases.

Several statistical and design considerations are critical to deriving robust estimates of population size/abundance. First, the approach should account for uncertainty in detection (i.e., detection probability) to be considered an unbiased estimator (White, 2005). In addition, the statistical framework used should account for various sources of uncertainty in density/abundance (Jathanna et al., 2015), resulting in estimates with a quantified standard error. Furthermore, the survey approach should consider spatial and temporal variability in population dynamics, as these factors can significantly impact population estimates. These could be addressed using a design-based and/or model-based sampling approach. In a design-based

approach, random, systematic, or stratified random sampling can be used to account for variation in abundance as necessary (Thomas et al., 2001). In a model-based sampling approach, incorporating covariates, such as habitat characteristics and/or environmental variables, can enhance the ability of a model to capture these variations and improve the accuracy of the abundance estimates (Royle et al., 2005). Ultimately, a comprehensive and rigorous approach that addresses both detection uncertainty and ecological factors is essential for obtaining reliable population size/abundance estimates.

The causes of Asian elephant population decline include, but are not limited to, habitat degradation resulting in fragmentation and loss, human-elephant conflict, and illegal killings for ivory, skin, and meat (Leimgruber et al., 2003; Sampson et al., 2018; Songer et al., 2016; Williams et al., 2020). Although the threats facing Asian elephants are clear, population status, abundance, and uncertainty around estimates across the species' range are not. While the cost of a monitoring program using abundance as the state variable is relatively higher, having accurate estimates/knowledge of population trends and abundance is key to endangered species management (Noon et al., 2012; Noon and Mckelvey, 1996). Here we highlight the gaps in the current knowledge of population biology for Asian elephants range wide. Our objectives in this review are to 1) summarize the state of knowledge on Asian elephant population abundance, 2) categorize methods used in survey reports, and 3) estimate the percentage of the extant range of Asian elephants with robust population assessments. Finally, we discuss the need and best approaches for conducting robust assessments to fill in current knowledge gaps regarding Asian elephant distribution and abundance.

## Method

We conducted a literature search on Google Scholar using the keywords, “Asian elephants”, “Population size”, “Abundance”, and “Density”, focusing on studies published between 2000 and 2022. Our literature search identified 880 articles fulfilling these criteria. We went through the titles and abstracts of the resulting articles to filter out any studies that did not provide original estimates of abundance and/or density and that lacked a description of the methodological approach used. In addition, we contacted our partner-network to ask about any governmental and non-governmental reports reporting abundance estimates and detailing methods used in surveys to ensure the review is as comprehensive as possible, given not all reports are available on Google Scholar.

Following the internal guidelines of the IUCN Asian elephant specialist group for categorizing the robustness of surveys (Williams et al., 2020), we categorized the identified reports/articles into three tiers: robust, probable, and guest estimates based on sampling and analysis methods. To calculate the area covered by the identified survey reports/articles, we obtained publicly available shapefiles of the study areas when available or georeferenced and digitized from the original articles/reports in QGIS (QGIS Development Team, 2019) when they were not. We extracted the year each assessment was conducted and summarized the time since the last assessment in years for each area. In each article/report, we determined the effective study area in square kilometers (km<sup>2</sup>). We summarized the area surveyed and the time since the last survey for each range state and calculated the percentage of the current estimated distribution of Asian elephants (Williams et al., 2020) per range state that had been assessed using a statistically robust sampling design and analytical framework. Summary statistics and figures in

this review were made in R using packages named ‘ggplot2’ and ‘dplyr’ (R Core Team, 2020; Wickham, 2016; Wickham et al., 2020).

## **Results**

After assessing the titles and abstract of the literature search for Asian elephant’s abundance and density and addition of gray literature, we found 26 articles and 9 governmental and non-governmental reports from 2000 to 2022 (Table 4.1) that provided estimates of elephant abundance or density, reported the methods used, and provided an area surveyed. Out of the 13 range states, only 7 had estimated population sizes of their Asian elephant populations using robust methods (Table 4.2), with the remainder lacking any quantitative and repeatable survey effort. Among the range states that had implemented robust surveys, only China had covered the entire range of their Asian elephant population. Furthermore, only 3 countries had conducted surveys using a robust sampling and statistical approach in the last 5 years (i.e., since 2018). In aggregate, we found that only 4.4 % of the estimated extant range of the Asian elephant had an assessment done using a statistically robust approach (Figure 4.1).

## **Discussion**

Knowledge of population status (i.e., abundance or density) is fundamental for conservation and making management decisions, particularly for endangered species like Asian elephants (Williams et al., 2002). However, estimating the abundance of Asian elephant populations is costly compared to other state variables such as occupancy because of their fragmented distribution, relatively smaller population sizes (Goswami et al., 2007), and large-ranging behavior resulting in strong differentiation in areas of use over time (Chan et al., 2022; Moßbrucker et al., 2016; Noon et al., 2012). Regardless, the current state of knowledge on the abundance of Asian elephants is limited, and this review highlights the dire need for population

assessments of the species across the range. The population estimates from some of the range states with unstable political environments, such as Myanmar, were not based on robust approaches and, likely were overestimates to avoid political and public pressure. Furthermore, estimates across most of the predicted species' range were informed guesses. Without clear knowledge of the population numbers, we cannot determine the trend in the species' population size and distribution, which means managers, policymakers, and other stakeholders cannot take informed management actions.

Information quality and availability of population status and trends varied across the range countries. Countries, such as Bangladesh, Myanmar, Nepal, Sri Lanka, Thailand, and Vietnam, have not assessed their elephant population using any robust approach. For example, in Myanmar, the widely used population abundance information was obtained from an expert workshop (Leimgruber and Wemmer, 2004). There had been a call for more robust abundance estimation methods in 2004 (Blake and Hedges, 2004), but only a few studies had lived up to this call (Goswami et al., 2007; Gray et al., 2014; Hedges et al., 2013; Zhang et al., 2015). This lack of action is likely due to difficulties posed by costs for surveys, lack of resources and/or technical capabilities and very small population sizes in some areas that make survey challenging (as in the case of Vietnam).

Currently, 7 of 13 range state countries have assessed their Asian elephant populations using a robust estimator, but only 3 have conducted such surveys within the last five years. The need to expand the number of populations and range countries/states undertaking robust surveys is critical. Asian elephants pose a unique challenge to study given the habitat they are primarily found in (i.e., disturbed forest with thick understory such as bamboo). Coupled with low density, such challenges can result in extremely low detection probability estimates for direct survey

methods (e.g., camera traps), leading to the risk of underestimation of population size. Similarly, distance sampling with direct counts likely violates the assumption that objects are detected at their initial locations (Buckland et al., 2015) given avoidance by elephants related to the habitat conditions and heightened sense of smell and hearing of the species. As such, appropriate techniques for robust surveys are relatively few. However, spatial mark and recapture approaches using fecal DNA (Hedges et al., 2013) and photographic capture-recapture methods where feasible (Goswami et al., 2007) have shown promising results in estimating abundance for Asian elephants. Methods using non-invasive SNP genotyping had been successfully used in nationwide efforts of estimating the abundance and density of African forest elephants in Gabon (Laguardia et al., 2021) and such protocols are recommended by CITES (Thomas et al., 2001). With the declining cost of processing DNA samples and the technology being more readily accessible across the world, we encourage researchers and governments across Asian elephant range states to explore this approach to estimate population sizes with more accuracy.

## Tables and Figures

**Table 4.1:** List of articles and reports (both governmental and non-governmental) reviewed in this study, ordered by year of publication.

Author	Title	Country	Sampling Method	Type of Study	Estimation Class
Hedges et al_2005	Distribution, status, and conservation needs of Asian elephants ( <i>Elephas maximus</i> ) in Lampung Province, Sumatra, Indonesia	Indonesia	Distance Sampling	Peer-reviewed	Robust
Goswami et al_2007	Application of photographic capture-recapture modeling to estimate demographic parameters for male Asian elephants	India	photographic capture-recapture	Peer-reviewed	Robust
Varma et al_2008	The status and conservation of the Asian elephant ( <i>Elephas maximus</i> ) in Cat Tien National Park, Vietnam	Vietnam	block survey	Peer-reviewed	Probable
DNPWC/MoFSC/GoN_2009	Elephant Conservation Action Plan for Nepal - 2009	Nepal	expert surveys and count	report	Guestimate
Alfred et al_2010	Density and population estimation of the Bornean elephant ( <i>Elephas maximus borneensis</i> ) in Sabah.	Sabah Malaysia	Distance Sampling	Peer-reviewed	Robust

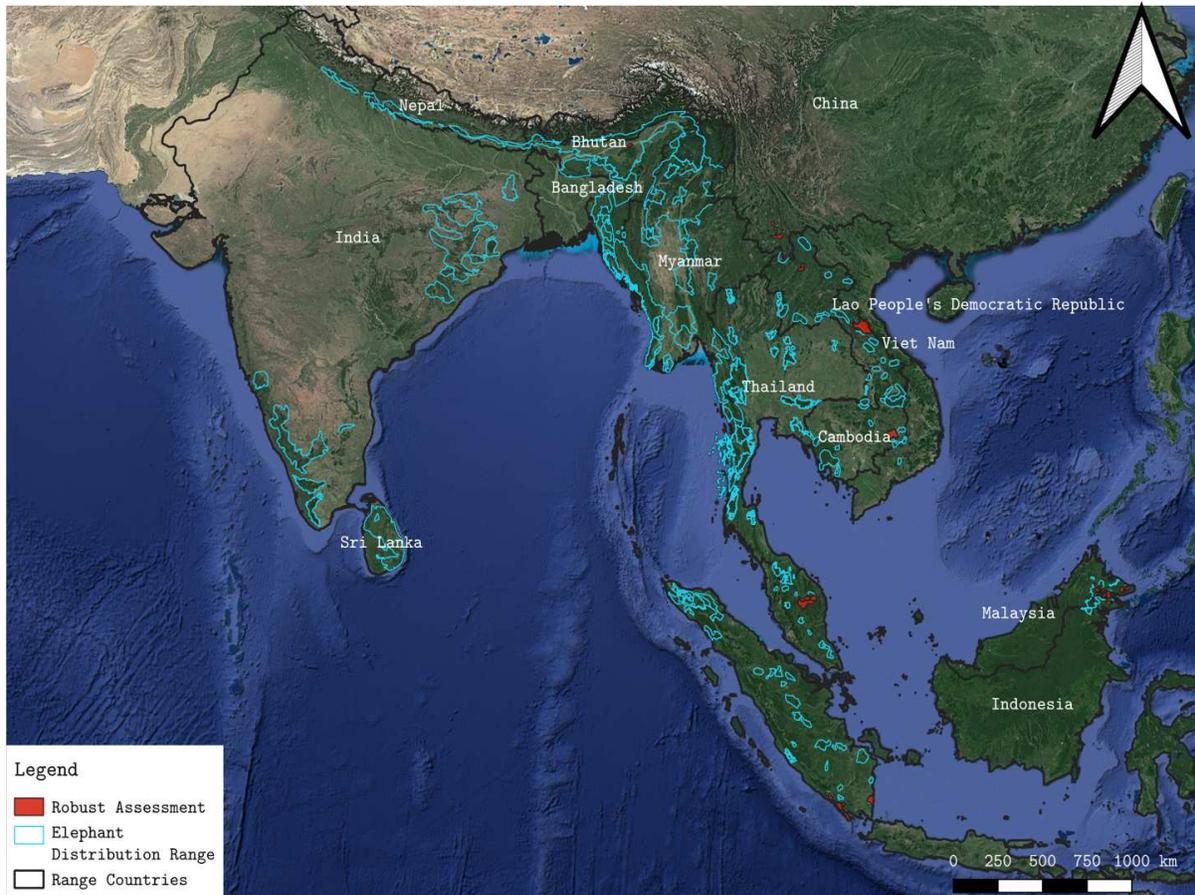
Kumarguru et al_2010	Estimating Asian Elephant Population in Dindugul, Kodaikanal	India	Dung transects	Peer-reviewed	Probable
Alfred et al_2011	Current Status of Asian Elephants in Borneo	Sabah Malaysia	referenced Alfred et al 2010	Peer-reviewed	Robust
Azmi and Gunaryadi_2011	Current Status of Asian elephants in Indonesia	Indonesia	no estimation method provided	Peer-reviewed	Guestimate
Baskara et al_2011	Current Status of Asian elephants in India	India	count and synchronized elephant census	Peer-reviewed	Probable
Cao Thi Ly_2011	Current Status of Asian elephants in Vietnam	Vietnam	no estimation method provided	Peer-reviewed	Guestimate
Fernando et al_2011	Current Status of Asian elephants in Sri Lanka	Sri Lanka	waterhole count	Peer-reviewed	Guestimate
Islam et al_2011	Current Status of Asian Elephants in Bangladesh	Bangladesh	dung counts, interviews, sightings	Peer-reviewed	Probable
Jigme and Williams_2011	Current Status of Asian Elephants in Bhutan	Bhutan	dung counts and line transact	Peer-reviewed	Robust
Khounboline_2011	Current Status of Asian Elephants in Laos	Laos	no estimation method provided	Peer-reviewed	Guestimate
Leimgruber et al_2011	Current Status of Asian Elephants in Myanmar	Myanmar	expert surveys and count	Peer-reviewed	Guestimate
Maltby and Bouchier_2011	Current Status of Asian Elephants in Cambodia	Cambodia	no estimation method provided	Peer-reviewed	Guestimate
Pradhan et al_2011	Current Status of Asian Elephants in Nepal	Nepal	no estimation method provided	Peer-reviewed	Guestimate
Saaban et al_2011	Current Status of Asian Elephants in Peninsular Malaysia	Peninsular Malaysia	dung counts and line transact	Peer-reviewed	Guestimate
Zhang_2011	Current Status of Asian Elephants in China	China	dung counts and line transact	Peer-reviewed	Robust

Hedges et al 2013	Accuracy, precision, and cost-effectiveness of conventional dung density and fecal DNA-based survey methods to estimate Asian elephant ( <i>Elephas maximus</i> ) population size and structure	Laos	fecal-DNA based survey	Peer-reviewed	Robust
MNREGM/DWNPM 2013	National Elephant Conservation Action Plan: Blueprint to Save Malaysian Elephants	Peninsular Malaysia	Distance Sampling and dung count	report	Robust
Gray et al 2014	Population size estimation of an Asian elephant population in eastern Cambodia through non-invasive mark-recapture sampling	Cambodia	non-invasive mark-recapture	Peer-reviewed	Robust
Jathannat et al 2015	Reliable monitoring of elephant populations in the forests of India: Analytical and practical considerations	India	Distance Sampling	Peer-reviewed	Robust
Madhusudan et al 2015	Distribution, relative abundance, and conservation status of Asian elephants in Karnataka, southern India	India	line transects, HEC records, media reports, sightings, signs, and interviews	Peer-reviewed	Probable
Zhang et al 2015	Asian Elephants in China: Estimating Population Size and Evaluating Habitat Suitability	China	DNA spatial capture-recapture	Peer-reviewed	Robust
AsERSN 2017	Asian elephants range states meeting final report	13 range countries		report	Varied

Sukumar_2017	Synchronized Elephant Population Estimation India	India	direct count method	report	Probable
FD_2018	Myanmar Elephant Conservation Action Plan (MECAP): 2018-2027	Myanmar	expert interviews	report	Guestimate
MOEF_2018	Bangladesh Elephant Conservation Action Plan (2018-2027)	Bangladesh	varied	report	Probable
NCD_2018	National Elephant Survey Report	Bhutan	photographic capture-recapture	report	Robust
Fernando et al_2019	First country-wide survey of the Endangered Asian elephant: towards better conservation and management in Sri Lanka	Sri Lanka	interview surveys	Peer-reviewed	Probable
Goswami et al_2019	Towards a reliable assessment of Asian elephant population parameters: the application of photographic spatial capture-recapture sampling in a priority floodplain ecosystem	India	photographic capture-recapture	Peer-reviewed	Robust
Menon and Tiwari_2019	Population Status of Asian Elephants <i>Elephas maximus</i> and key threats	13 range countries	dung counts, interviews, sightings	Peer-reviewed	Guestimate
GDANCP_2020	Asian elephant conservation action plan for Cambodia	Cambodia		report	Robust
Sabah WD_2020	Bornean Elephant Action Plan for Sabah 2020-2029	Sabah Malaysia	expert knowledge	report	Guestimate

**Table 4.2:** A breakdown of the sampled area using robust methods by country with respect to the current distribution range (Williams et al. 2020). The percentage of the distribution range sampled using robust methods is 4.4%.

<b>Country</b>	<b>Distribution Range (km<sup>2</sup>)</b>	<b>Robust Sampling Covered (km<sup>2</sup>)</b>	<b>Percent Sampled</b>
Bangladesh	14340	0	0.0%
Bhutan	2342	800	34.2%
Cambodia	19485	2225	11.4%
China	4548	5580	122.7%
India	250005	3080	1.2%
Indonesia	45515	4802	10.6%
Laos	27433	1988	7.2%
Malaysia	25529	6555	25.7%
Myanmar	78571	0	0.0%
Nepal	12646	0	0.0%
Sri Lanka	36432	0	0.0%
Thailand	52916	0	0.0%
Vietnam	629	0	0.0%



**Figure 4.1:** Showing only 4.4% of the elephant distribution range were assessed for population status using statistically robust methods since 2000.

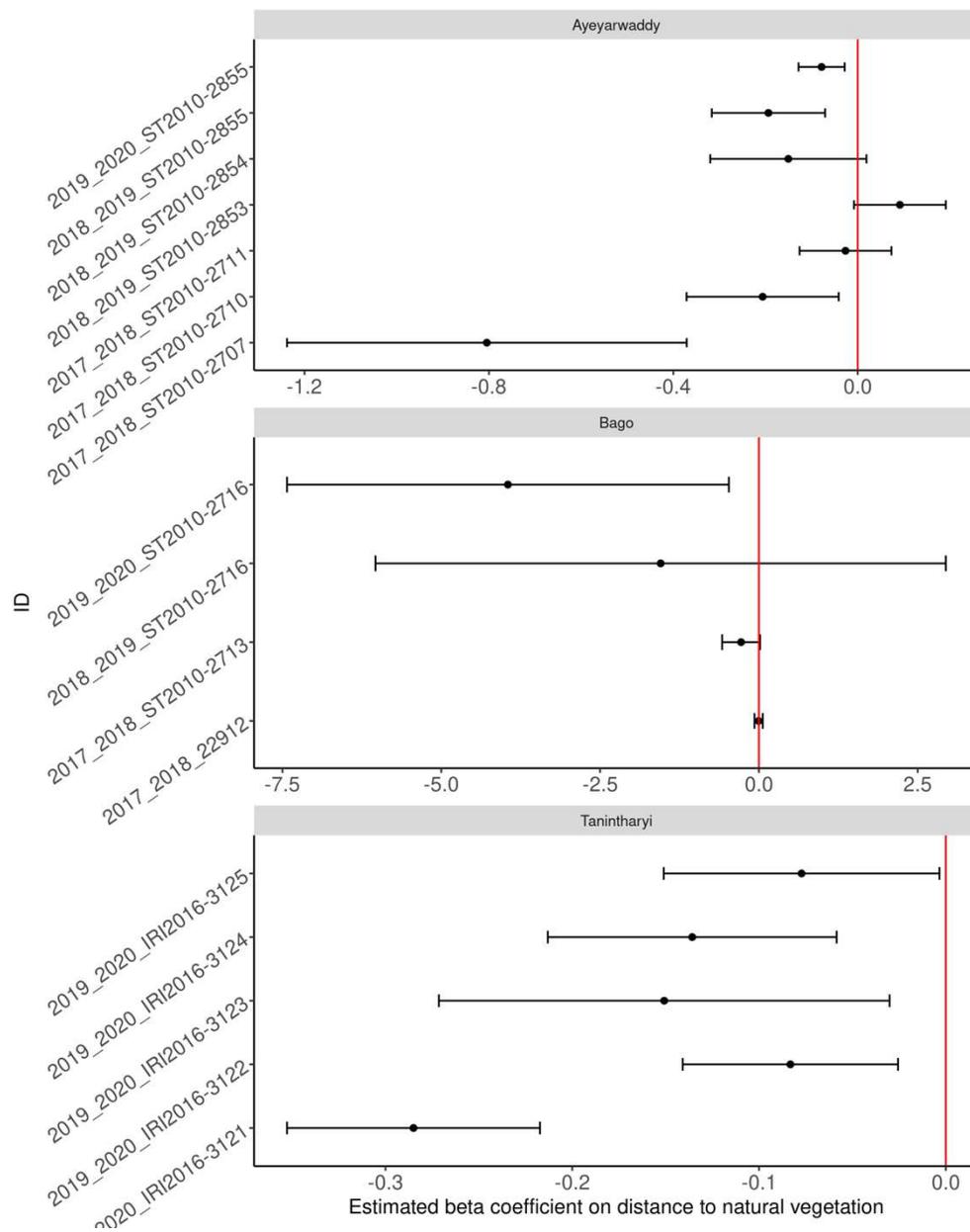
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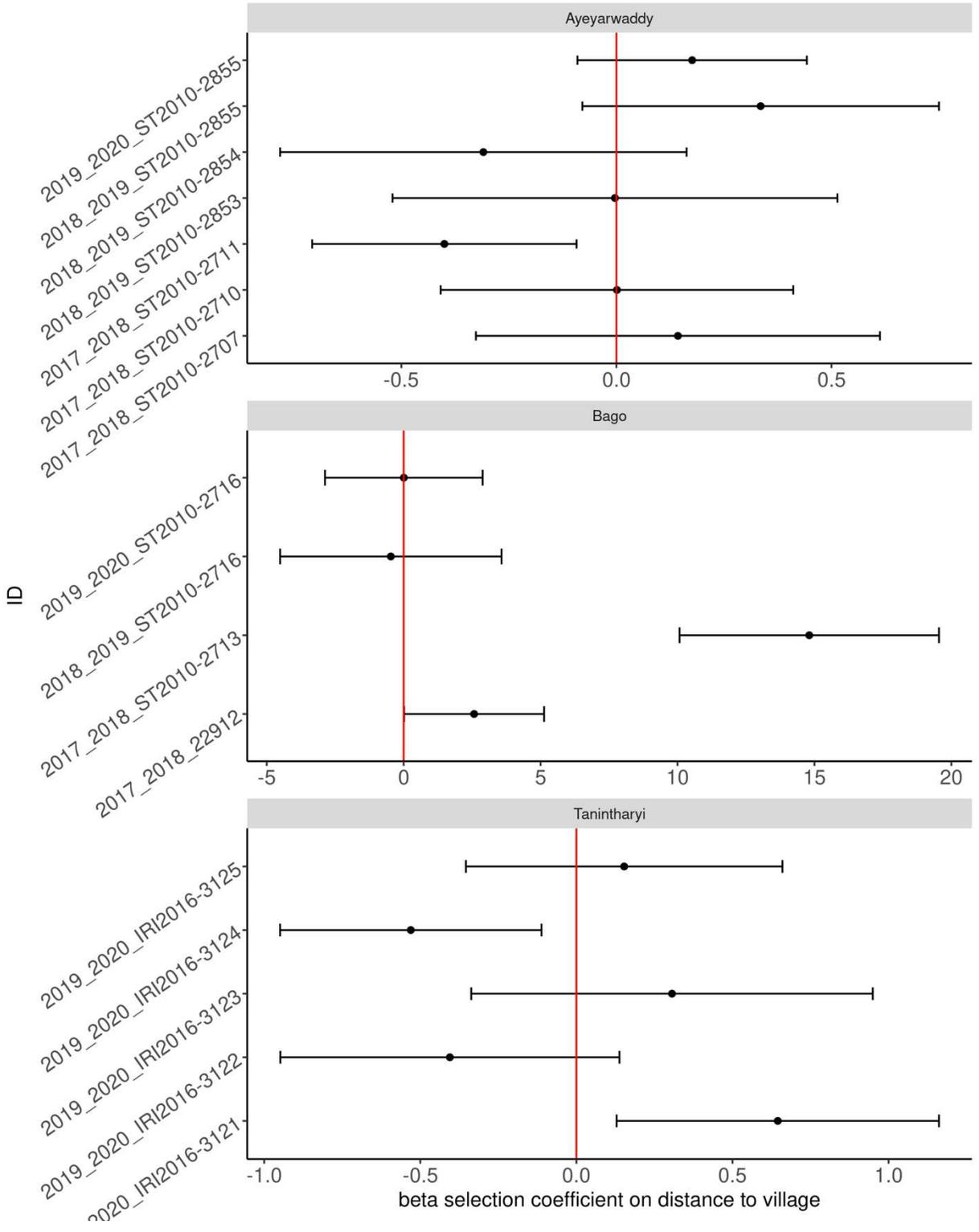
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## APPENDIX 1: Supplementary materials for Chapter 2

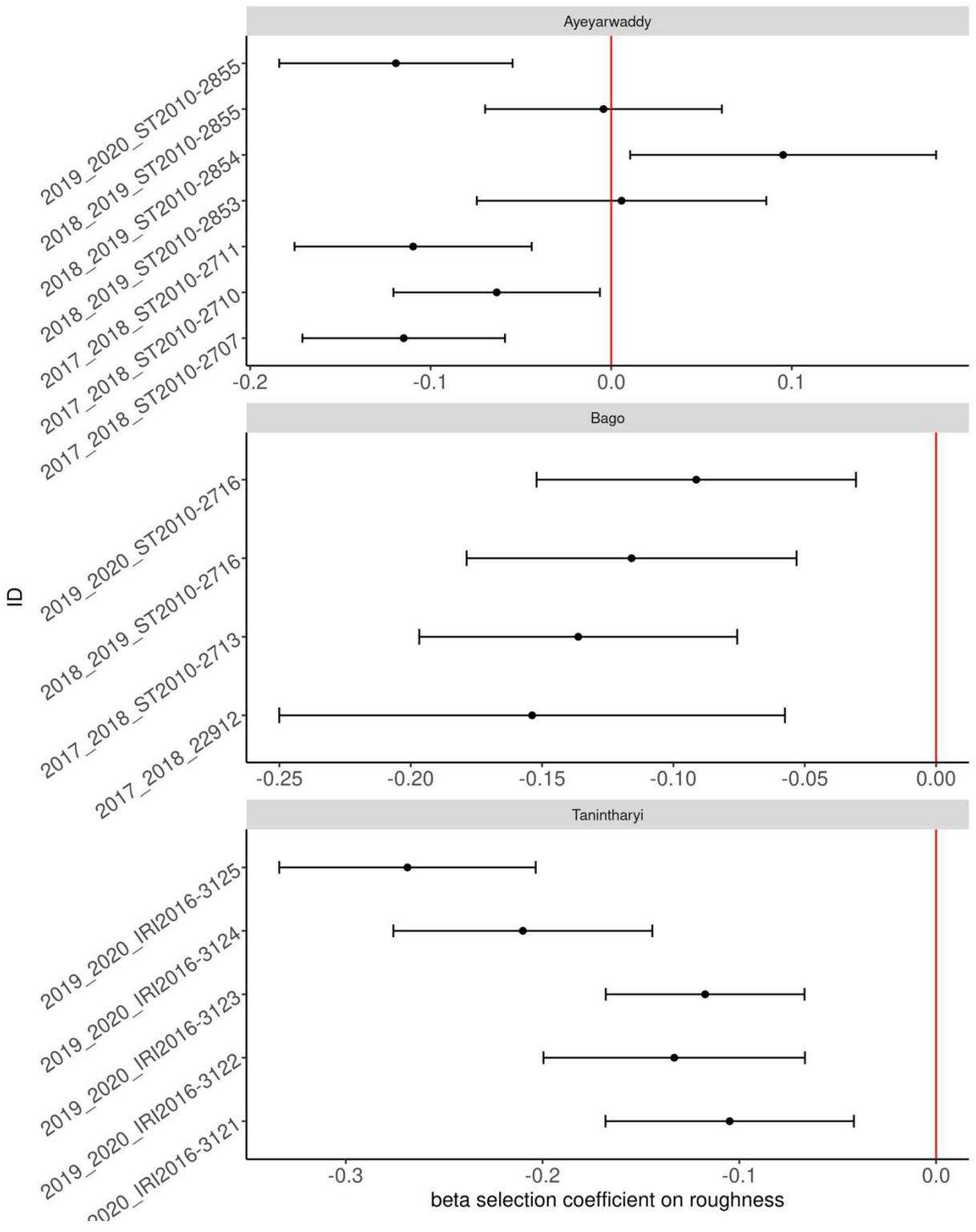
### Selection Coefficients at the individual step scale



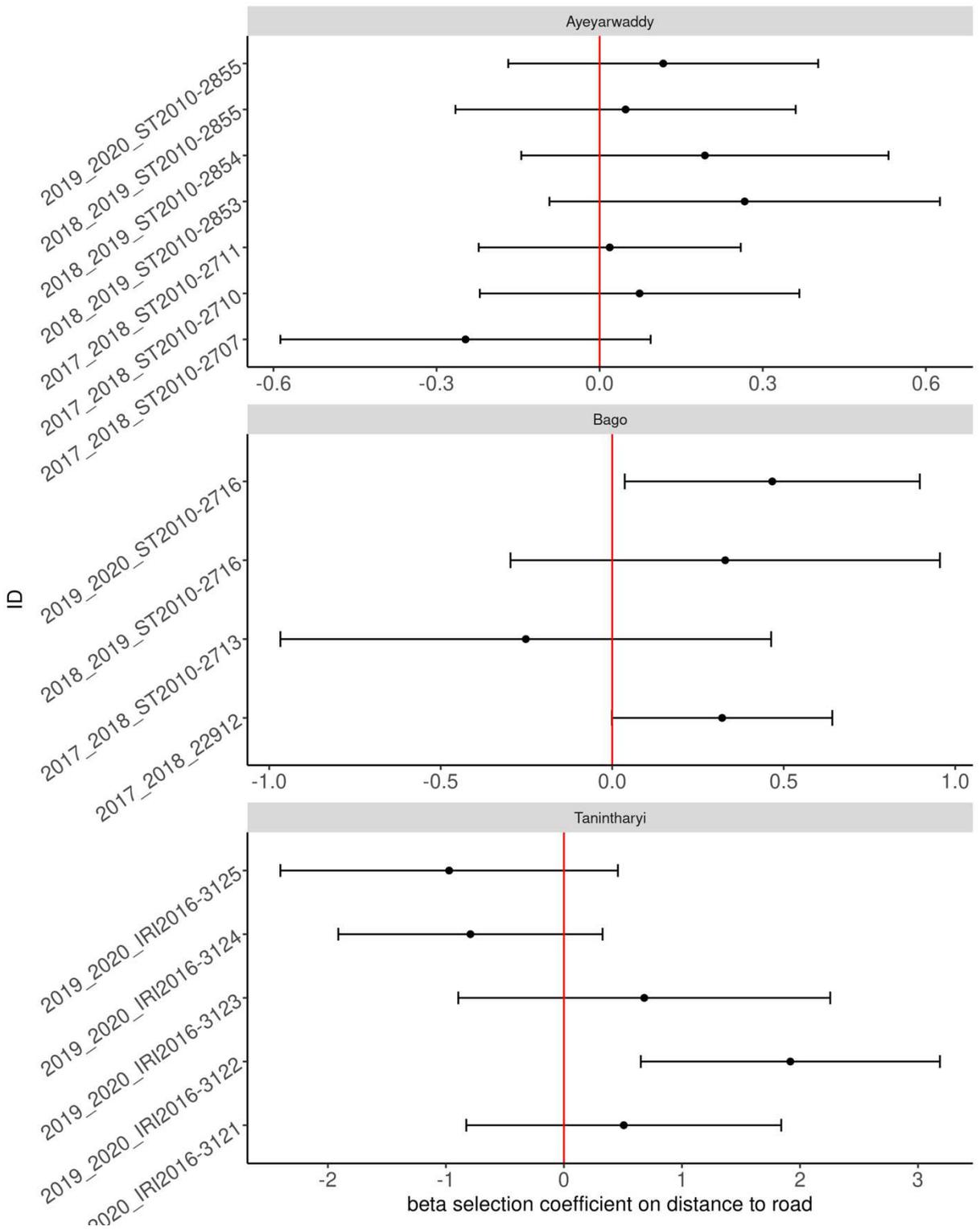
**Figure S1.1:** Beta selection coefficient for distance to natural vegetation estimated from integrated step selection analysis.



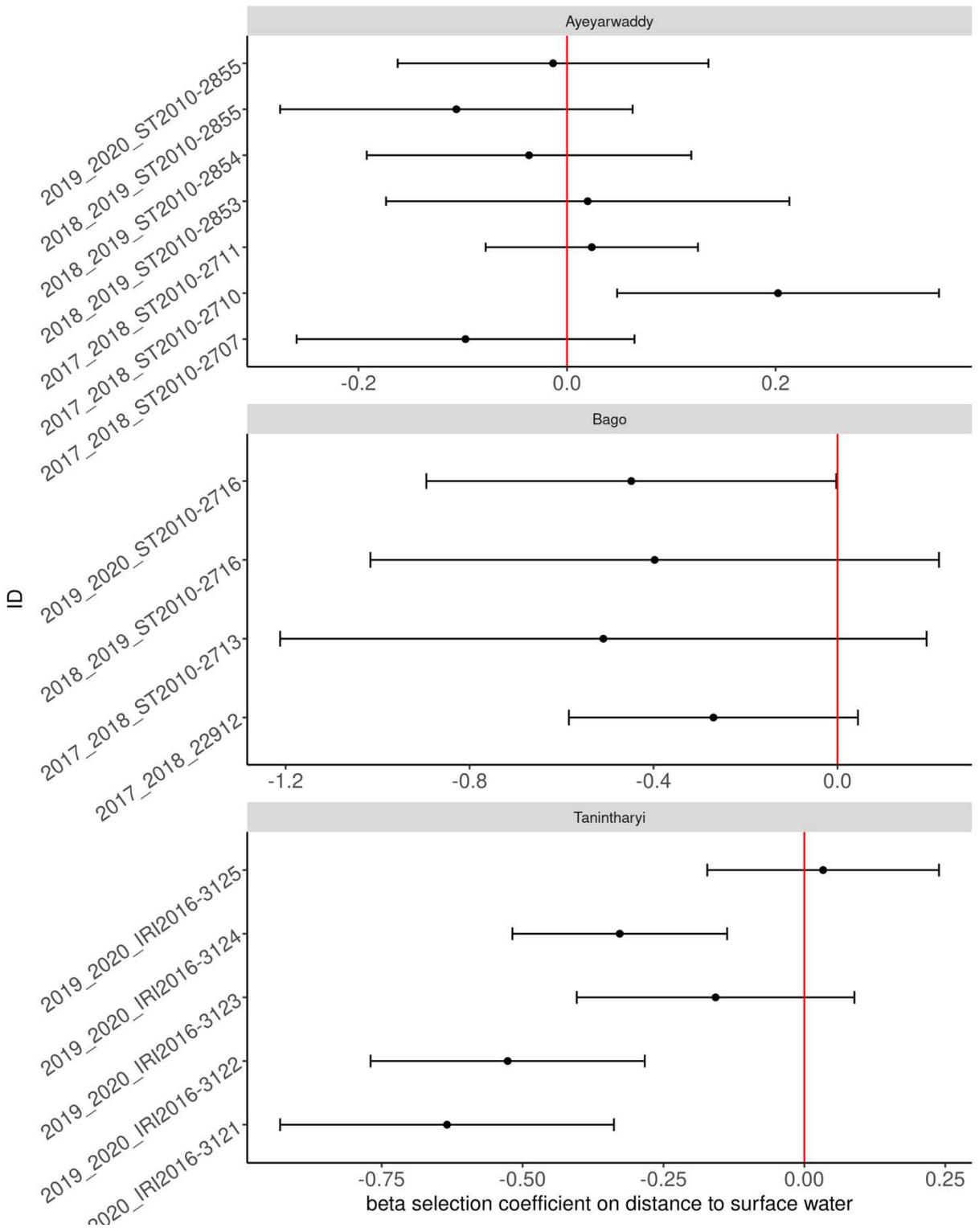
**Figure S1.2:** Beta selection coefficient for distance to village estimated from integrated step selection analysis.



**Figure S1.3:** Beta selection coefficient for terrain roughness estimated from integrated step selection analysis.

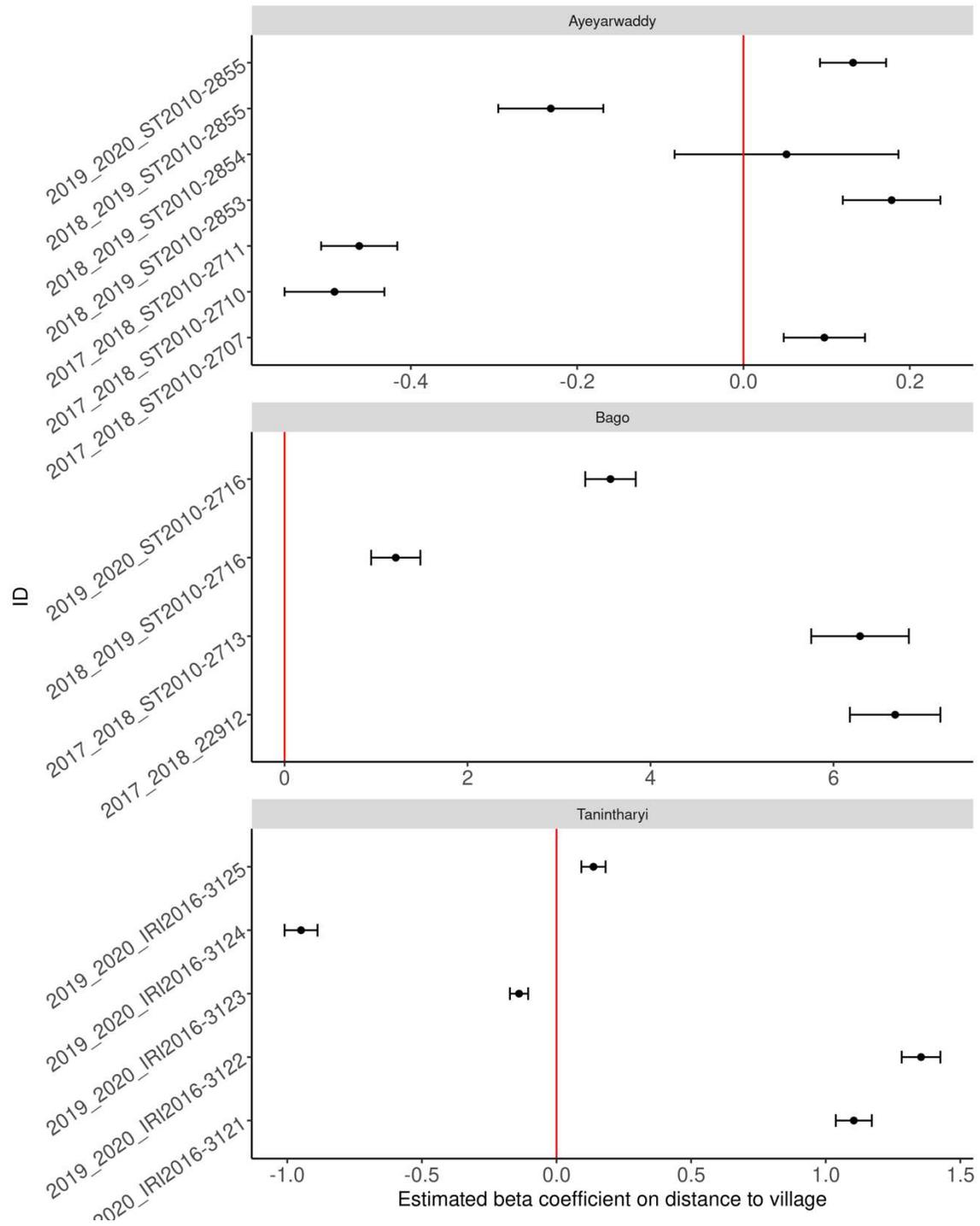


**Figure S1.4:** Beta selection coefficient for distance to road estimated from integrated step selection analysis.

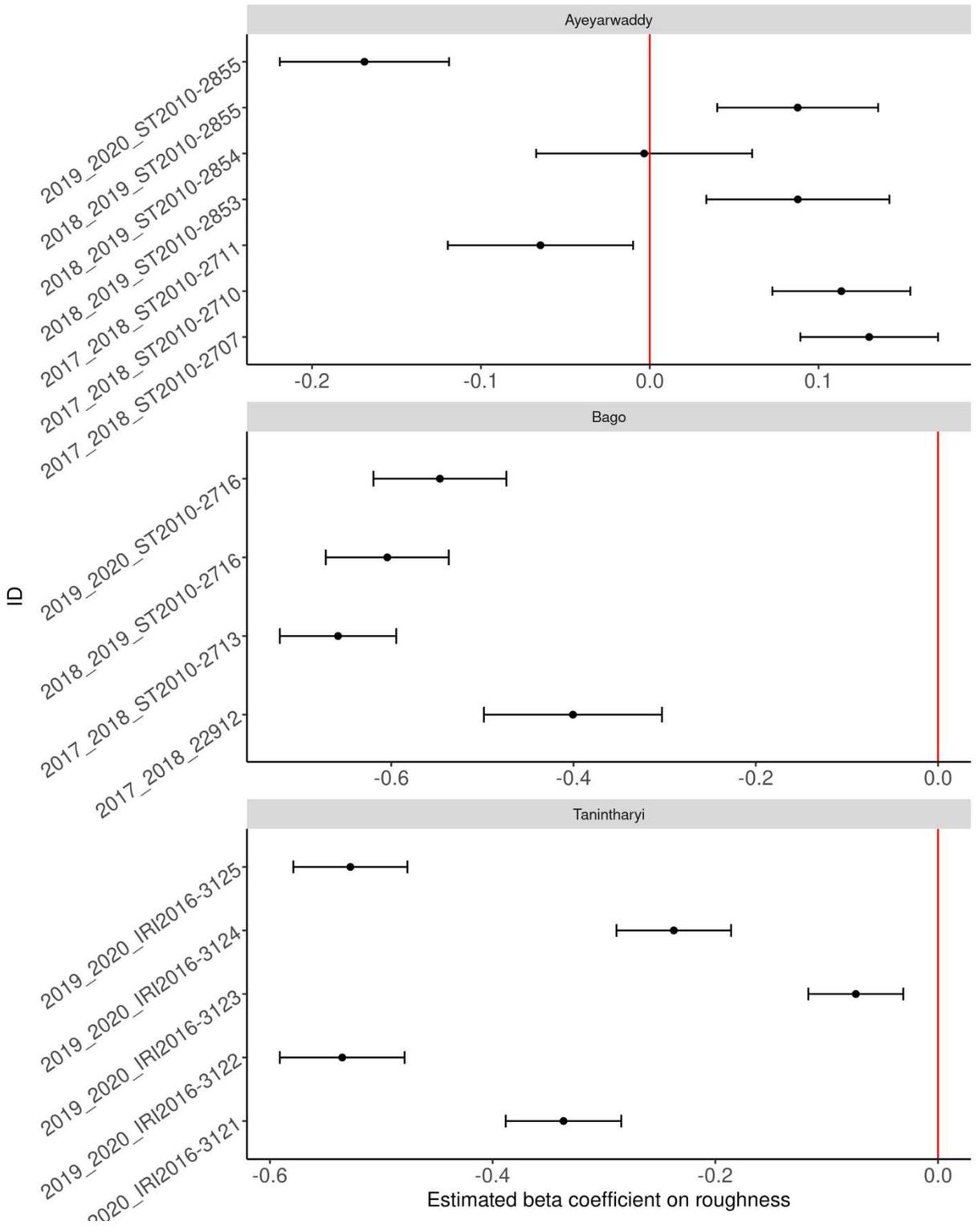


**Figure S1.5:** Beta selection coefficient for distance to surface water estimated from integrated step selection analysis.

**Selection coefficients estimated at range scale**



**Figure S1.6:** Beta selection coefficient for distance to village estimated from third-order resource selection analysis.



**Figure S1.7:** Beta selection coefficient for terrain roughness estimated from third-order resource selection analysis.

**APPENDIX 2: Supplementary materials for Chapter 3**

**Table S2.1:** Model selection table evaluating environmental features explaining the most variation in the connectivity of a pixel (betweenness value). All the models have spatial auto-covariate term to account for unexplained spatial autocorrelations in the residual.

<b>Model names</b>	<b>K</b>	<b>BIC</b>	<b>Delta BIC</b>	<b>Model Lik.</b>	<b>BIC Wt.</b>	<b>LL</b>	<b>Cum. Weight</b>
Global	13.00	4456679.04	0.00	1.00	1.00	-2228250.76	1.00
Geographic	8.00	4458008.57	1329.53	0.00	0.00	-2228949.66	1.00
Human	7.00	4459771.76	3092.72	0.00	0.00	-2229838.09	1.00
Water	7.00	4459869.15	3190.11	0.00	0.00	-2229886.78	1.00
Environment	9.00	4459896.17	3217.13	0.00	0.00	-2229886.64	1.00

**Table S2.2.1:** Model selection table of the candidate model set evaluating the most parsimonious model to explain the difference between corridor v. non corridor pixels for male elephants in the study.

<b>Model names</b>	<b>K</b>	<b>BIC</b>	<b>Delta BIC</b>	<b>Model Lik.</b>	<b>BIC Wt.</b>	<b>LL</b>	<b>Cum. Weight</b>
Global	14	77953.92	0.00	1.00	0.99	-38897.34	0.99
Water	6	77964.50	10.57	0.01	0.01	-38948.12	1.00
Environment	8	77987.14	33.22	0.00	0.00	-38948.07	1.00
Human	8	78013.55	59.62	0.00	0.00	-38961.27	1.00
Geographic	7	78039.63	85.71	0.00	0.00	-38980.00	1.00

**Table S2.2.2:** Model selection table of the candidate model set evaluating the most parsimonious model to explain the difference between corridor v. non corridor pixels for female elephants in the study.

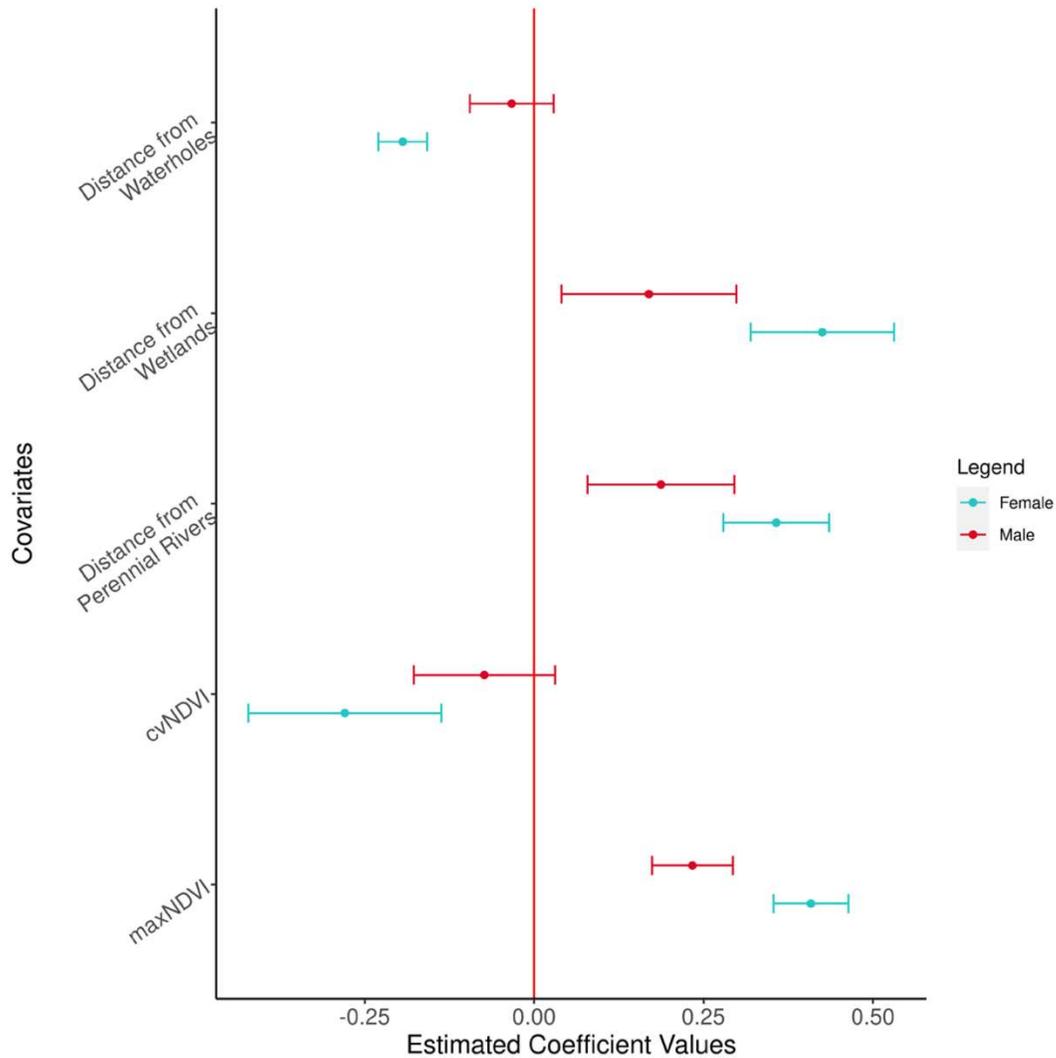
<b>Model names</b>	<b>K</b>	<b>BIC</b>	<b>Delta BIC</b>	<b>Model Lik.</b>	<b>BIC Wt.</b>	<b>LL</b>	<b>Cum. Weight</b>
Global	14.00	144716.68	0.00	1.00	1.00	-72274.30	1.00
Geographic	7.00	144835.29	118.61	0.00	0.00	-72375.62	1.00
Environment	8.00	144972.26	255.58	0.00	0.00	-72438.10	1.00
Human	8.00	144980.38	263.70	0.00	0.00	-72442.16	1.00
Water	6.00	145013.74	297.06	0.00	0.00	-72470.85	1.00

**Table S2.3.1:** Model selection table of the candidate model set evaluating the most parsimonious model to explain the difference between fast and slow corridor types for male elephants in the study.

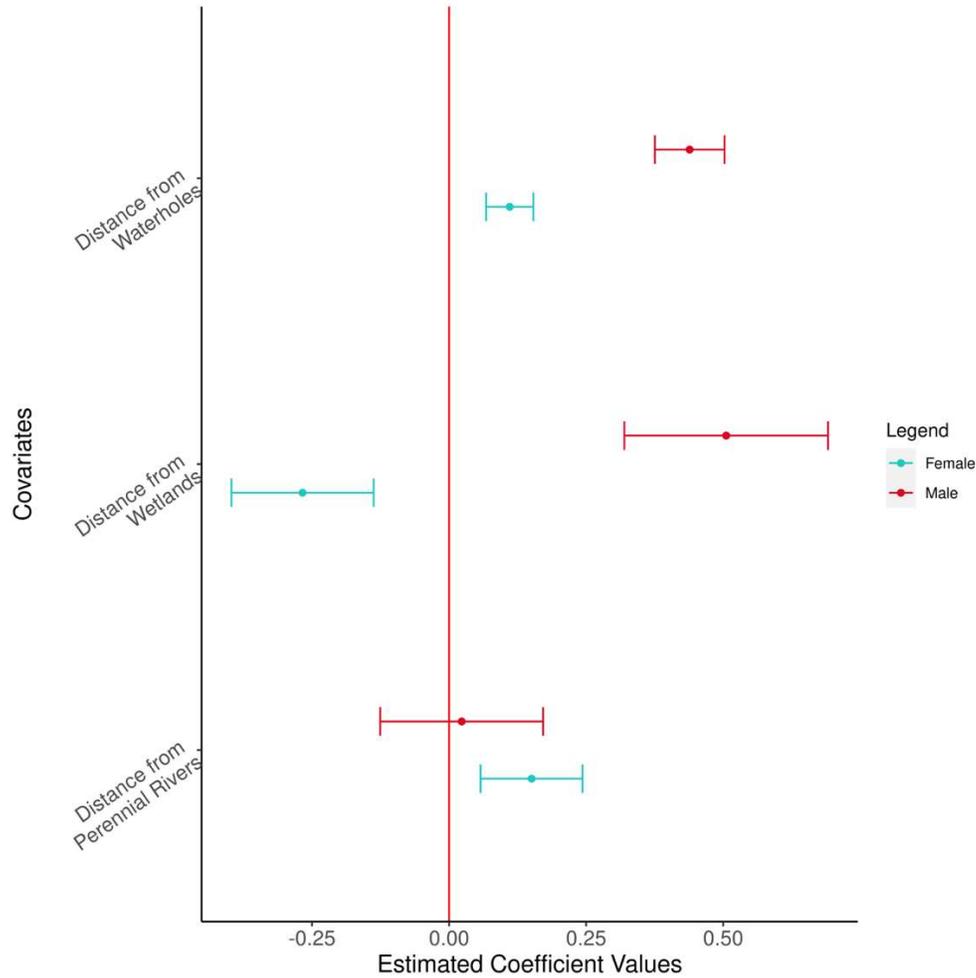
<b>Model names</b>	<b>K</b>	<b>BIC</b>	<b>Delta BIC</b>	<b>Model Lik.</b>	<b>BIC Wt.</b>	<b>LL</b>	<b>Cum. Weight</b>
Global	14.00	11590.17	0.00	1.00	1.00	-5727.12	1.00
Water	6.00	11609.23	19.06	0.00	0.00	-5775.49	1.00
Environment	8.00	11622.35	32.18	0.00	0.00	-5772.34	1.00
Human	8.00	11786.23	196.06	0.00	0.00	-5854.28	1.00
Geographic	7.00	11862.67	272.50	0.00	0.00	-5897.36	1.00

**Table S2.3.2:** Model selection table of the candidate model set evaluating the most parsimonious model to explain the difference between fast and slow corridor types for female elephants in the study.

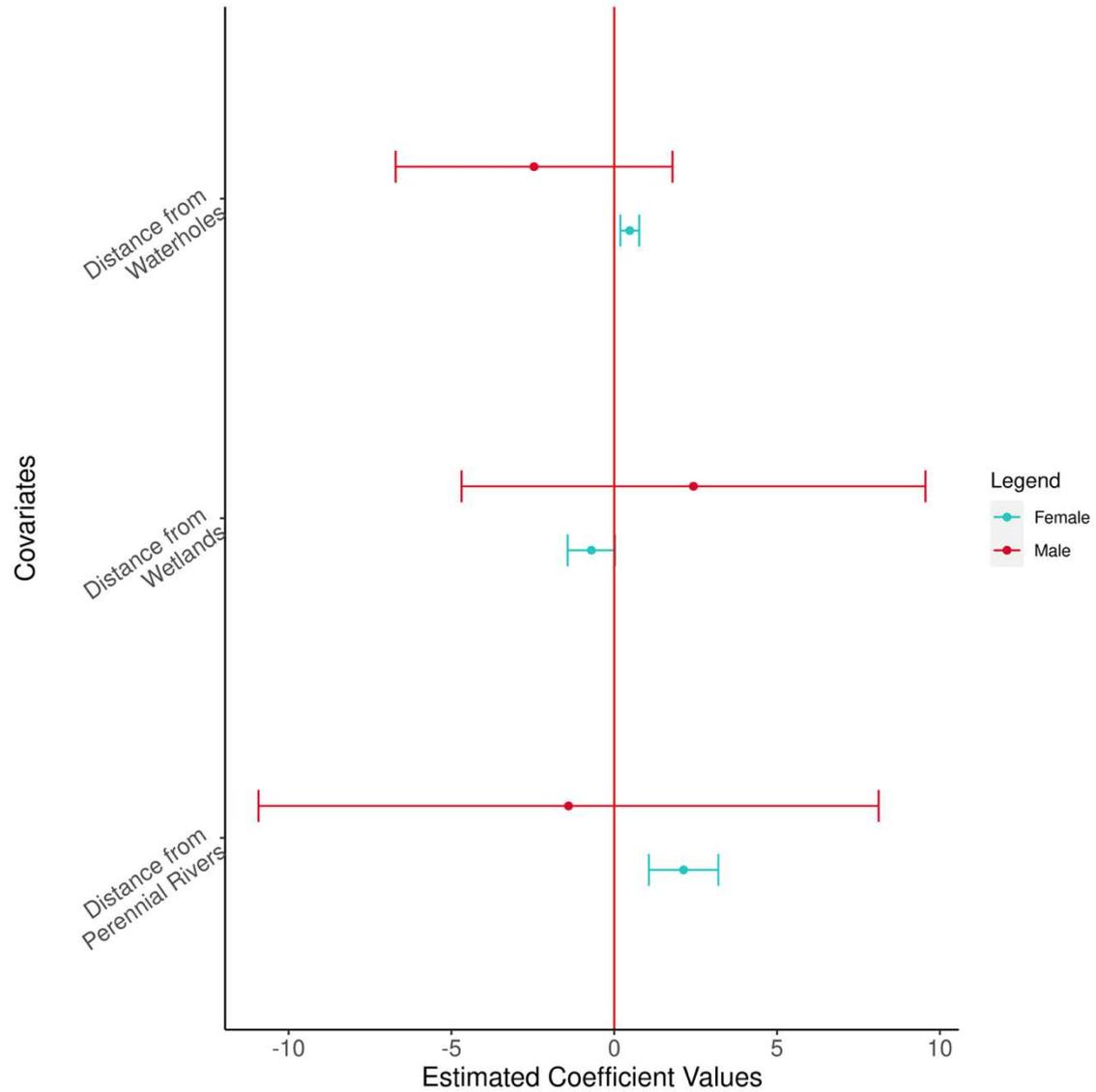
<b>Model names</b>	<b>K</b>	<b>BIC</b>	<b>Delta BIC</b>	<b>Model Lik.</b>	<b>BIC Wt.</b>	<b>LL</b>	<b>Cum. Weight</b>
Water	6.00	18022.90	0.00	1.00	0.92	-8981.34	0.92
Environment	8.00	18027.67	4.77	0.09	0.08	-8973.69	1.00
Geographic	7.00	18046.80	23.90	0.00	0.00	-8988.27	1.00
Human	8.00	18049.81	26.92	0.00	0.00	-8984.76	1.00
Global	14.00	18064.34	41.45	0.00	0.00	-8961.92	1.00



**Figure S2.1:** Subset of coefficient estimates, and associated confidence intervals from the best-performing model evaluating differences between high-use and low-use pixels for both males and females. The area under the curve (AUC) was 0.7378 and 0.6704 for males and females, respectively. Model structure was similar. High-use pixels on the landscape were negatively correlated with distance from waterholes, distance from towns and settlements, and cattle abundance for both male and female elephants, while slope and max NDVI values are positively associated with high-use pixels. Additionally, variation in productivity negatively impacts the use intensity of female elephants (i.e., the use intensity of a given pixel was low when it experienced high variability in productivity).



**Figure S2.2:** Subset of coefficient estimates, and associated confidence intervals included in the best-performing model for both males and females evaluating differences between hubs and corridors pixels. For male elephants the global model was the most parsimonious model with an AUC of 0.7891, while the environment model, containing variables describing distance from water sources and productivity metrics, had the lowest BIC value and AUC value of 0.7336 for females. All the covariates for both males and females behave similarly. Distance from wetlands, distance from perennial rivers, and max NDVI were positively correlated with hub pixels, while the distance from waterholes and coefficient of variation of NDVI are correlated with corridor pixels. In general, pixels with high productivity closer to waterholes are likely to be hubs for elephants.



**Figure S2.3:** Coefficient estimates, and associated confidence intervals included in the best-performing model (the water model) for both males and females evaluating differences between the highest-use and the second highest-use clusters. The water model was the best-performing model for both male and female datasets with AUC values of 0.999 and 0.995, respectively. Distance from waterholes and distance from perennial rivers were positively correlated with the highest-use clusters for females, while the distance from wetlands was negatively correlated. Both cluster types were similar for males.