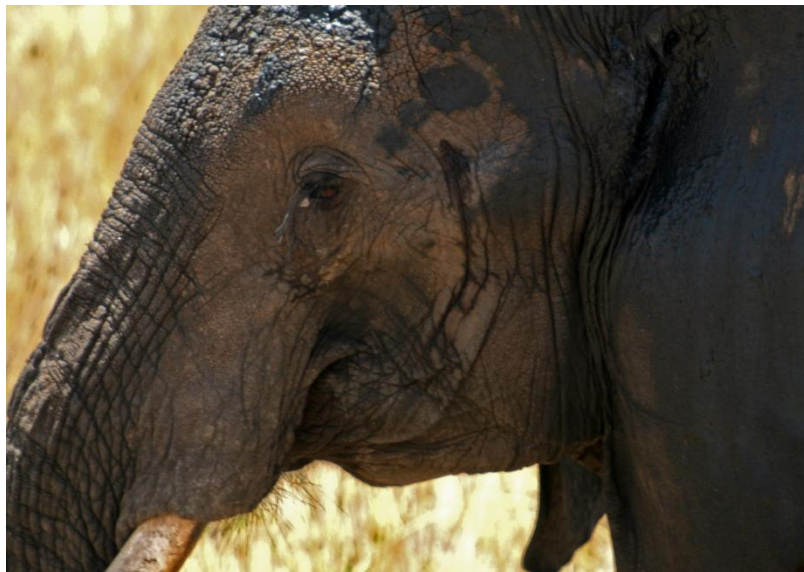




DEPARTMENT OF BIOLOGICAL AND
ENVIRONMENTAL SCIENCES

EFFECTS OF VEGETATION TYPES AND HUMAN BORDERS ON ELEPHANT HABITAT SELECTION

A study on male *Loxodonta africana* in northeast
Botswana



Anton Nyström

Biology: Bachelor's degree project

BIO603, Examination course in Biology, 30 credits

First cycle

Semester/year: Spring 2025

Supervisors: Søren Faurby, Department of Biological and Environmental Sciences

Kate Evans, Elephants for Africa & Department of Biological and Environmental
Sciences

Examinator: Catharina Olsson, Department of Biological and Environmental Sciences

Frontpage figure: elephant in Tarangire National Park, Tanzania. Photograph taken by Dennis Nyström.

Table of Contents

Abstract	2
Sammanfattning	2
Introduction	3
Background	3
Population status	3
Ecology	3
Human-elephant conflict.....	3
Objectives	4
Hypotheses	4
Methods.....	4
Study area	4
Data collection.....	6
Analysis	8
Results.....	9
Protected areas.....	9
Seasonal variation	9
Individual variation.....	10
Ecosystem utilisation.....	11
Seasonal variation	12
Individual variation.....	14
Leaf area index to presence ratio	14
Villages.....	15
Walking speed	15
Discussion	16
Protected areas.....	16
Ecosystem utilisation.....	16
Village presence	17
Walking speed	17
Conclusion	18
Acknowledgements	18
References	19
Attachments.....	21

Abstract

Botswana has reserved approximately a third of its area for wildlife protection and holds the largest amount of African savanna elephant (*Loxodonta africana*) out of any country. Even so, elephants' large ranges extend outside these areas, and may overlap with human settlements, causing potential conflict. The aim of this project was to determine what types of habitats male adult elephants prefer in different seasons regarding vegetation types and human borders, to establish when and where the risk of a human-elephant encounter is highest. Tracker collars recorded the GPS coordinates and speed of seven adult bulls every hour over 2.5 years, which was analysed by examining average speed and time spent in different ecosystems with leaf area index (LAI) values, protected areas and local villages. The results showed that during the wet season, the elephants roamed beyond protected areas, villages were generally avoided, and no particular ecosystems were preferred. During the dry season, individuals stayed almost exclusively inside protected areas, but villages were preferred when venturing outside them, and higher LAI ecosystems were preferred. It was concluded that attraction to high LAI areas was likely a consequence of the search for food, water and shade in combination. Walking speed was low in the ecosystem with the most time spent, suggesting that elephants deliberately spend time there. It was concluded that speed might depend on area protection level. No preference for villages was observed in wet season, but as only the season peak was included in the analysis, the height of crop raids may have been missed as crop harvest occurs after this period. As these results show what habitats elephants prefer, they may be used to reduce human-elephant conflict by decreasing encounter risk.

Sammanfattning

Botswana har åsidosatt ungefär en tredjedel av sin totala yta åt skyddad natur och landet innehåller det största antalet afrikans savannelefant (*Loxodonta africana*) i världen. Elefanter stora utbredningsområden sträcker sig utanför de skyddade områdena och in bland mänsklig bebyggelse, vilket potentiellt kan leda till konflikter. Målet med detta projekt var att avgöra vilka typer av habitat vuxna elefanttjurar föredrar i avseende på naturresurser och gränser dragna av människan, för att visa när och var risken för möte mellan människor och elefanter är som störst. Data på geografisk position och gånghastighet för sju vuxna elefanttjurar insamlades under 2,5 år med hjälp av spårarhalsband. Dessa jämfördes med olika sorters ekosystem med leaf area index (LAI), skyddade områden och byar. Resultaten för regnperiod visade att elefanter vistades utanför skyddade områden, undvek byar och hade ingen särskild preferens för någon typ av ekosystem. Under torrperiod befann sig elefanterna nästan helt och hållet innanför skyddade områden men föredrog byar när de vandrade utanför, samt föredrog ekosystem med högt LAI. Skälet till att områden med högt LAI var attraktiva var förmodligen tillgång till en kombination av mat, vatten och skugga. Gånghastighet var låg i ekosystemet där mest tid tillbringats vilket antyder att elefanterna avsiktligt tillbringar tid där. Det fastställdes att hastighet kan bero på områdets skyddsstatus. Byar var inte särskilt attraktiva under regnperiod, men eftersom skördetid infaller efter den definierade regnperioden kan den största andelen plundring av grödor ha missats i analysen. Eftersom resultaten i denna studie visar vilka habitat elefanter föredrar kan de användas för att minska antalet möten och konflikter mellan elefanter och människor.

Keywords:

Adult Bull, Human-Elephant Conflict, Protected Areas, Seasonality, Villages, Walking Speed

Introduction

Background

Population status

African savanna elephants (*Loxodonta africana*) are listed by the International Union for Conservation of Nature as endangered (IUCN, 2020.). According to the IUCN's latest status report, the total number of individuals in Africa is estimated to be around 415 000 and Botswana is the country that holds the highest number of individuals at circa 131 000 (Thouless et al., 2016). Southern Africa's collective elephant population declined by around 10% in the nine years between the report by Thouless et al. (2016) and the previous report. Botswana's population was a main contributor to the total reduction. Reasons for this decline include miscounting due to wider ranges and varying survey methods, as well as population reduction through poaching. Botswana holds responsibility for protecting a large fraction of elephants due to the high local number of individuals. The success of Botswana's conservation efforts thus have a great effect on the species' survival.

Ecology

African savanna elephants have significant effects on their surroundings and are thus considered a keystone species. They are strong enough to topple trees with relatively weak root systems and/or trunks, partly in search of food, but often as part of some kind of social display (Guy, 1976). Elephants are also responsible for increasing germination rate of seeds that pass through their guts, serving as "tree planters" (Lewis, 1987). Since these behaviours contribute to shaping the habitats the elephants inhabit, conserving the species is important for preserving their environment.

In addition to habitat shaping, another important attribute of African savanna elephants' behaviour is the size of the areas they utilise. About a third of Botswana's total land and inland water area is protected to some degree (UNEP-WCMC, 2025), but while protected areas are generally preferred due to the lack of humans, elephants' total ranges are much larger (Douglas-Hamilton, 2005; Graham, 2009). Since absolute protection of elephant habitats is not feasible, coexistence with humans is key to elephants' survival.

Elephants' preferred food sources vary between seasons. Most plants thrive during the wet season, giving elephants a range of options. At this time, grasses have high protein contents, making them a favoured food source (Guy, 1976; Sinclair, 1975). Dried plant material is however significantly less nutritious, meaning that elephants choose to adopt browsing behaviour as tree leaves overtake grasses as preferred food items during dry season (Buss, 1961), while the availability of grasses also diminishes. This habitat switch may not necessarily happen due to the food the trees provide, but the shade that protects them from the dry season's heat (Buss, 1961).

A measurement of elephants' preference for certain areas (such as those with few humans and bountiful resources) is walking speed, which can show whether elephants "stay" in an area or simply pass it. For example, higher walking speeds have been observed outside national parks, suggesting that those areas are obstacles to move through rather than the target destination (Douglas-Hamilton, 2005).

Human-elephant conflict

A main point of conflict is crop raiding, where elephants, bulls in particular, wander into fields to eat farmers' produce (Jackson et al., 2008). These raids result not only in potential physical harm to humans, but also economic damage (Jackson et al., 2008). Furthermore, elephants possess an intimidating presence and can even cause psychological harm to locals, who might hesitate to go outside and perform tasks and activities as they normally would when living near elephants (Mayberry et al., 2017).

While crop raiding is a well-known problem in human settlements close to protected areas, it has also been established that elephants avoid humans when possible to avoid unnecessary conflict (Graham, 2009). Areas with low levels of human activity are generally preferred, and individual elephants traveling outside protected areas have shown to assess the risk of human contact in certain areas and have thus adapted their roaming grounds (Graham, 2009).

It's been suggested that promoting dispersal of local elephant populations to other, less burdened areas might prove an effective method of decreasing conflict (Cushman et al., 2010). Since protected areas are preferred by elephants, development of protected wildlife corridors can ensure elephants' safe passage them.

Objectives

The aim of this study was to evaluate the preferred areas of adult male elephants in a region in northeastern Botswana. The area in question is relatively understudied; this project thus contributes to knowledge about habitat selection of bulls in this particular region. Preference for different ecosystems, protected areas and human settlements were be examined. For these factors, wet and dry seasons were compared since behaviour might vary with precipitation levels. Results were analysed to determine when and where elephants are most likely to appear and to estimate the risk of encounter and possible conflict with humans.

Hypotheses

For this project, I proposed the following hypotheses:

1. The elephants will spend more time within protected areas than outside, since it can be expected based on general elephant behaviour.
2. Grass should be a preferred diet during wet season when it is a rich food source, while trees and bushes are expected to be preferred during dry season, both due to leaves being a better nutritional option than dry grass, and to the temperature relief woodlands can provide through shade. Therefore, elephants should be expected to reside in areas with high tree canopy density during dry season, while areas with low tree canopy density might see more activity during wet season.
3. The elephants will deliberately visit human settlements, at least during dry season. Although elephants mostly avoid humans, drought might cause them to go to further lengths in search of food, as regular food sources are scarce. Local communities should thus experience more interactions with elephants during dry season than during wet season, when food is more abundant and there is no real reason to occupy human settlements.
4. Walking speed will generally be higher in unpreferred areas, either because the elephants simply pass through those areas in search for resources, or because they have a specific preference to spend as little time as possible in those areas. Again, unpreferred areas should be those with low tree density during dry season and high tree density during wet season.

Methods

Study area

The study was concentrated in a region in northeast Botswana, close to the border to Zimbabwe. The area in which the elephants were present was called the focus area, defined as the convex hull of all geographical points (i.e., a polygon that contains all coordinates measured from the

elephants). As different analyses utilised different subsets of points (dry/wet season points, for example), the focus area had a new definition for each analysis (i.e. the convex hull of those specific points). Areas visited by the elephants outside Botswana were removed from all analysis, since ecosystem definitions consistent with Botswana's were not attainable. The focus areas were used as the total area when calculating area fractions. Figure 1 shows the total focus area, i.e. the convex hull of all geographical points recorded regardless of season (about 26 000 km²).

Ecosystems defined by the Department of Environmental Affairs (DEA, 2022) using dominant tree species are displayed in figure 1 and later described in table 1. The protected areas were defined as the two national parks present in the study area: Nxai Pan National Park and Makgadikgadi Pans National Park, which cover a total of around 7 500 km². Both protected area and ecosystem polygons were downloaded through the ArcGIS online portal.

There were five villages in the focus area: three close to the border of the national parks and two further outside the parks (figure 1). The villages were identified through a report by Statistics Botswana (2022), and Google Maps images from 2023 were used to estimate their sizes.

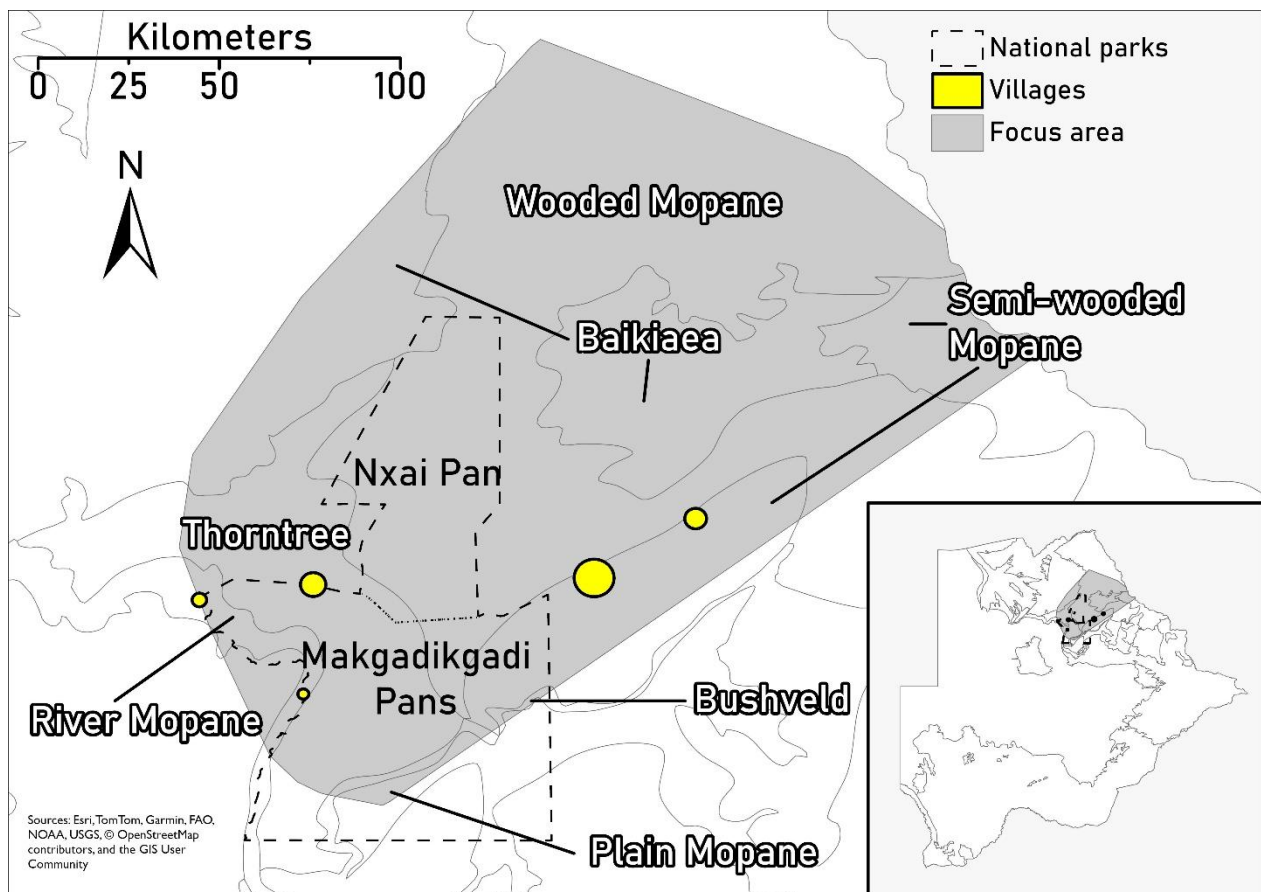


Figure 1. An overview of the study area, including national parks, total focus area, ecosystems and villages. The size of the village circles are determined by physical village size (they are to scale in the map), defined as the approximate area covered by buildings and crop fields. Ecosystem borders are defined using dominant and secondary tree species, dividing the focus area into chunks. Parts of the focus area outside Botswana's borders (north-east) are removed. The figure in the lower right corner shows where in the country the study takes place.

Data collection

Data on geographical position and walking speed were collected over a 2.5-year period (from August 16th, 2022 to April 17th, 2025) using African Wildlife Tracking, IR SAT (GPS/UHF) collars for elephants. Recordings were downloaded hourly, meaning that one geographical point represents one hour spent in that area, as it can be assumed that an individual will be in the vicinity of that point until the next measurement. Each point also contains data of the elephant's current speed.

These collars were fitted to 10 male adult (30+ years) African savanna elephants (*Loxodonta africana*) after sedation by tranquiliser (figure 2). A permit to do this was provided by Botswana's Ministry of Environment and Tourism, permit number ENT 8/36/4 XXXXIII (88). For this analysis I only used data from seven of the elephants as two individuals died in the middle of data collection, and one dropped its collar. Collar placement and data collection was carried out by the Botswana NGO Elephants for Africa.



Figure 2. The team at Elephants for Africa placing a collar on a sedated bull. Photograph by Kate Evans.

Subsets of the data that fall within the peaks of the dry and the wet seasons were created for seasonal analysis. In this context, the dry season is defined as the 90 days before the first rains of the wet season, and the wet season was defined as the 90 days preceding moderate rain. The weather data was sourced from Elephants for Africa's camp near the Khumaga entry gate of the Makgadikgadi Pans National Park by the Boteti River, at latitude -20.471, longitude 24.514.

Leaf area index (LAI) was used to estimate the variation in vegetation by calculating the average value for each ecosystem. LAI values describe the average number of "leaf layers" in a given area, i.e. a summary average thickness and density of tree canopies. An area with higher LAI contains more trees with thicker canopies, and vice versa. LAI will consequently be higher in wet

season for example, especially in areas with a lot of trees, due to the onset of rains allowing leaves to grow. The primary purpose of this was to provide clarity on the availability of shade and leaves as a food source in the peaks of the dry and wet seasons. LAI data from October 2019 (dry season peak) and February 2020 (wet season peak) were downloaded from European Union’s Copernicus Land Monitoring Service (2020).

When making analyses at dry season, only a subset of the measurements taken during the dry season peak, defined as the 90 days before first rain (late July to late October), was used. A similar subset of the measurements was made for the wet season peak, defined as 90 days following moderate rain (early December to early March). In the “general” analyses, data from the entire study period were used, i.e. data from the dry and wet season peaks plus data collected during the rest of the year.

As the ecosystem names were very long, they are henceforth referred to using the shortened names in table 1, which provides leaf area index (LAI) data that gives insight into each ecosystem’s basic vegetative structure. Dry LAI and wet LAI are the average values across the entire ecosystem in the respective seasons.

Table 1. Ecosystems in the focus area with basic descriptions based on dry and wet season LAI. Shortened names are also provided for simplification.

Ecosystem	Shortened name	Dry LAI	Wet LAI	Description
Baikiaea woodlands with <i>Pterocarpus angolensis</i> and <i>Baikiaea plurijuga</i>	Baikiaea	0.238	1.331	Forested
Bushveld with <i>Colophospermum mopane</i> and <i>Senegalia nigrescens</i>	Bushveld	0.219	0.957	Forested/grassy
Mopane woodlands with <i>Philenoptera nelsii</i> and <i>Terminalia sericea</i>	River Mopane	0.338	1.250	Forested (river)
Mopane woodlands with <i>Terminalia sericea</i> and <i>Adansonia digitata</i>	Plain Mopane	0.072	0.210	Grassy
Mopane woodlands with <i>Terminalia sericea</i> and <i>Combretum imberbe</i>	Semi-wooded Mopane	0.233	1.029	Forested/grassy
Mopane woodlands with <i>Vachellia nilotica</i> and <i>Combretum spp</i>	Wooded Mopane	0.260	1.393	Forested
Thorntree and deciduous woodland with <i>Senegalia mellifera</i>	Thorntree	0.176	0.914	Forested/grassy

Baikiaea, Bushveld and Thorntree are named after their corresponding dominant tree species. Mopane is a dominant species in several ecosystems; they are thus named with additional details: River Mopane is named after the Boteti River that the ecosystem surrounds at the western border of Makgadikgadi Pans National Park. Plain Mopane has low LAI value in both dry and wet season, indicating a grassy environment with low tree density. Wooded Mopane and Semi-

wooded Mopane are quite similar regarding LAI value, with Wooded Mopane having slightly higher tree canopy density than Semi-wooded Mopane.

Analysis

Most of the analytical work was performed in R, version 4.3.1 (Beagle Scouts), using the programme RStudio. Before analyses, the data were cleaned with readings outside Botswana removed (as ecosystems weren't defined in those areas), as well as measurements from before each individual first left a protected area (since data collection started when the elephants were in protected areas, they could not be considered to "select" for that area until they had the time to move elsewhere). Temporal gaps in the data were filled with artificial measurements (randomly selected copies of adjacent recordings) to ensure each reading represented one hour spent in the area.

By examining map data, the ecosystems the elephants preferred were determined, both when utilising protected areas and when venturing outside them. The number of geographical points (hours spent) per ecosystem were counted and then recalculated into fractions to be compared to the fractions of ecosystem area coverage, i.e. expected frequencies. This is later referred to as a usage concentration plot.

$$\frac{\text{Points in ecosystem}}{\text{Total points}} = \text{Ecosystem point fraction}$$

$$\frac{\text{Area in focus area covered by ecosystem}}{\text{Total focus area}} = \text{Ecosystem area fraction}$$

Just like the ecosystems, the utilisation of villages was estimated and compared to general utilisation of other areas outside protected areas and areas inside protected areas, i.e. usage concentration plots.

For all of these usage concentration plots, chi-square goodness-of-fit tests were made to examine whether there was a significant difference between the fraction of usage and fraction of area for each variable. The level of significance (α) was chosen as 0.05, meaning that p-values from test statistics below 0.05 indicate significance. Note that chi-square goodness-of-fit tests for these plots assumed that all points were independent and thus have incorrect test statistics, as the independent variable is not point but individual. The purpose of these tests was simply to determine whether selection is completely random or not as the test only would give non-significance if usage and area fractions were exactly the same.

The seasonal data subsets were used in tandem with other analyses to determine potential variations based on precipitation. Using the LAI data, the average value for each ecosystem during the dry and wet seasons was compared against the usage/area fraction ratio in a scatterplot, and a line of best fit was applied to identify any potential relationship between LAI and over/underutilisation. R^2 values show the relationship's strength: a large positive or negative value indicates a strong positive or negative relationship, while small values suggest that the relationship is weak.

$$\frac{\text{Ecosystem point fraction}}{\text{Ecosystem area fraction}} = \text{Usage/area ratio}$$

The average walking speed in each ecosystem was also calculated and then fitted into a linear mixed model (LMM) as a response, with ecosystem as a predictor and individual as a random effect to account for different walking speeds among the bulls.

$$\frac{\text{Sum of speed at all points in ecosystem}}{\text{Number of points in ecosystem}} = \text{Average speed in ecosystem}$$

Additionally, ArcGIS Pro version 3.5.2 was used as a tool to detect potential data errors, as well as for visualising and picturing data. ChatGPT with GPT-4 was used as a coding assistance tool.

Results

Protected areas

Figure 3 shows that nearly 80% of the total time (throughout the entire data collection period) was spent inside national parks. Preference for protected areas was strong considering that the parks only covered about 20% of the focus area, giving a usage/area ratio of around 4:1. Selection was non-random, $X^2(1) = 299395$, $p < 0.001$.

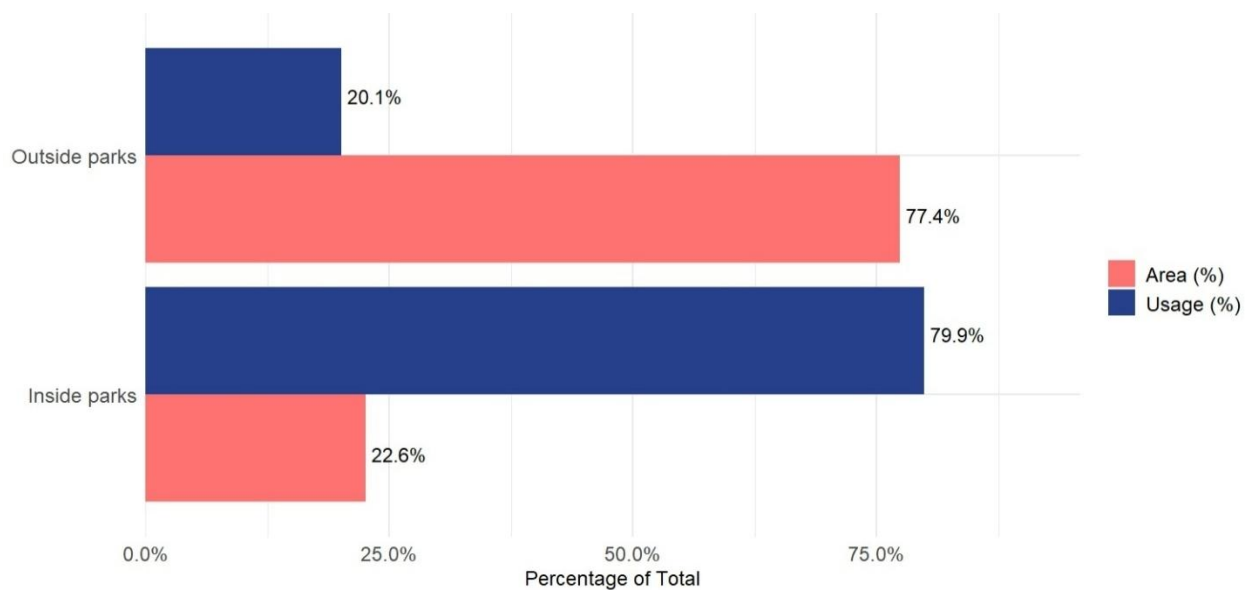


Figure 3. General (through the entire study period) usage of areas outside and inside national parks compared to the fraction of the focus area covered.

Seasonal variation

At dry season, preference for protected areas was even stronger, with over 95% of time spent inside national parks (figure 4a). The nearly as large area fraction (~93%) is due to the focus area being much smaller at this time, as the elephants very seldom went outside protected areas (see figure 7). Usage/area ratio was thus 1:1, meaning that selection for areas inside national parks was as expected. Selection was non-random, $X^2(1) = 609$, $p < 0.001$.

During wet season, time spent inside versus outside protected areas was nearly evenly distributed (figure 4b). Area fractions (~78% outside, ~22% inside) are similar what was generally observed during the entire study period in figure 3. Given the usage/area fraction of nearly 3:1, areas inside national parks were still preferred. Selection was non-random, $X^2(1) = 24405$, $p < 0.001$.

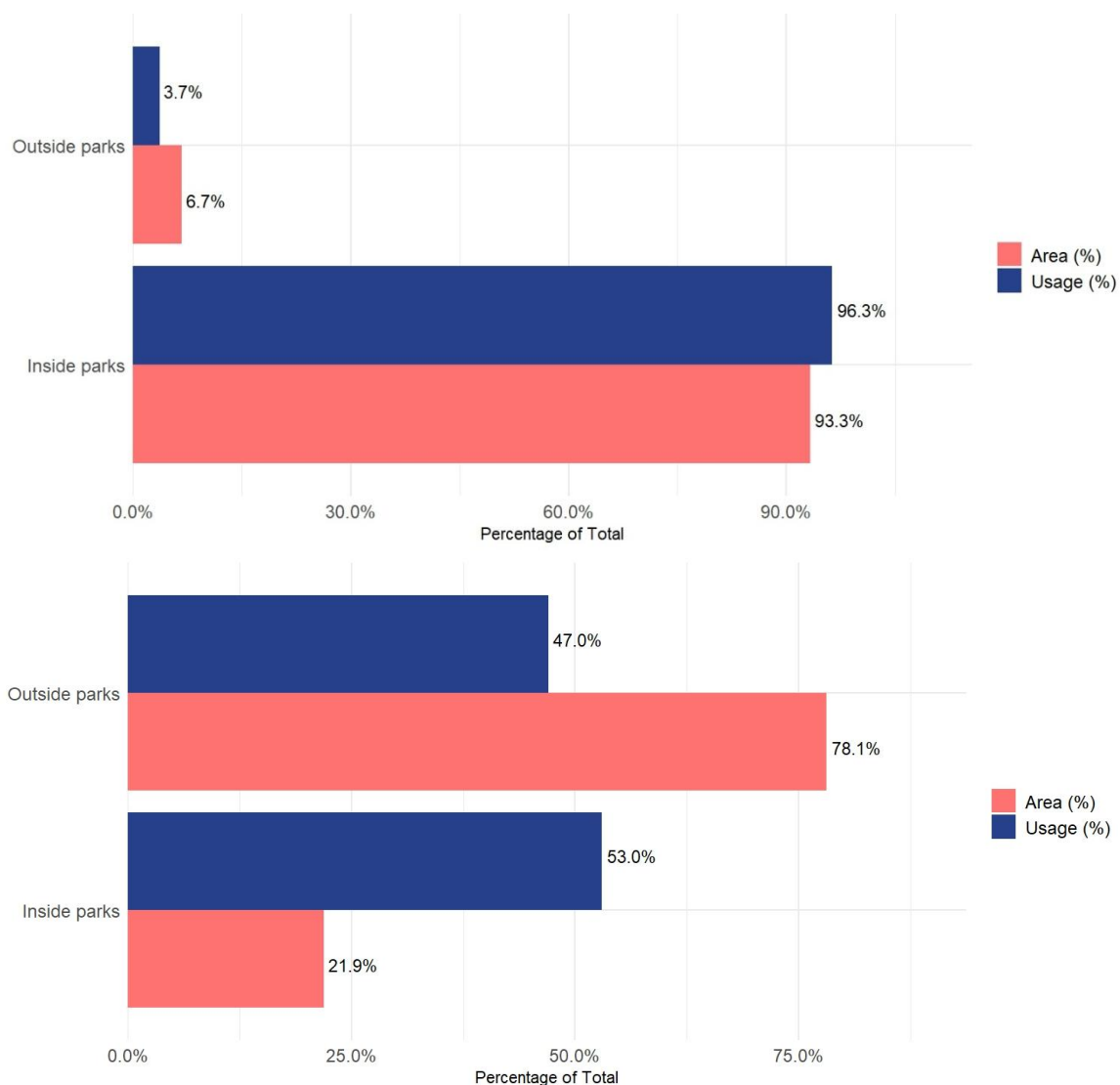


Figure 4a (top) and 4b (bottom). Dry (a) and wet (b) season usage of areas outside and inside national parks compared to the fraction of the focus area covered.

Individual variation

Usage/area plots for each individual are displayed in attachments 1–7. All of the bulls seemed to prefer protected areas. There was some variation in time spent outside protected areas; some individuals spent almost all their time inside protected areas while others wandered further outside. Table 2 show that selection was non-random for each individual.

Table 2. Chi-square goodness-of-fit tests for selection of national parks for each individual.

Individual	X ²	Degrees of Freedom	p-value
6207	36033	1	<0.001
6208	36069	1	<0.001
6210	2485	1	<0.001
6212	34346	1	<0.001
6213	7187	1	<0.001
6214	19158	1	<0.001
6216	16044	1	<0.001

Ecosystem utilisation

For the plots in figures 5, 6 and 8, the total area was drawn from areas inside and outside national parks together, meaning that the area fraction of an ecosystem represents how much of the total focus area that ecosystem covers. The same is true for the usage fractions in those plots.

Inside national parks, Thornrtree was the clear favourite with 50% of the time spent and over a 5:1 usage/area ratio (figure 5). Wooded Mopane and River Mopane also exhibited large usage fractions compared to their respective areas. Outside national parks, River Mopane was the only with a usage/area ration more than 1:1 (figure 5). A chi-square goodness-of-fit test was made, with the usage as observed frequency and area fraction as expected frequency. It showed that selection was non-random as the usage did not conform to what would be expected with the area coverage for each ecosystem, $X^2(12) = 521\ 036$, $p < 0.001$.

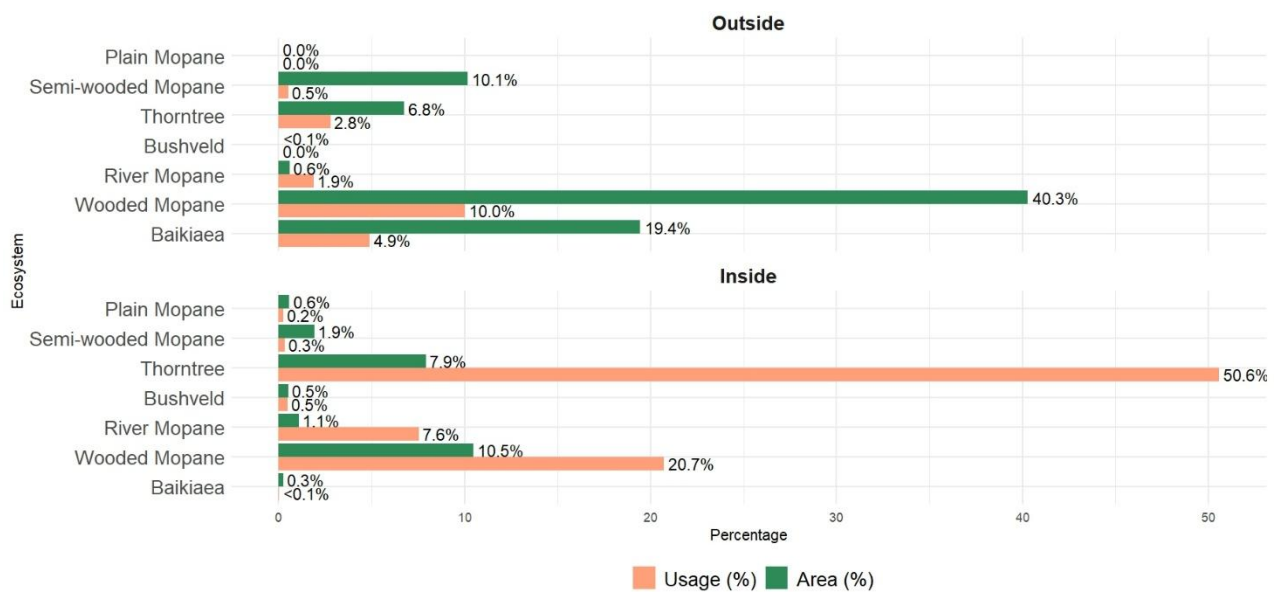


Figure 5. Comparisons between the fraction of usage and area coverage per ecosystem, split by outside/inside protected areas. The usage fractions can be viewed as observed frequency, and the area fractions as expected frequency. Usage is in this context the percentage of hourly coordinates measured in each ecosystem, i.e. the fraction of total time spent there.

Seasonal variation

Separate usage/area plots were made for the dry and wet seasons, respectively. During the dry season, most time was spent in Thorntree but it also covered the largest area so usage/area ratio was close to 1:1. Only River Mopane stands out as a selected ecosystem with a usage/area ratio of around 4:1, but this time only within protected areas (see figure 6). According to the chi-square test, selection was not random, $X^2(6)$, $p < 0.001$.

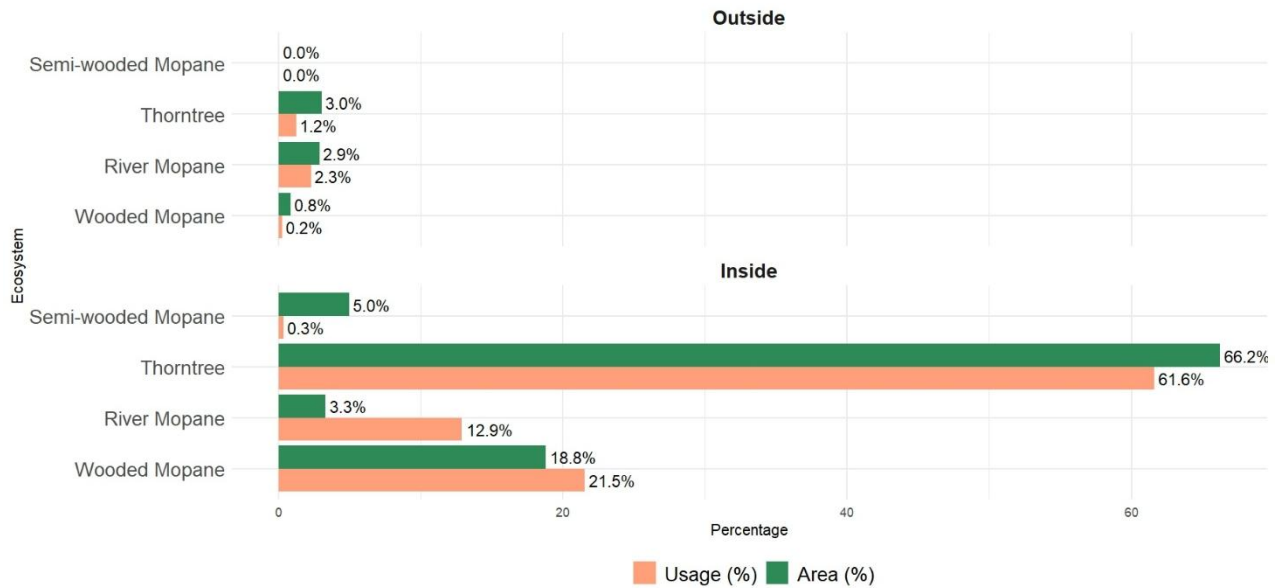


Figure 6. Dry season usage/area comparison.

Figure 7 displays the dry season focus area together with leaf area indexes for each ecosystem. The small focus area (2 193 km²) was nearly entirely within national parks.

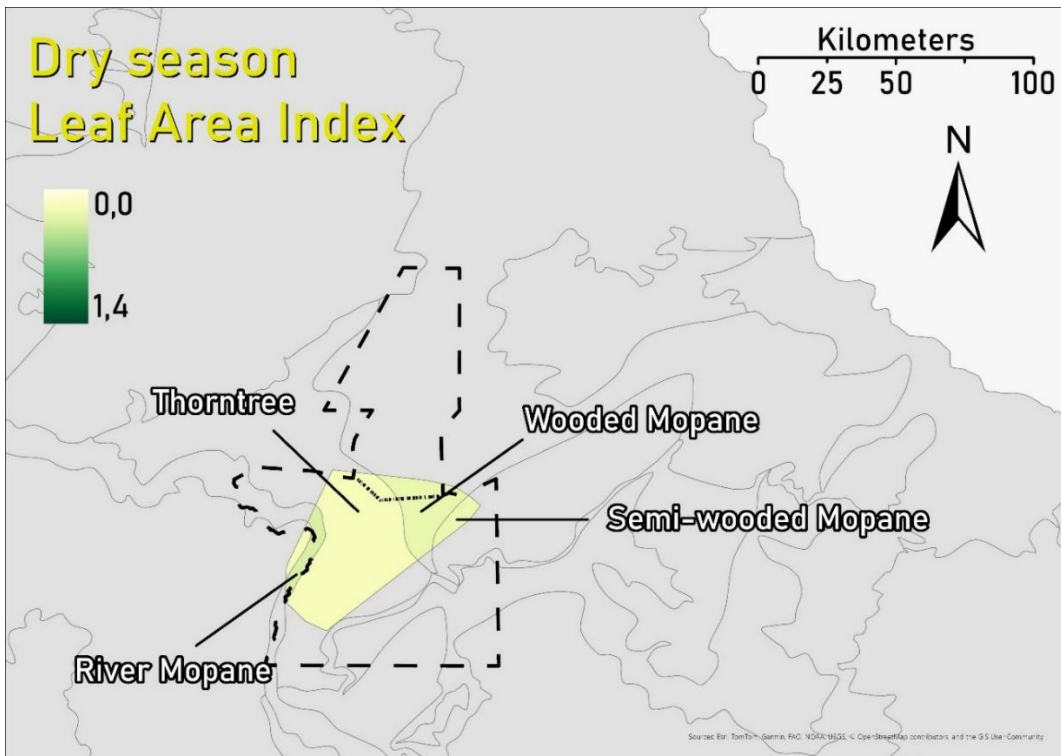


Figure 7. Dry season leaf area index map. The dashed line represents national parks.

At wet season, the elephants utilised much larger areas than at dry season (figure 9). As previously mentioned, this means more time spent outside national parks. There was however no preference for any ecosystem outside national parks. Inside national parks, Thorntree was clearly favoured with a usage/area ratio of almost 5:1 (figure 8). Selection was again non-random, $X^2(12) = 50376$, $p < 0.001$.

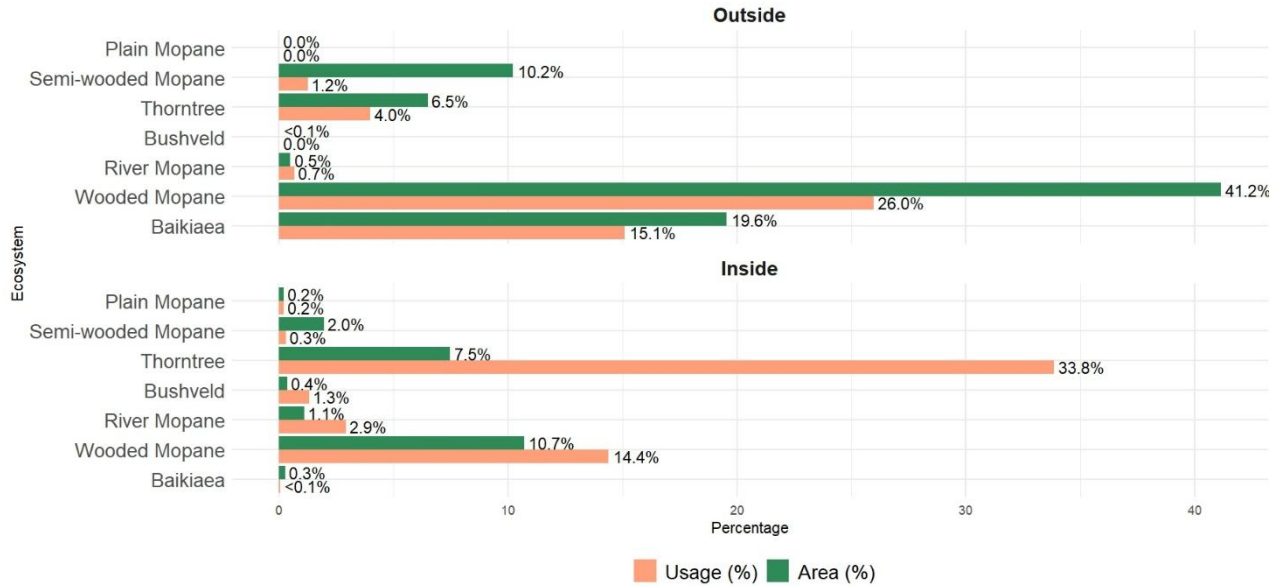


Figure 8. Wet season usage/area comparison.

The wet season map in figure 9 shows the much greater focus area (25 523 km²) and higher LAI values. Unlike during the dry season, the bulls ventured far outside protected areas.

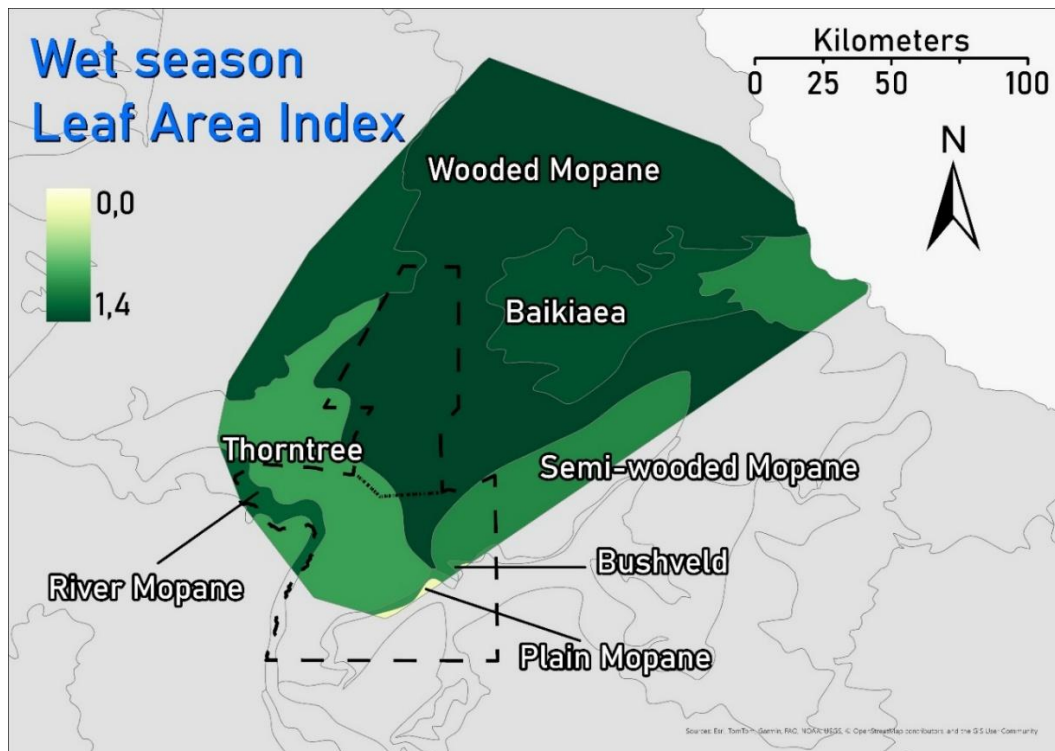


Figure 9. Wet season leaf area index map. The dashed line represents national parks.

Individual variation

Every individual showed selection for Thorntree and River Mopane inside protected areas, following the general pattern, while results for Wooded Mopane inside protected areas were mixed (attachments 8–14). Outside protected areas, ecosystem selection varied greatly, suggesting that bulls ventured in different directions. Chi-square test statistics (table 3) show that every individual, just like the total summary, had non-random selection.

Table 3. Chi-square goodness-of-fit tests for each individual, where the observed values are each individual's number of hours spent in each ecosystem, and the expected fractions are the area fractions of those ecosystems based on that individual's convex hull focus area.

Individual	X ²	Degrees of Freedom	p-value
6207	640 077	8	<0.001
6208	1 191 087	8	<0.001
6210	695 574	9	<0.001
6212	949 065	8	<0.001
6213	145 291	7	<0.001
6214	267 515	10	<0.001
6216	1 167 774	7	<0.001

Leaf area index to presence ratio

For the dry season, the usage seemed to increase with the ecosystem's LAI at a relatively high rate. A line of best fit was included together with its corresponding R² value. 0.567% of the variance is explained by the model (figure 10a). This relationship between the usage/area ratio and the average LAI was not observed at wet season, as the model gave the very small R² of 0.003 (figure 10b).

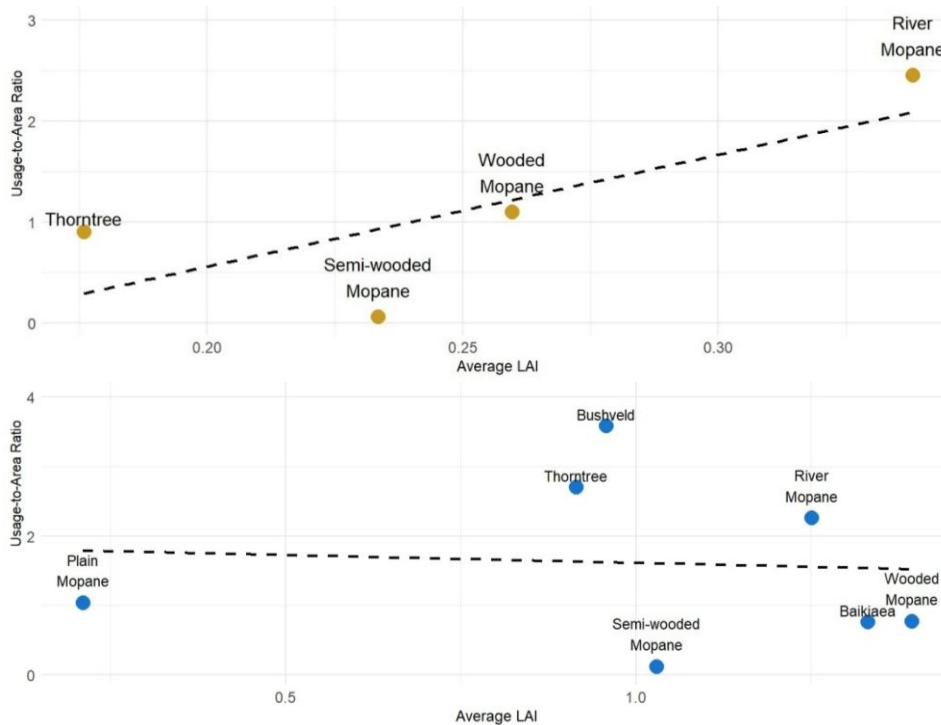


Figure 10a (top) and 10b (bottom). Scatterplots of the dry season (a) and wet season (b) ecosystems, where the average leaf area index is fitted on the x-axis, and the ratio between the usage and area fractions for those ecosystems fitted on the y-axis.

Villages

Preference for villages was summarised in usage/area plots. Attachment 15 shows that in general, villages seemed to be of no special interest, as the usage/area ratio was nearly 1:1 (0.4% usage, 0.5% area). A chi-square goodness-of-fit test gave evidence for non-random selection, $X^2(2) = 299\ 801$, $p < 0.001$. For the dry season, selection for villages seemed to be stronger compared to what should be expected given the area fraction with a usage/area ratio of 3:1 (0.6% usage versus 0.2% area), as seen in attachment 16. Selection was non-random, $X^2(2) = 1106.4$, $p < 0.001$. At wet season, villages did not look like they were selected for with a usage/area ratio of almost 1:3 (0.2% usage versus 0.5% area), shown in attachment 17. Selection was non-random, $X^2(2) = 24\ 464$, $p < 0.001$.

Usage/area plots for village selection were also made for each individual, see attachments 18–24. Between bulls, there was some variation in time spent near villages. Table 4 displays chi-Square goodness-of-fit tests for each individual, all of which showed non-random selection.

Table 4. Chi-Square goodness-of-fit tests for each individual's usage and area fractions outside/inside protected areas and villages.

Individual	X²	Degrees of Freedom	p-value
6207	36076	2	<0.001
6208	36070	2	<0.001
6210	2900	2	<0.001
6212	34399	2	<0.001
6213	7619	2	<0.001
6214	19245	2	<0.001
6216	16088	2	<0.001

Walking speed

Finally, the results of the LMM for the walking speed is displayed in table 5. A baseline ecosystem was chosen to show whether the elephants walked faster or slower than “normal”. Wooded Mopane was chosen as the baseline, since it covers the largest fraction of the total focus area, and can thus be reasonably considered the “average” ecosystem. The model suggested that walking speed was slightly higher for Baikiaea, Plain Mopane and River Mopane. Walking speed was moderately lower in Bushveld and Thorntree, and significantly higher in Semi-wooded Mopane. Given a level of significance at 0.05, the associated p-values indicated relatively strong significance for the difference between Wooded Mopane/Semi-wooded Mopane and Wooded Mopane/Thorntree, at 0.002 and 0.006, respectively (table 5). In summary, there was strongly significant evidence that the elephants moved slower in Semi-wooded Mopane and faster in Thorntree. The random effect of individual explained some of the variance (0.016), but most of it was residual (0.029).

Not every individual ventured into every ecosystem. Therefore, each individual's walking speed was plotted to spot any outliers that could have skewed the random effect results. No striking outliers were found based on these plots, although variation was present for several ecosystems. Speed was consistently lower in Thorntree and higher in Semi-wooded Mopane compared to the baseline (attachments 25–31).

Table 5. Fixed effects of the LMM for walking speed. The number in parentheses show the difference between the ecosystem's speed and the baseline. The level of certainty for the differences are given by the associated p-values.

Ecosystem	Average walking speed (km/h)	p-value
Wooded Mopane (baseline)	0.67	<0.001
Baikiaea	0.84 (+0.17)	0.095
Bushveld	0.45 (-0.22)	0.142
Plain Mopane	0.53 (+0.14)	0.340
River Mopane	0.77 (+0.10)	0.269
Semi-wooded Mopane	1.06 (+0.39)	0.002
Thorn tree	0.40 (-0.28)	0.006

Discussion

This study's results have shown that adult elephant bulls prefer protected areas, especially during dry season but also during wet season. Preference for protected areas at dry season can be explained by the high tree canopy density in an ecosystem in one of the national parks. At wet season it did not seem to matter whether an area has a relatively high or low tree density, as the bulls showed no particular preference for either alternative. Rather than tree density, preference for protected areas during wet season can be explained by convergence to and from these areas as the seasons change. Villages were preferred at dry season but not at wet season. Walking speed seemed to be lower in one preferred ecosystem, but results for other ecosystems were difficult to interpret.

Protected areas

My first hypothesis, stating that protected areas would be preferred, can be confirmed as true. Nearly 80% of the total time was spent inside protected areas, which matches results of previous research (Douglas-Hamilton, 2005; Graham, 2009). This pattern was especially pronounced at dry season, during which elephant ranges have shown to decrease, as suggested by Chamaille-Jammes (2008). The bulls explored areas outside the national parks at wet season, which coincides with conclusions from other papers claiming that bulls spread out during the rains when resources are abundant (Wittemyer, 2001; Osborn & Parker, 2003).

Ecosystem utilisation

During dry season, elephants can be expected to travel to woodier areas and switch to a browsing diet. However, the attraction to trees might be a result of other environmental factors, such as heat relief in the form of shade (Buss, 1961). There's also reason to consider that permanent water sources, such as the Boteti River, also are attractive features of the dry season focus area. Elephants gather around permanent water sources during dry season (Wittemyer, 2001) and, according to Chamaille-Jammes (2008), their effective range at periods of drought can shrink to within a few kilometres of permanent water sources. The elephants' small ranges at dry season in this study matches the conclusions of these papers. Douglas-Hamilton (2005) also mentions that elephants tend to prefer specific vegetative-rich regions close to rivers within protected areas, similar to this study's implications. Conclusively, attraction to woody areas could be due to some combination of food, water and shade. Whatever the reason for targeting woody areas, the study's results reflect previous research, as elephants seemed to have a slight preference for ecosystems with higher LAI values. This result is logical since LAI values in are by necessity high near water, as it allows trees to grow leaves which in turn provides shade. The aforementioned

relationship between LAI and usage is however determined with little certainty since there only were four ecosystems available for analysis during the dry season.

During wet season however, the elephants showed no particular preference for either high or low LAI ecosystems. Other research shows that African savanna elephants adapt to grazing during wet season as they exhibit a preference for grass in their diet (Guy, 1976). This is likely due to the high protein content in green grass compared to dried plant material (Sinclair, 1975). While grassier areas with lower LAI such as Plain Mopane can be expected to be preferred given the concentration of highly nutritional food items, other ecosystems should also have grasses present in addition to species of trees and bushes. There might therefore be a limit to how dense patches of grass need to be in order to qualify as an ecosystem preferred by elephant bulls.

The second hypothesis was thus partly supported by the study's results. As though, areas with low tree canopy density (LAI) were attractive at dry season, but there wasn't any preference for high or low tree canopy density at wet season. Note that these patterns would be even more pronounced had the total focus area been used for comparison, instead of the redefined dry and wet season focus areas.

Village presence

The risk of crop raids can vary greatly depending both on when the produce ripens and how abundant other food sources are (Chiyo et al., 2005). The wet season features comparatively low village interactions, suggesting that wild resources are sufficient enough that local crops are not worth the effort at that time. However, crop raiding frequency increases steadily from January and is highest during the harvest of crops in March–April (Stevens, 2018). This is right after the defined wet season peak, meaning that the most crop raids might be unrepresented in the current analysis for the wet season. Usage fraction within villages during dry season was about three times larger than what would be expected at random area selection. This interaction is especially noteworthy given the elephants' limited range at drought. Village presence could be explained by search for food as natural sources are scarce, but human–elephant competition for water sources might also contribute to risk of conflict (Jackson et al., 2008). Conclusively, the third hypothesis can be confirmed as true, but with some uncertainty.

Crop raid frequency has also been shown to increase with age and also increases if another older male is present (Chiyo et al., 2012; Stevens, 2018). As this study handled males over the age of 30, presence inside villages could be expected to be higher than with younger bulls. Moreover, crop raids are largely performed by “problem elephants” with more aggressive tendencies (Hoare, 1999). Thus, knowing studied individuals' behaviour is a pivotal factor for determining the risk of conflict. The results showed that there's some variation between bulls in this facet; elephants 6210, 6213 and 6214 spent noticeably more time in or near villages than the others. It is however difficult to ascertain whether this difference qualifies as deviant “problem elephant” behaviour or if it's a product of chance. A random selection of seven or more other bulls may produce noticeably different results than what was found in this study, especially if males of other ages were studied. Nevertheless, behavioural tendencies vary between elephants. Therefore, other methods, such as individual or village monitoring, may be more efficient in this matter.

Walking speed

Results from the LMM show that the random effect (individual) explains some of the variance in the model, but most can be explained by residuals. Therefore, elephants have somewhat different speeds, but the difference is not enough to discredit the results from the model's fixed effects. When compared to the baseline, walking speed in Bushveld and Thorntree was lower and could thus be considered to be preferred ecosystems, as it suggests that the frequent usage represents willingness to remain in the area and not just an obstacle to pass through to reach other ecosystems. Wooded Mopane also seems like a relatively “slow” ecosystem since most other

ecosystems show a higher walking speed. Thorntree and Wooded Mopane walking speed correlates well with the usage inside national parks, as they were preferred in that aspect as well. Bushveld was neither selected for nor against, but it is of note that both Bushveld and Thorntree are entirely or largely situated inside national parks, respectively. Douglas-Hamilton (2005) found that elephants crossing unprotected areas tend to move faster, potentially as a way to avoid dangerous territory. Consequently, they can be expected to move slower inside safer areas like national parks, which can be partially deducted from this study's findings. Walking speed was the highest in Semi-wooded Mopane. Most of the ecosystem is outside protected areas. Baikiaea in its entirety is outside national parks and walking speed was somewhat higher there when compared to the baseline. These correlations could be a result of the aforementioned "streaking" behaviour Douglas-Hamilton (2005) describes, but no solid conclusions about the causalities of walking speed can be made with the current data. It is, however, possible to determine with relatively high certainty that Thorntree is likely an attractive ecosystem type, as it had a high usage fraction in addition to having the lowest average walking speed. The fourth hypothesis can thus be confirmed for one ecosystem, but the relationship between walking speed and preference is difficult to determine for other ecosystems.

Conclusion

In total, nearly 80% of the time was spent inside protected areas. At wet season, elephants showed no particular interest in low or high LAI ecosystems, as most ecosystems likely contained sufficient resources. Ecosystems with high LAI values were preferred at dry season, probably because of food, water, and shade availability. Elephants spread out and moved outside protected areas while avoiding human settlements during wet season. Ranges shrunk substantially during dry season, keeping the elephants nearly exclusively inside protected areas, but villages were preferred when moving outside protected areas. It was concluded that dry season village presence was caused by search for food and/or water, and that the sufficient natural resources caused the lack of village presence at wet season. However, it was also noted that peak crop raiding times occur after the defined wet season and may have been missed in the analysis. Individuals showed some variation in village presence. Individual walking speed was low in Thorntree, an ecosystem that the elephants spent the most time in in relation to its area coverage. It was thus concluded that Thorntree was an attractive ecosystem, likely due to it largely overlapping protected areas. Walking speed varied between individuals in most ecosystems.

Acknowledgements

First of all, I want to offer my sincere thanks to my fantastic supervisors. Without Kate and her team at Elephants for Africa, this project would not be possible. I'm very happy that you accepted me as a student so I could learn so much about these incredible creatures. I'm also grateful that Søren could act as a supervisor on such short notice, you've offered great guidance on writing and conducting analyses. This paper would not be nearly as good without your advice. Additionally, I want to thank Luc Bussière, who aided me in search of projects and introduced me to Kate.

I'm incredibly grateful for my mum, dad and sister for supporting me in life. You are the best family I could ask for. I love you!

I'd like to acknowledge my fellow biologists and peers of other degrees. I'm truly lucky to have such good friends who offer consultation and encouragement in our common endeavours.

And finally, I'm thankful for my love Ella, who I never would have met had I not decided to study biology. I'm so blessed to have you in my life.

References

- Buss, I.O. (1961). Some Observations on Food Habits and Behavior of the African Elephant. *The Journal of Wildlife Management*, 25(2), 131–148.
- Chiyo, P.I., Cochrane, E.P., Naughton, L., Basuta, G.I. (2005). Temporal patterns of crop raiding by elephants: a response to changes in forage quality or crop availability?. *African Journal of Ecology*, 43(1), 48–55. <https://doi.org/10.1111/j.1365-2028.2004.00544.x>
- Chiyo, P.I., Moss, C.J., Alberts, S.C. (2012). The Influence of Life History Milestones and Association Networks on Crop-Raiding Behavior in Male African Elephants. *PLOS ONE* 7(2). <https://doi.org/10.1371/journal.pone.0031382>
- Cushman, S.A., Chase, M., Griffin, C. (2010). Mapping Landscape Resistance to Identify Corridors and Barriers for Elephant Movement in Southern Africa. *Spatial Complexity, Wildlife Informatics, and Wildlife Conservation*. Springer.
- Department of Environmental Affairs (DEA) (2022). *Botswana Ecosystem Types Protection Levels and Threat Status MBP2 2021 WGS84*. ArcGIS Online Portal. Sourced 2025-05-19 from <https://www.arcgis.com/home/item.html?id=7ed236ef0d4e43498623207b3e3aa3ee>
- Douglas-Hamilton, I., Krink, T., Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften*, 92, 158–163. <https://doi.org/10.1007/s00114-004-0606-9>
- European Union's Copernicus Land Monitoring Service information (2020). *Leaf Area Index 1999-2020 (raster 1 km), global, 10-daily – version 2*. Sourced 2025-07-02 from <https://land.copernicus.eu/en/products/vegetation/leaf-area-index-v2-0-1km>
- Graham, M. D., Douglas-Hamilton, I., Adams, W. M., Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12(5), 445–455. <https://doi.org/10.1111/j.1469-1795.2009.00272.x>
- Guy, P.R. (1976). The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area, Rhodesia. *South African Journal of Wildlife Research*, 6(1), 55–63.
- Hoare, R. E. (1999). Determinants of human–elephant conflict in a land-use mosaic. *Journal of Applied Ecology*, 36(5), 689–700. <https://doi.org/10.1046/j.1365-2664.1999.00437.x>
- IUCN (International Union for Conservation of Nature). (2020). *African Savanna Elephant*. IUCN Red List of Threatened Species. Sourced 2025-07-17 from <https://www.iucnredlist.org/species/181008073/223031019>
- Jackson, T.P., Mosojane, S., Ferreria, S.M., van Aarde, R.J. (2008). Solutions for elephant *Loxodonta africana* crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx*, 42(1), 83-91. <https://doi.org/10.1017/S0030605308001117>
- Lewis, D. M. (1987). Fruiting Patterns, Seed Germination, and Distribution of *Sclerocarya caffra* in an Elephant-Inhabited Woodland. *Biotropica*, 19(1), 50–56. <https://doi.org/10.2307/2388459>
- Mayberry, A.L., Hovorka, A.J., Evans, K.E. (2017). Well-Being Impacts of Human-Elephant Conflict in Khumaga, Botswana: Exploring Visible and Hidden Dimensions. *Conservation and Society* 15(3): 280-291. DOI: 10.4103/cs.cs_16_132
- Osborn, F.V., & Parker, G. E. (2003). Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. *African Journal of Ecology*, 41(1), 68–74. <https://doi.org/10.1046/j.1365.2028.2003.00413.x>

Sinclair, A.R.E. (1975). The Resource Limitation of Trophic Levels in Tropical Grassland Ecosystems. *Journal of Animal Ecology*, 44(2), 497–520. <https://doi.org/10.2307/3608>

Statistics Botswana. (2022). *Population of Cities, Towns and Villages* (version 2).

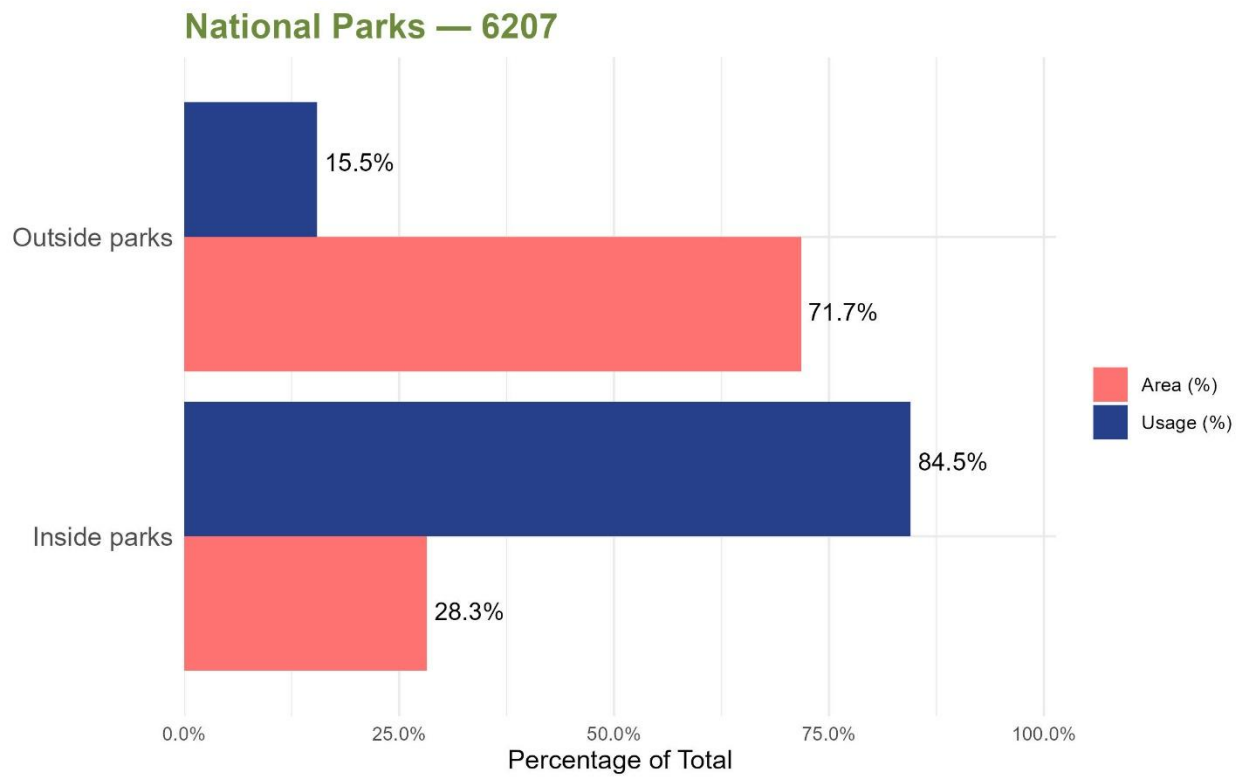
Stevens, J. (2018). *Understanding human-elephant interactions in and around Makgadikgadi Pans National Park, Botswana* [PhD]. University of Bristol.

Thouless, C.R., Dublin, H.T., Blanc, J.J., Skinner, D.P., Daniel, H.T., Taylor, R.D., Maisels, F., Frederick, H.L., Bouché, P. (2016). *African elephant status report 2016*. IUCN.

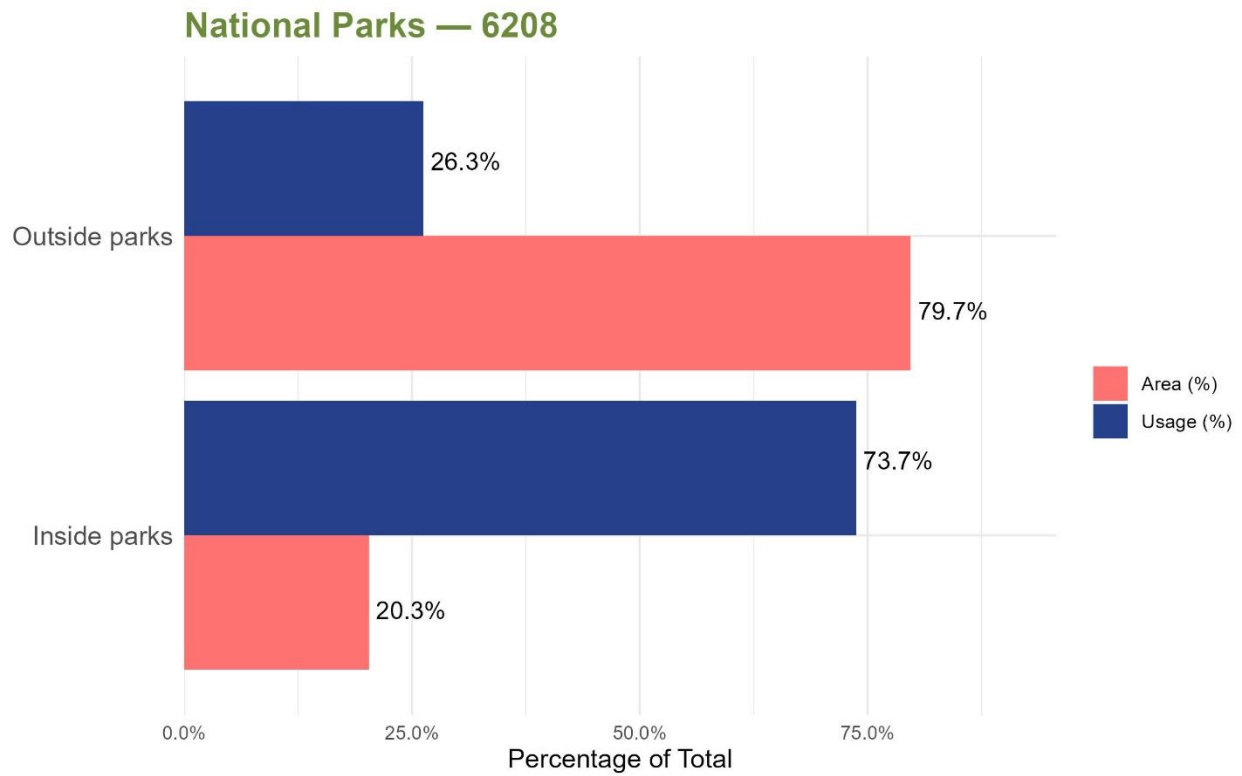
United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) (2025). *Protected Area Profile for Botswana from the World Database on Protected Areas*. Protected Planet. Sourced 2025-08-19 from <https://www.protectedplanet.net/country/bwa>

Wittemyer, G. (2001). The elephant population of Samburu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology*, 39(4), 357–365. <https://doi.org/10.1046/j.1365-2028.2001.00324.x>

Attachments

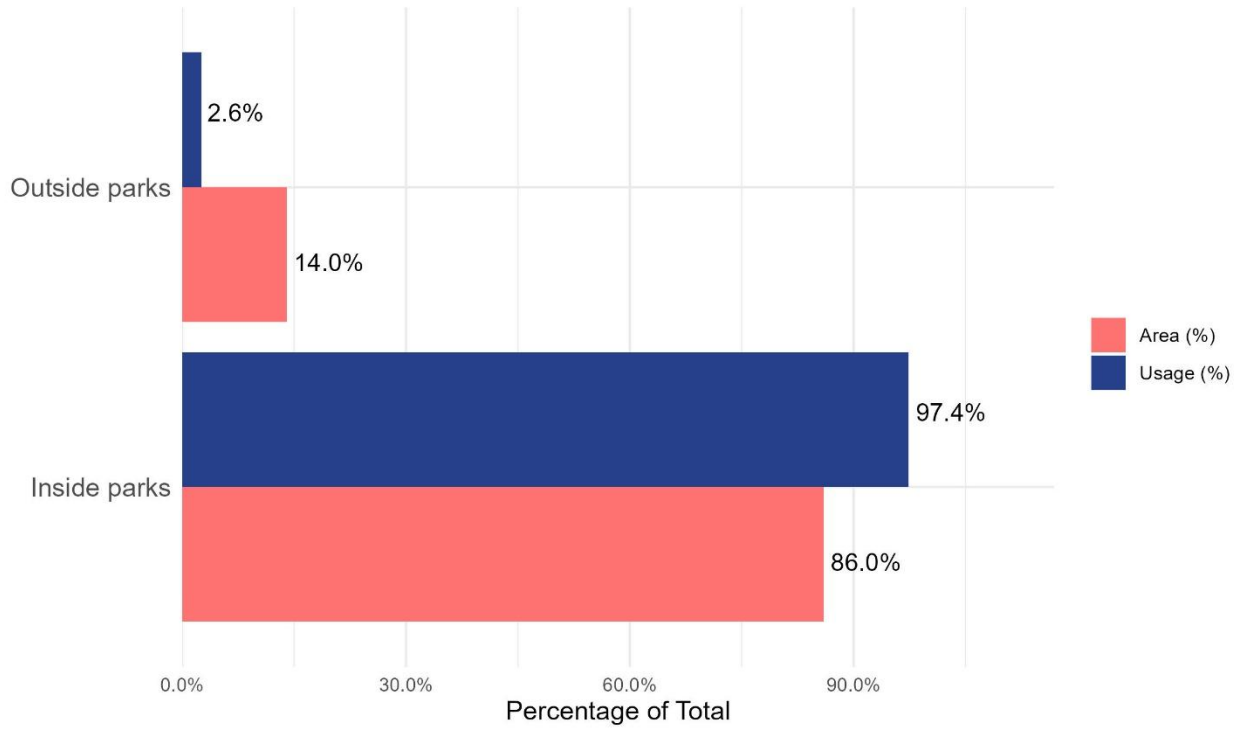


Attachment 1.



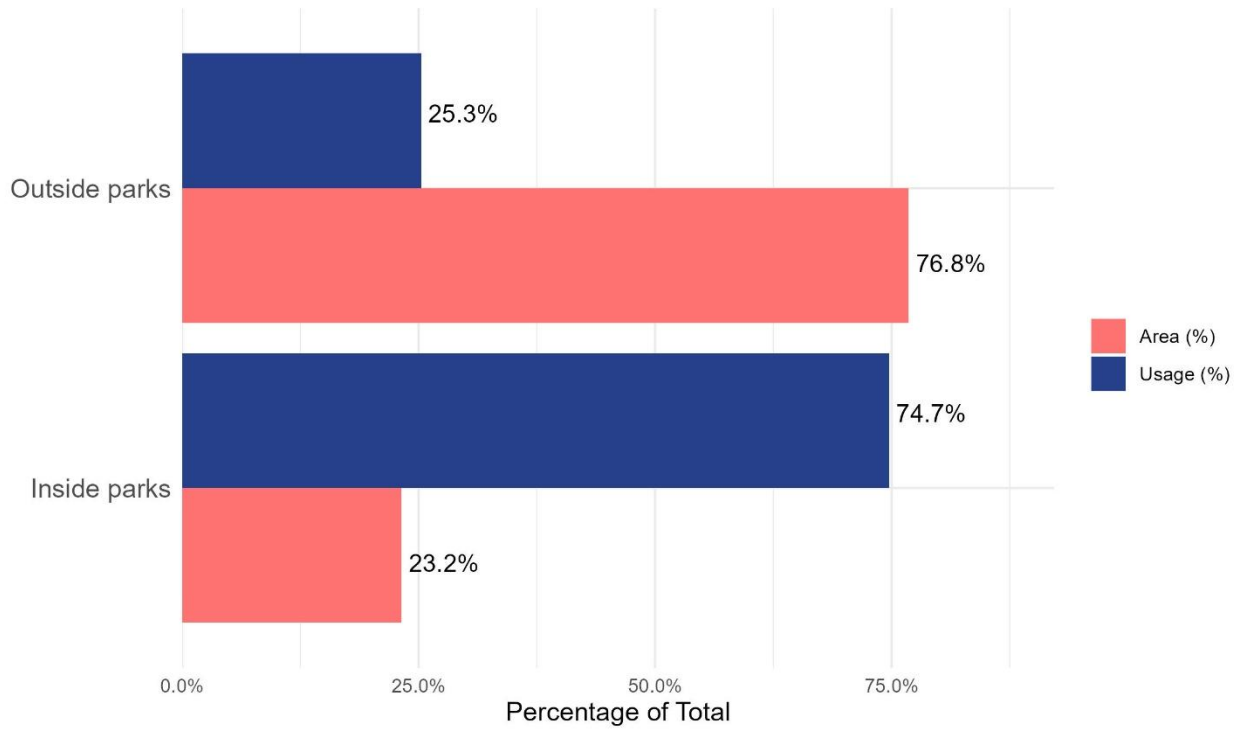
Attachment 2.

National Parks — 6210



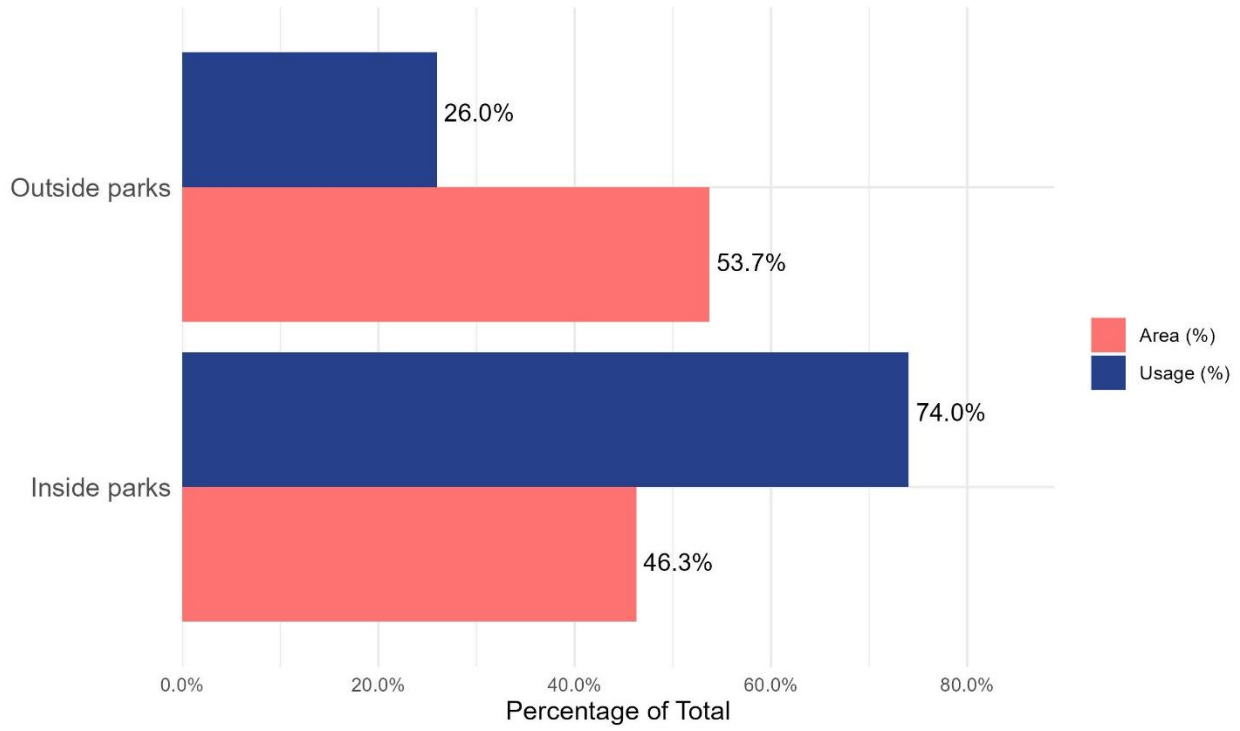
Attachment 3.

National Parks — 6212



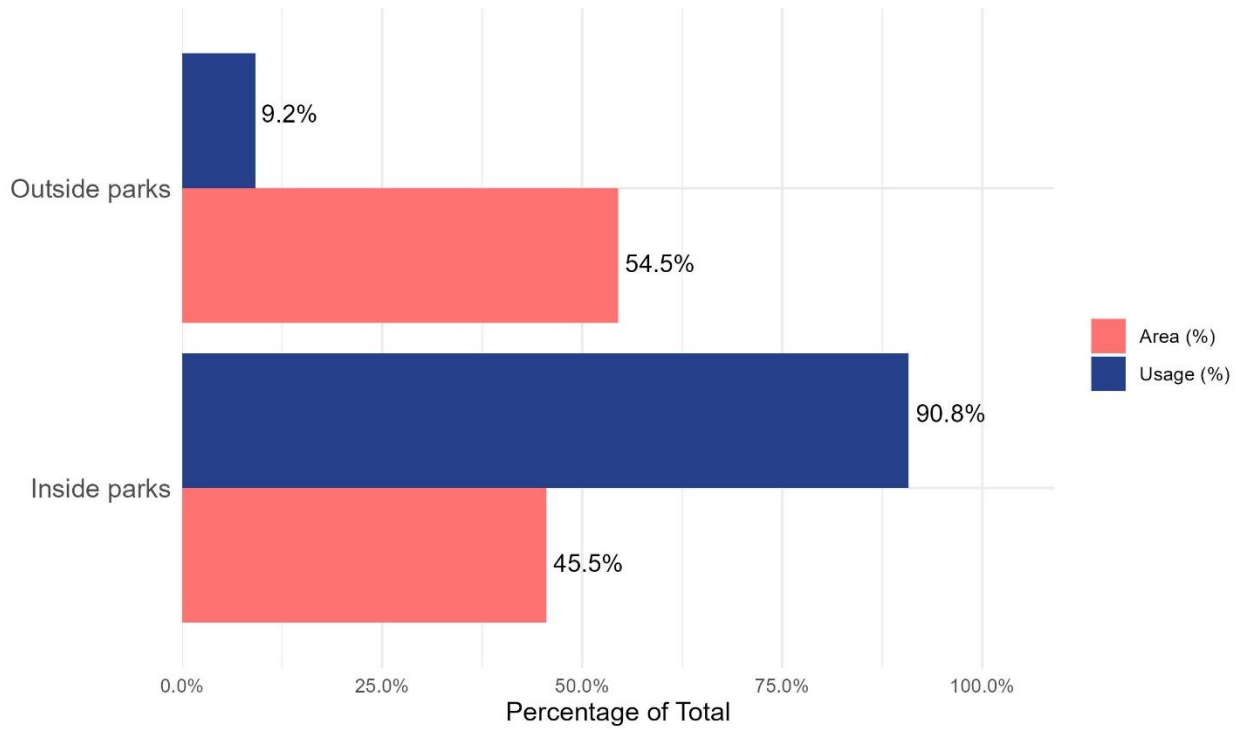
Attachment 4.

National Parks — 6213



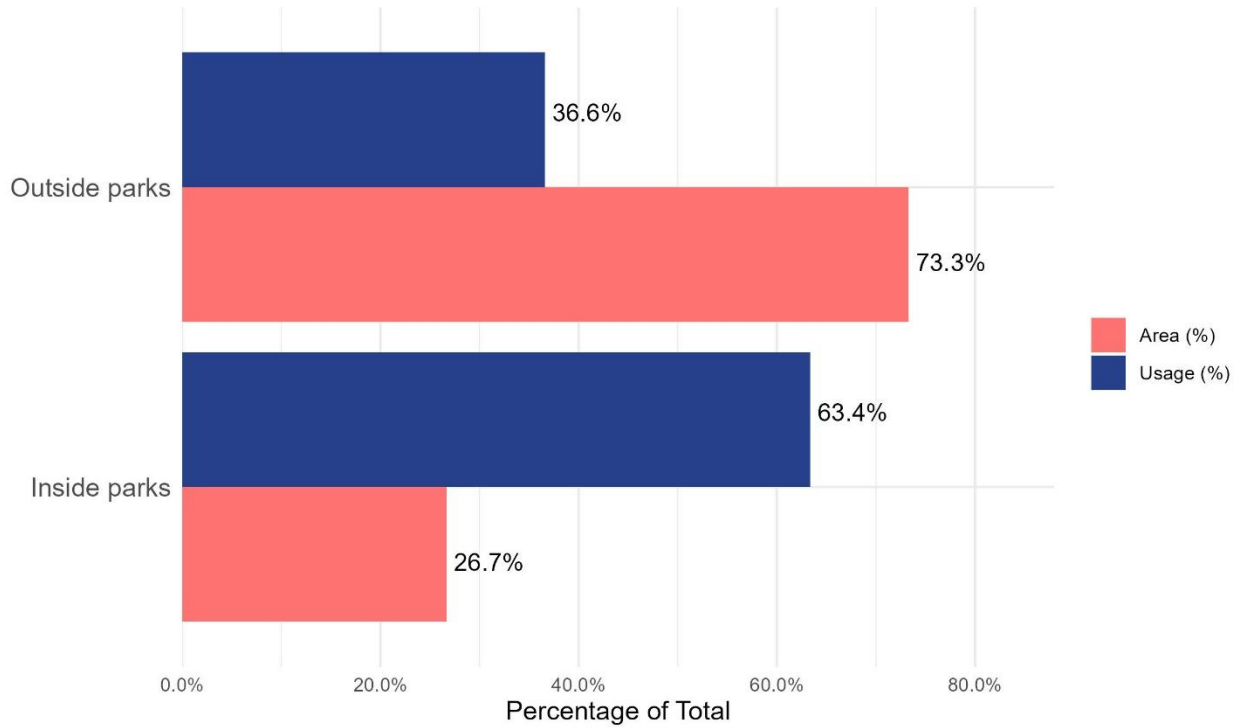
Attachment 5.

National Parks — 6214



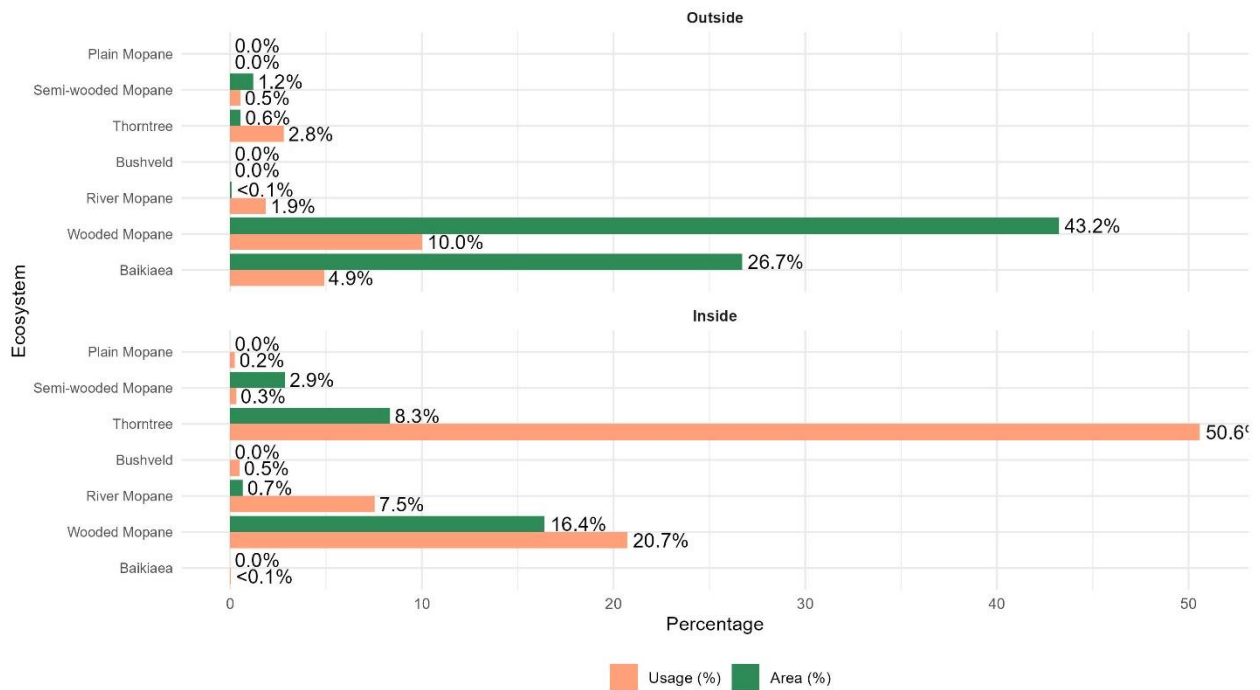
Attachment 6.

National Parks — 6216



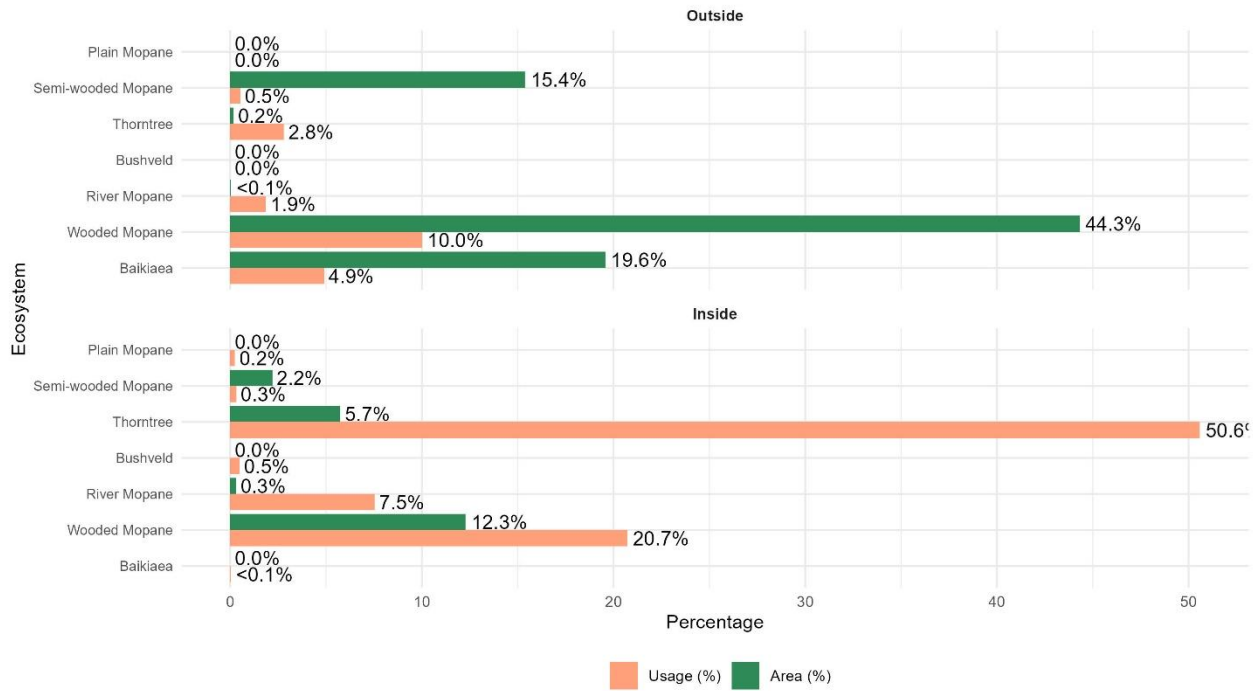
Attachment 7.

Ecosystems - 6207



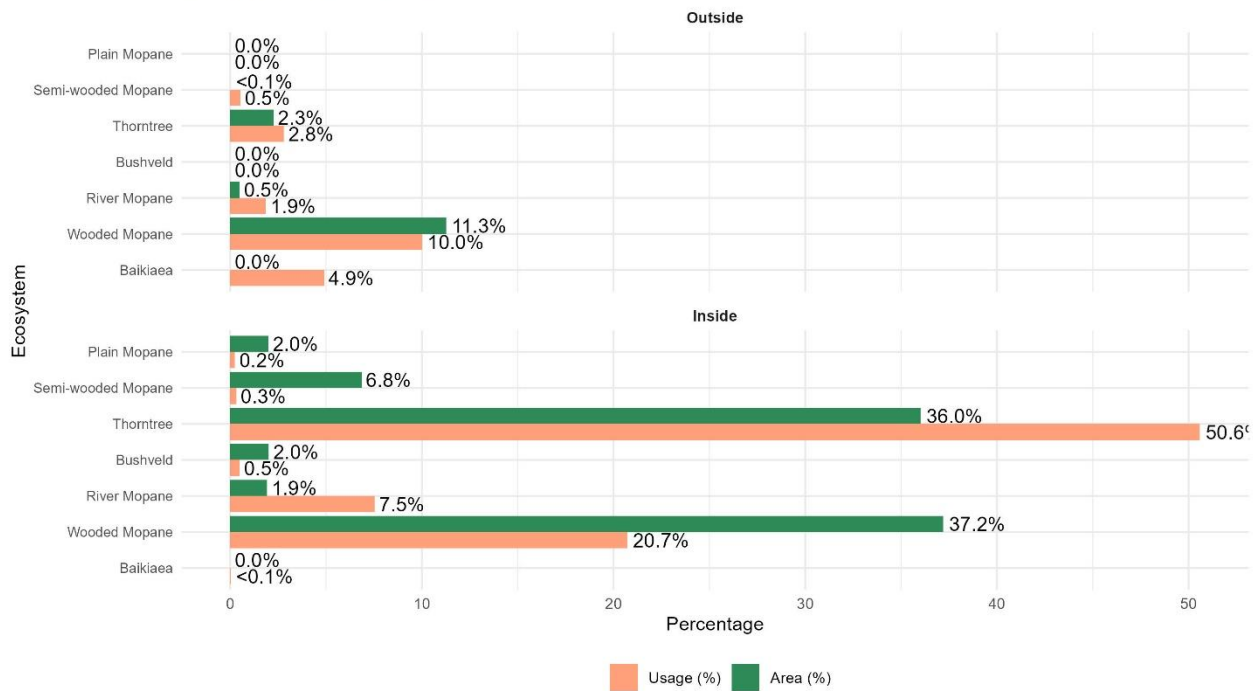
Attachment 8.

Ecosystems - 6208



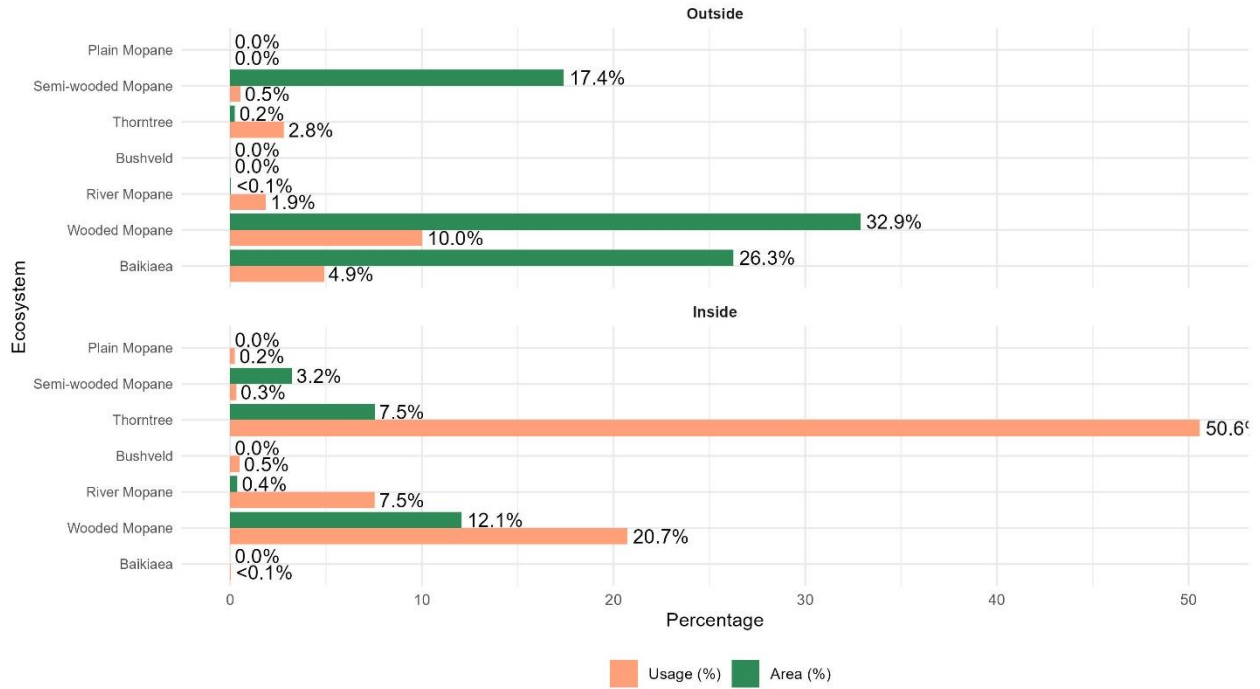
Attachment 9.

Ecosystems - 6210



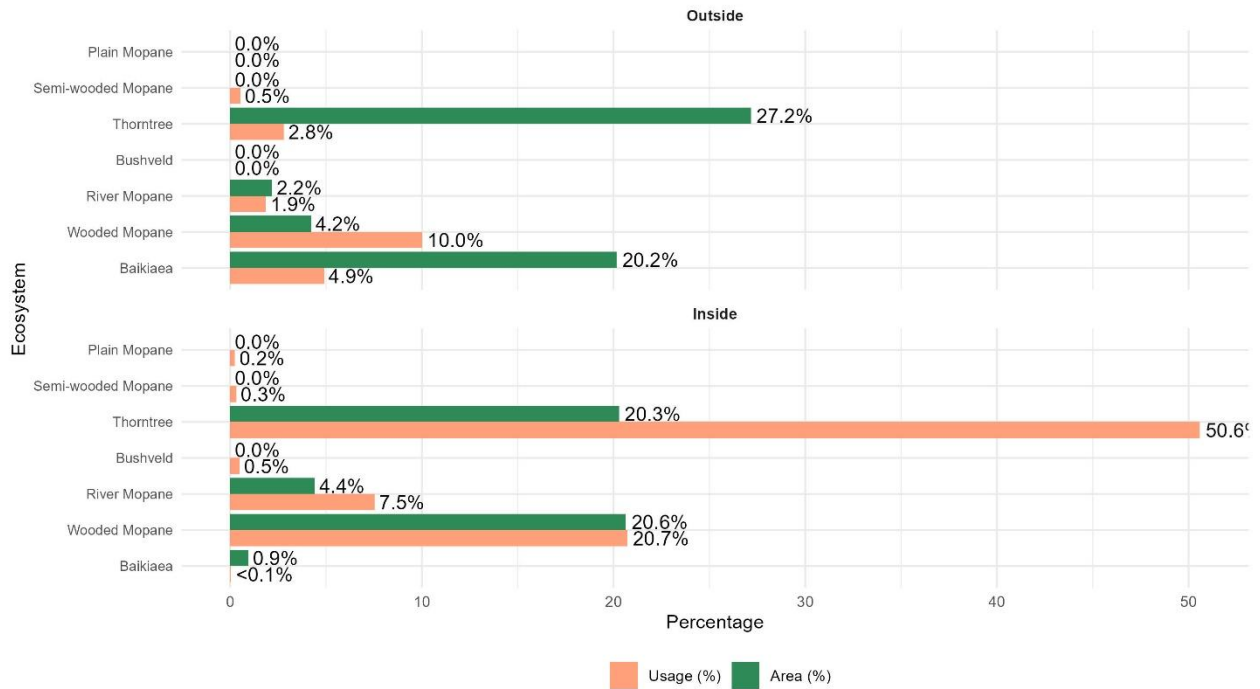
Attachment 10.

Ecosystems - 6212



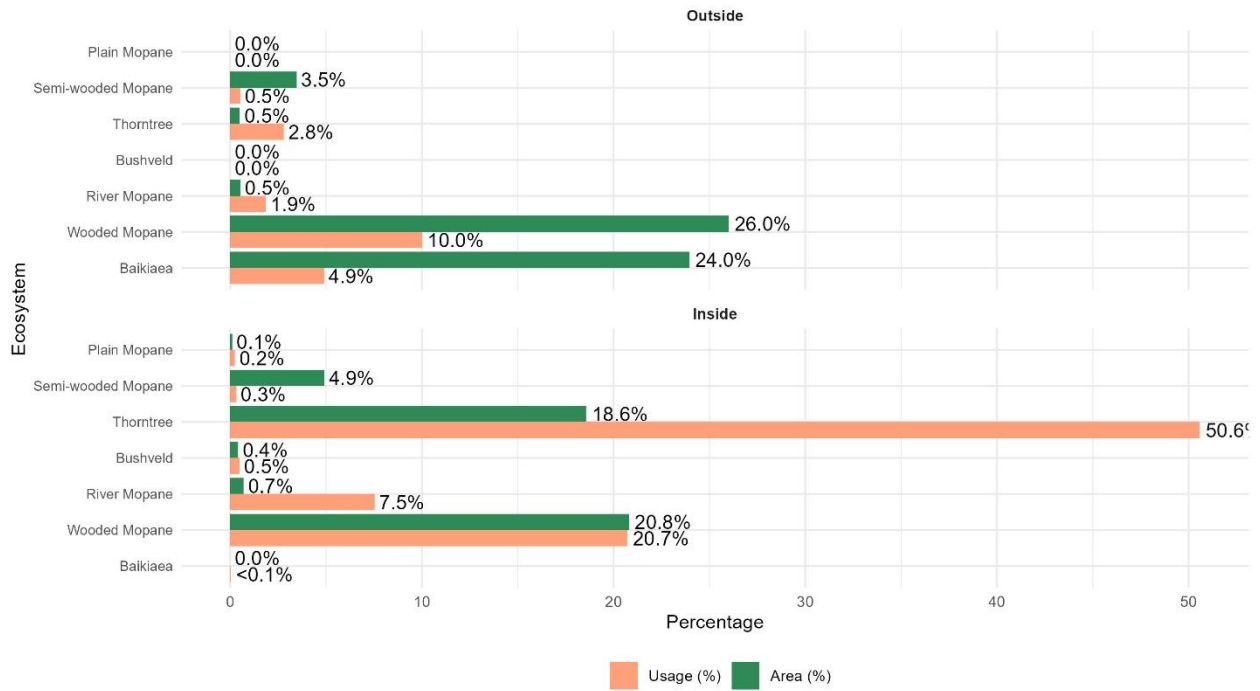
Attachment 11.

Ecosystems - 6213



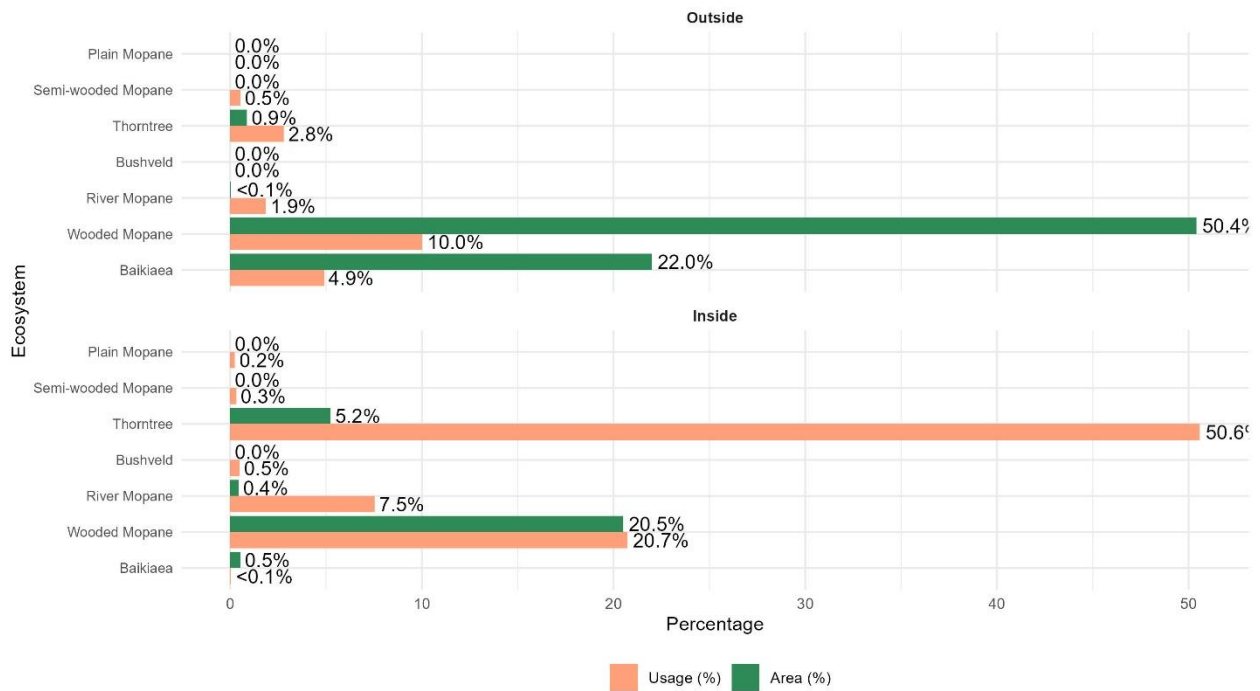
Attachment 12.

Ecosystems - 6214



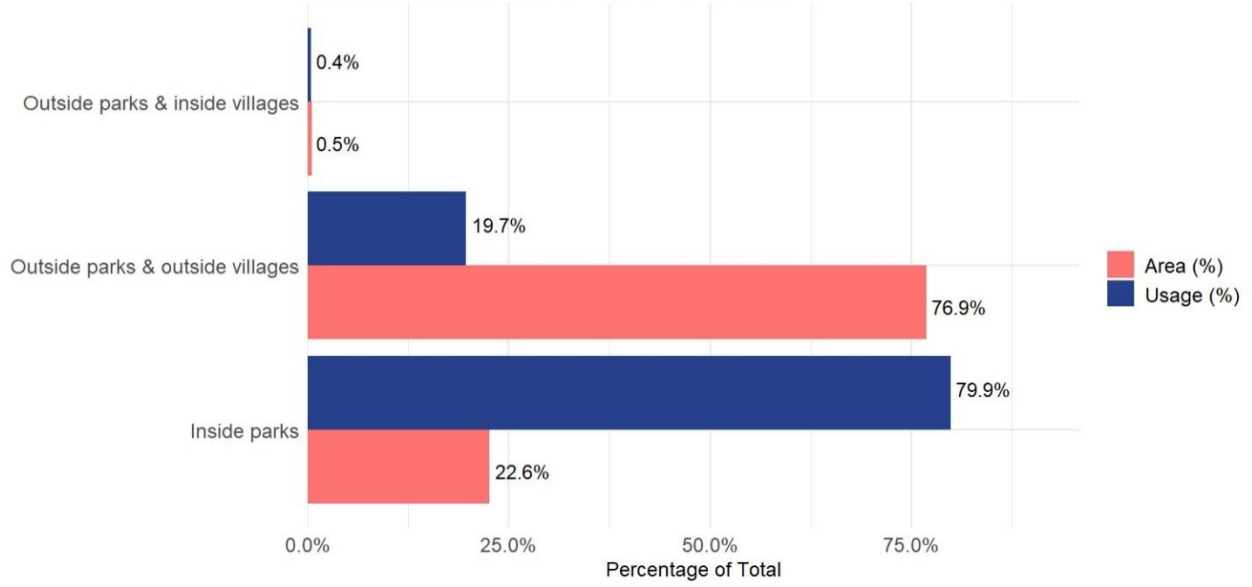
Attachment 13.

Ecosystems - 6216



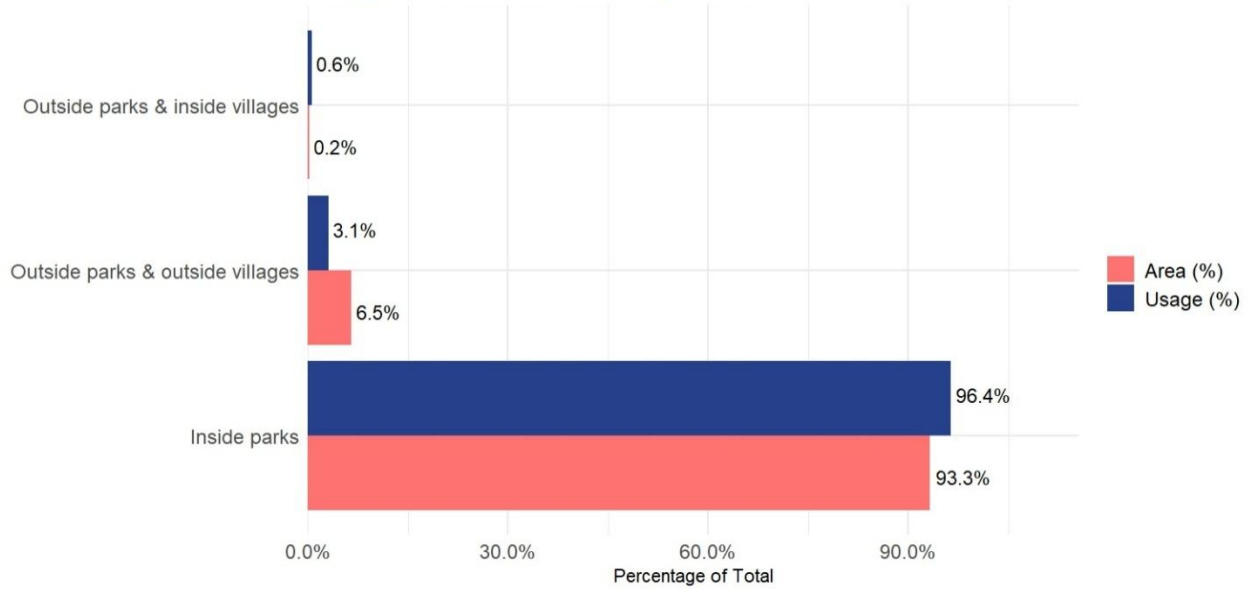
Attachment 14.

Villages and National Parks - General



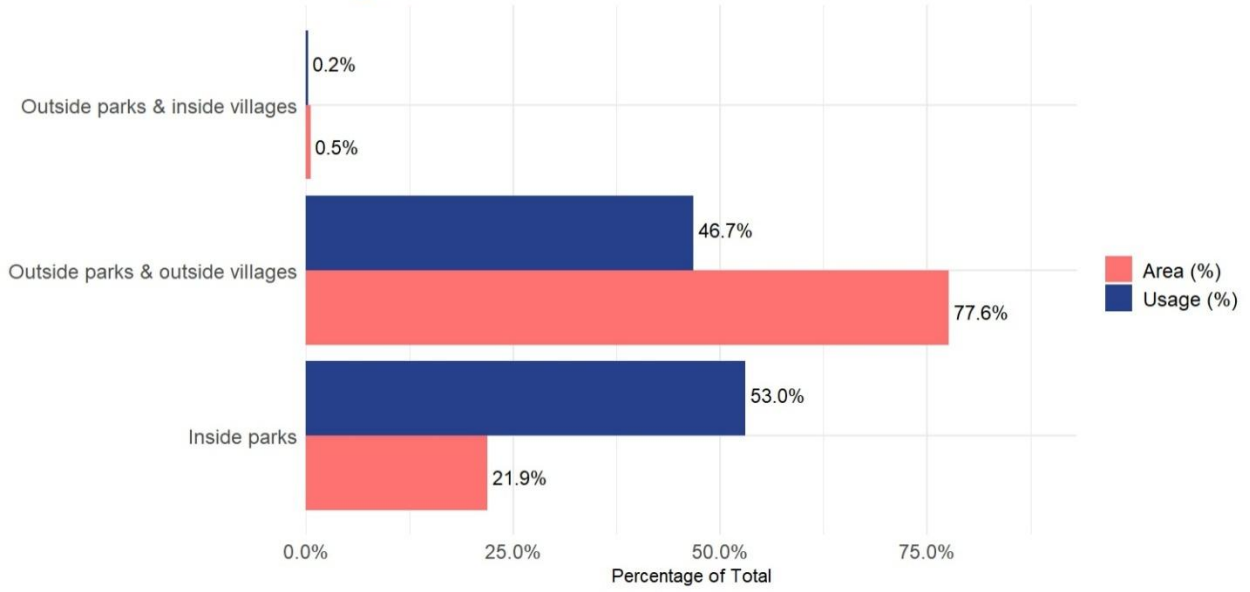
Attachment 15.

Villages and National Parks - Dry season



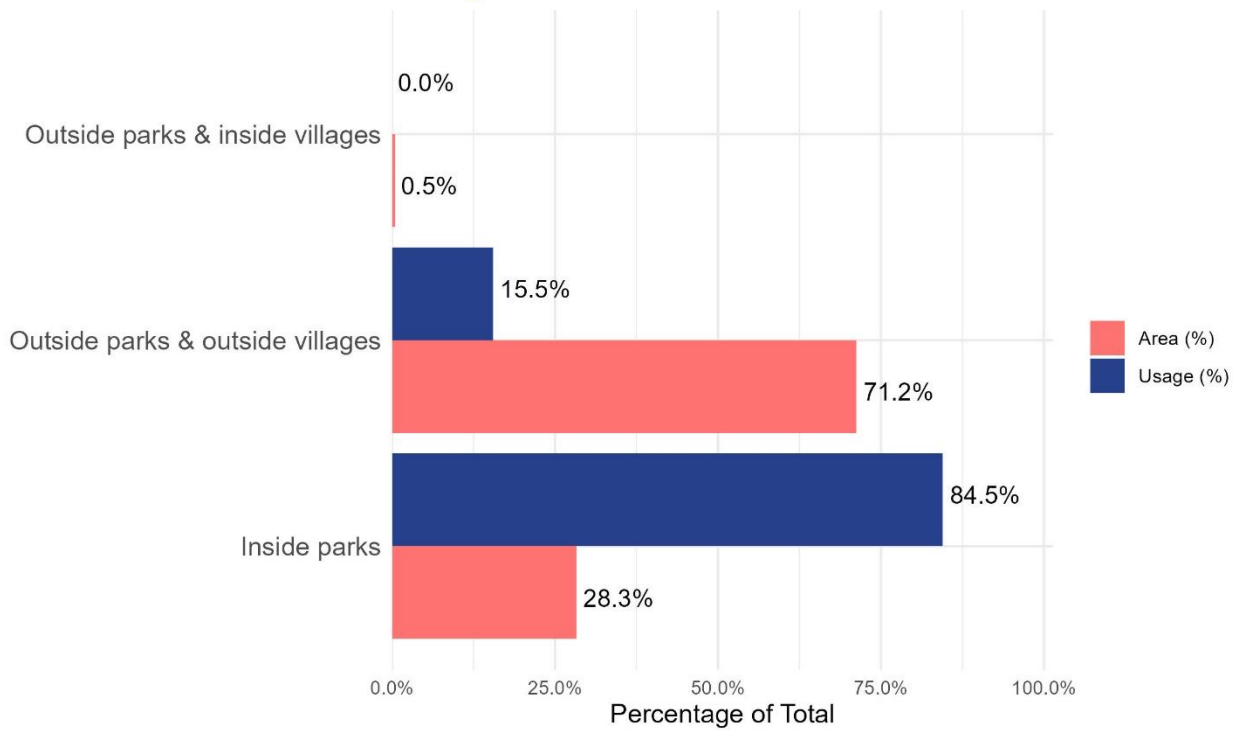
Attachment 16.

Villages and National Parks - Wet season



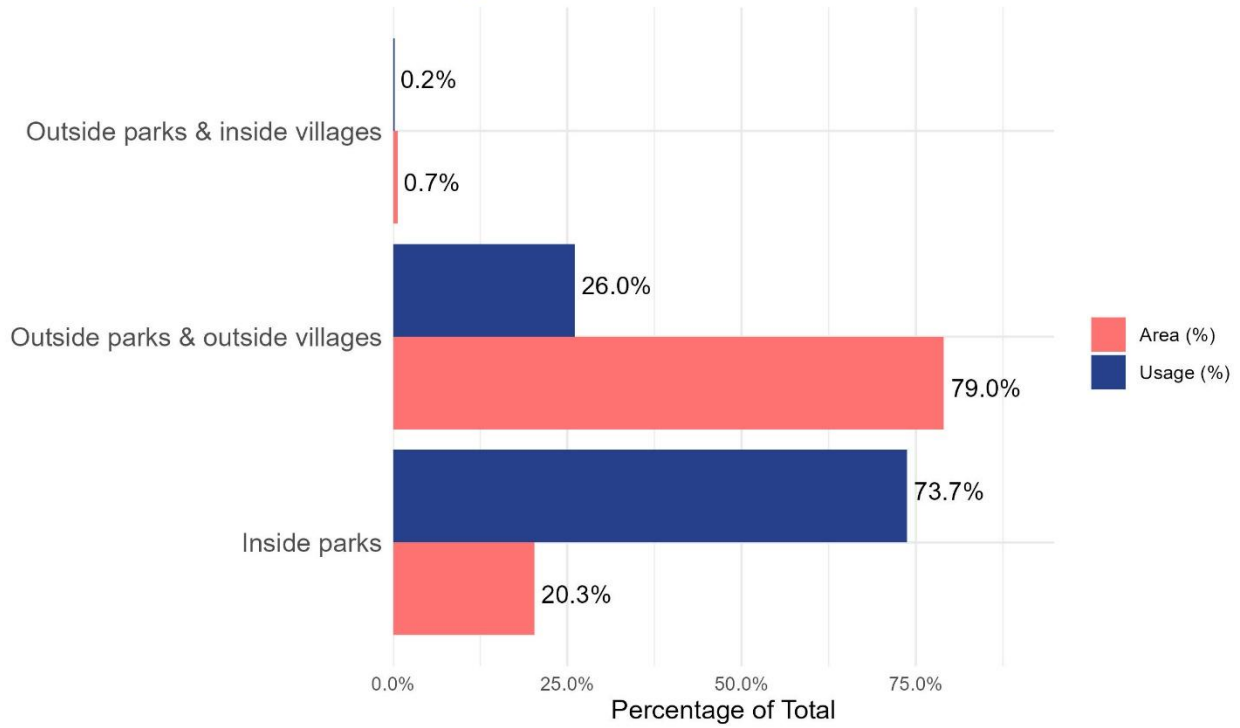
Attachment 17.

Villages and National Parks — 6207



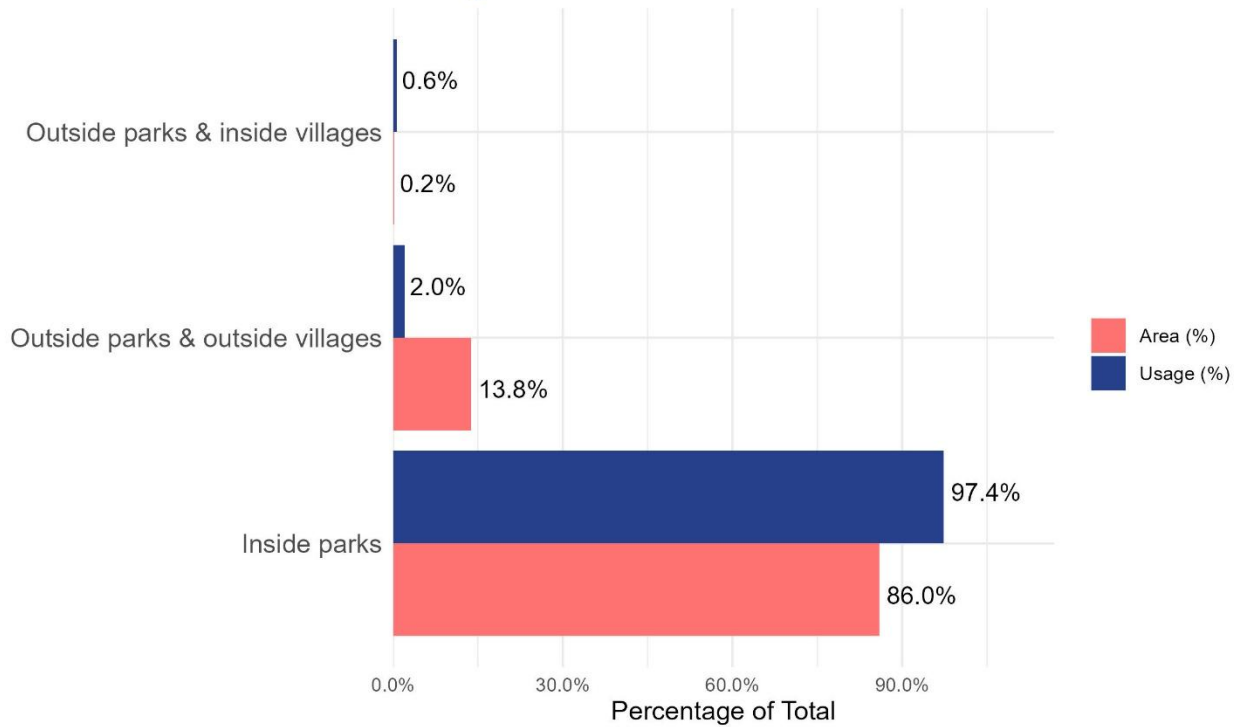
Attachment 18.

Villages and National Parks — 6208



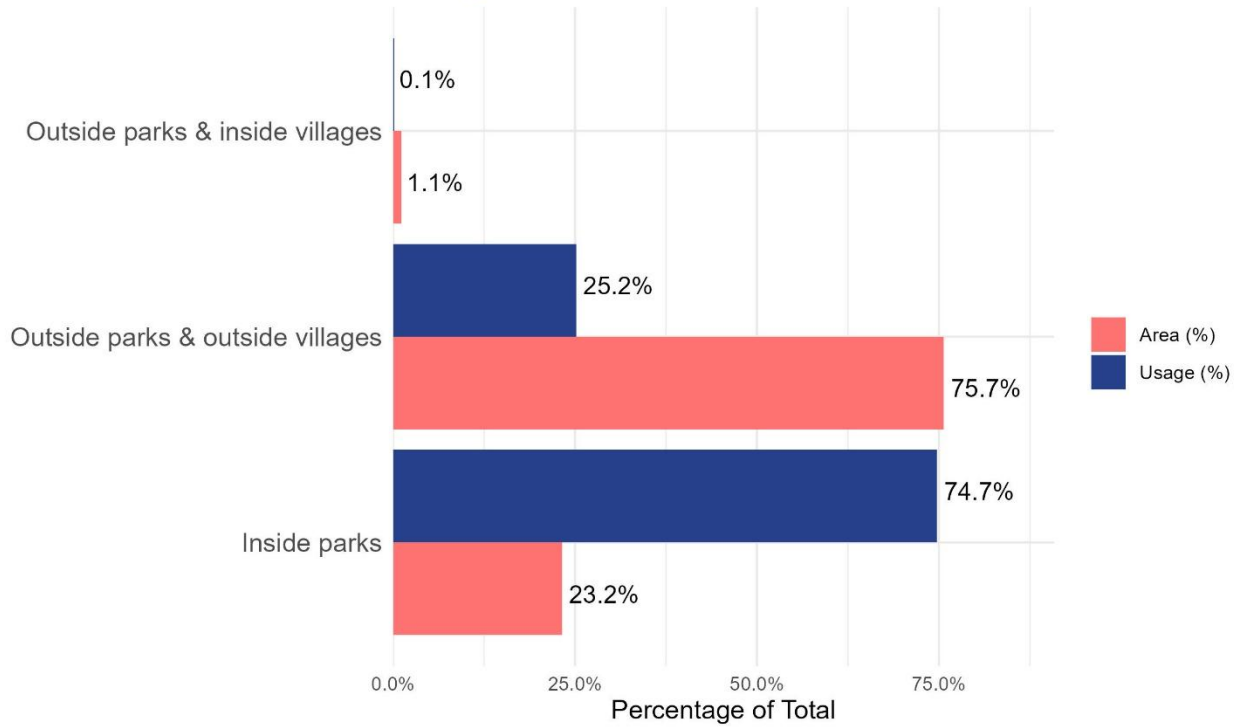
Attachment 19.

Villages and National Parks — 6210



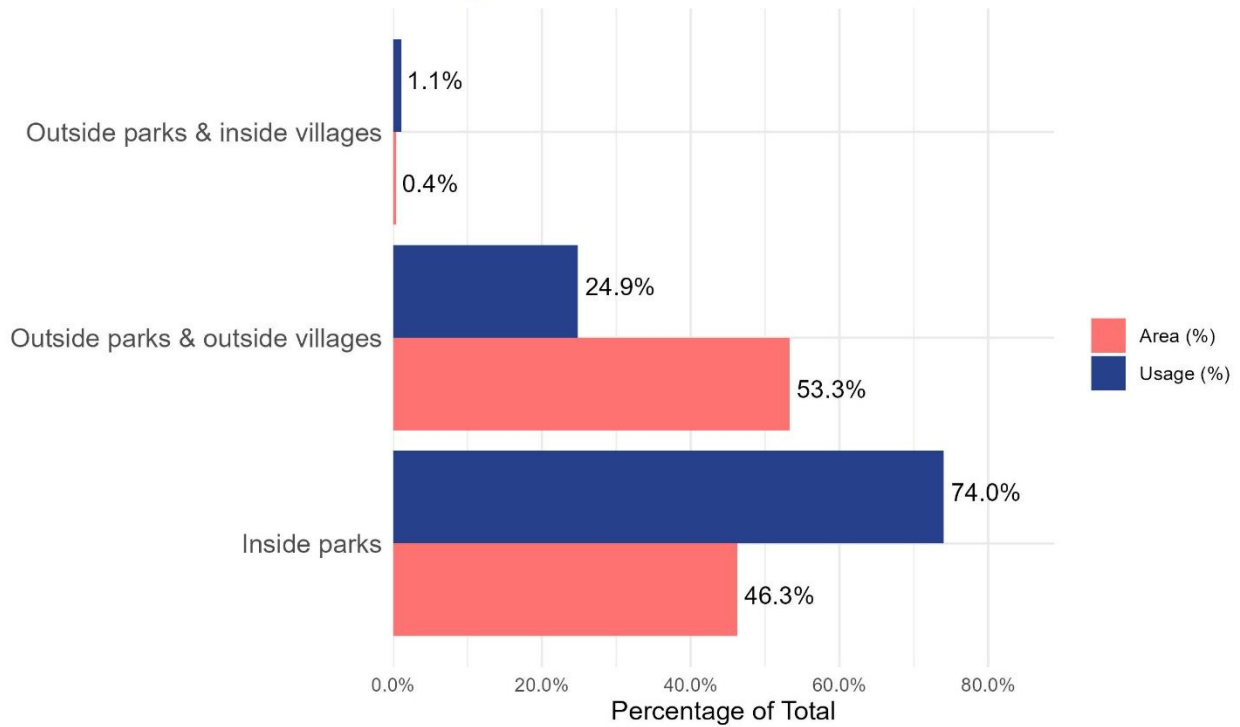
Attachment 20.

Villages and National Parks — 6212



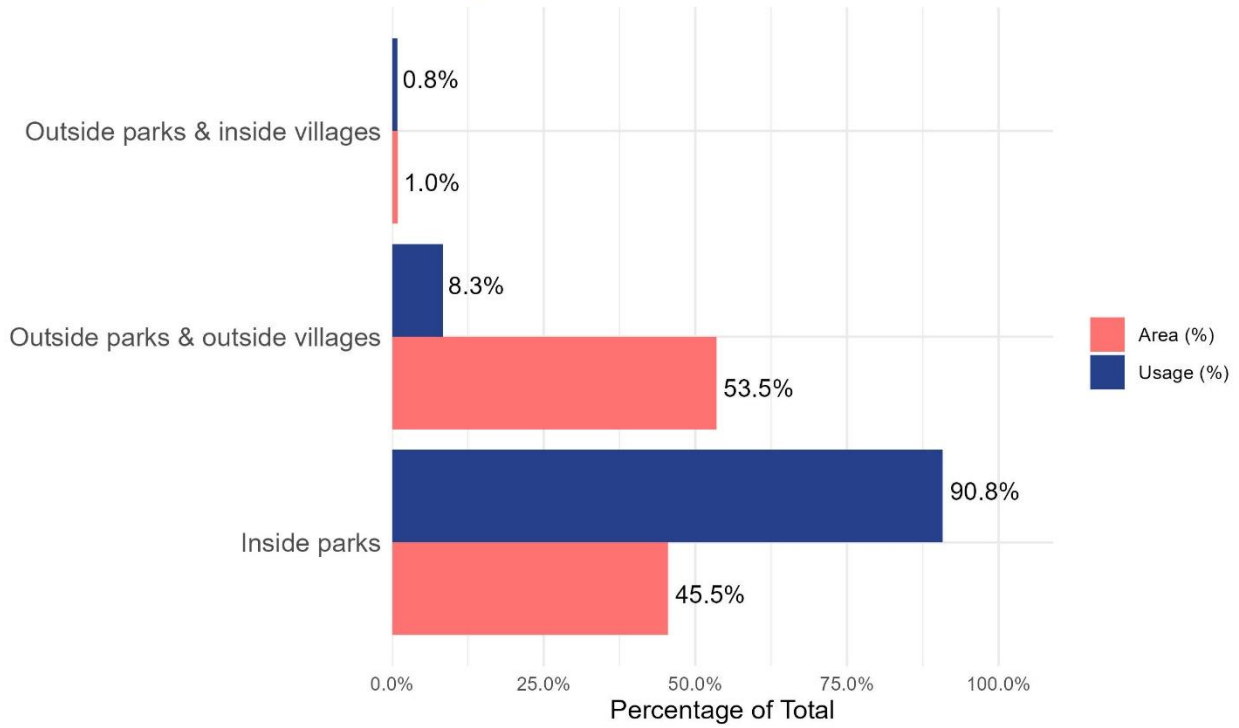
Attachment 21.

Villages and National Parks — 6213



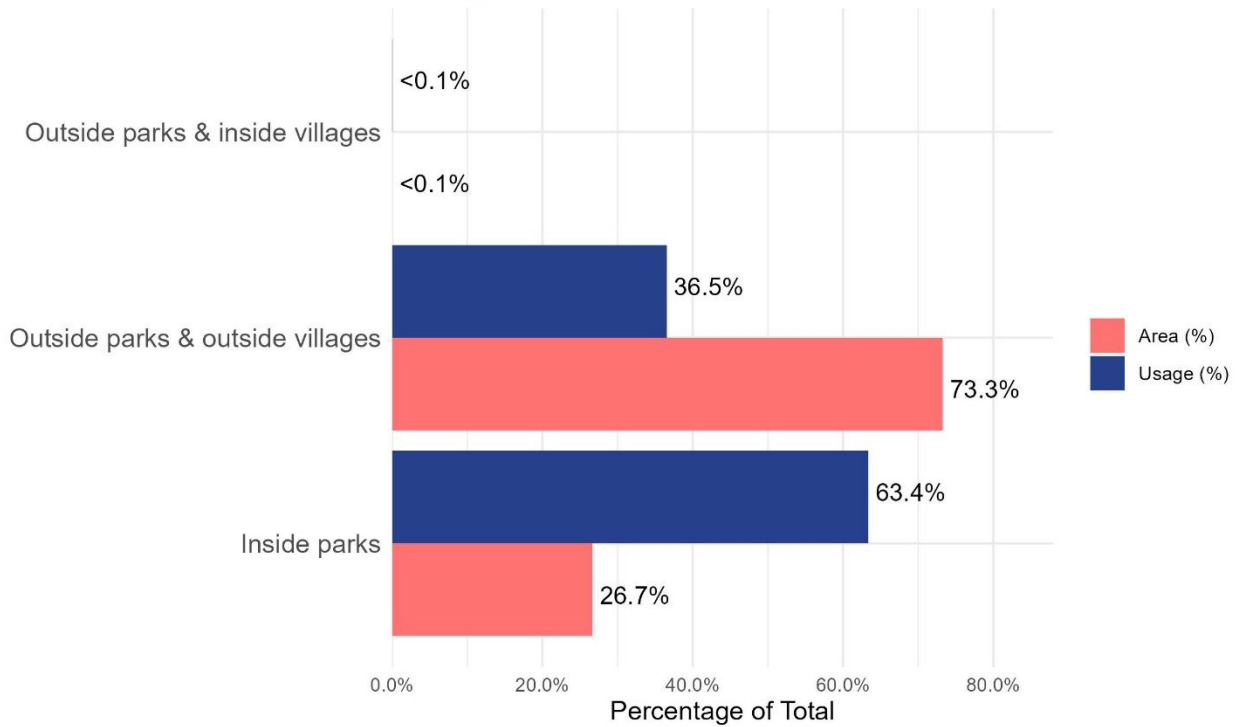
Attachment 22.

Villages and National Parks — 6214

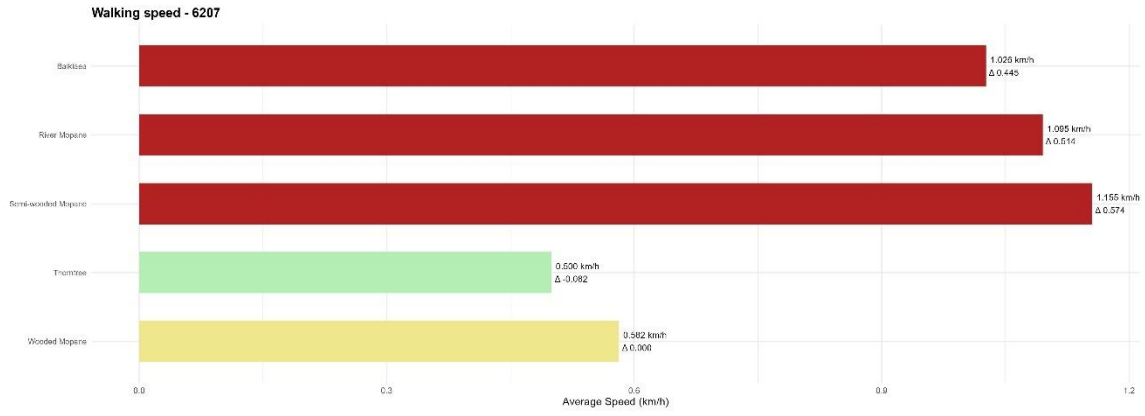


Attachment 23.

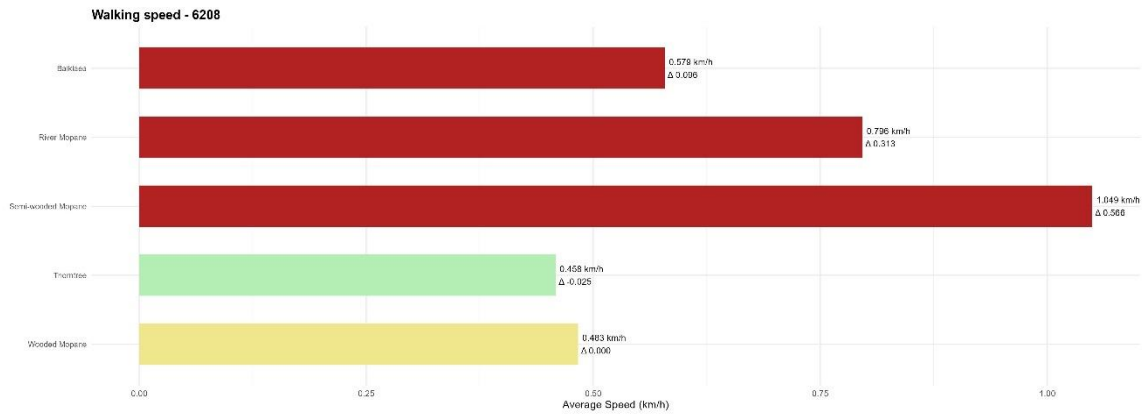
Villages and National Parks — 6216



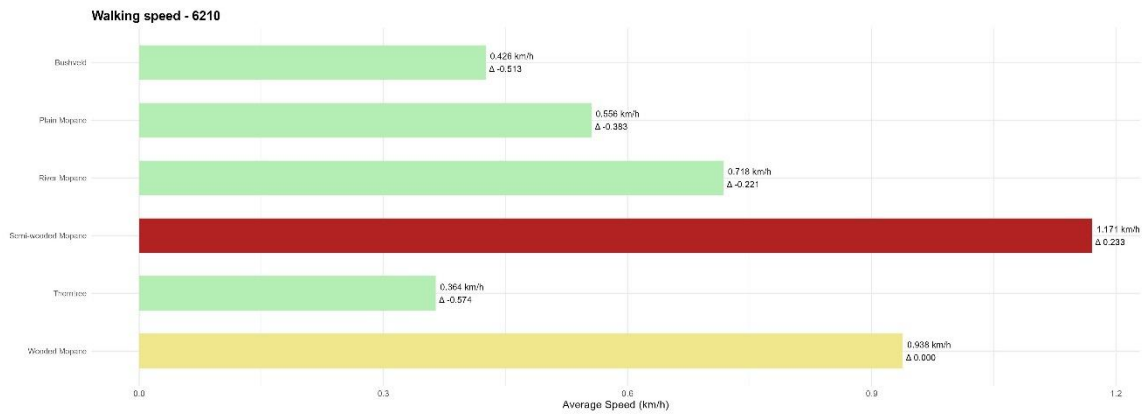
Attachment 24.



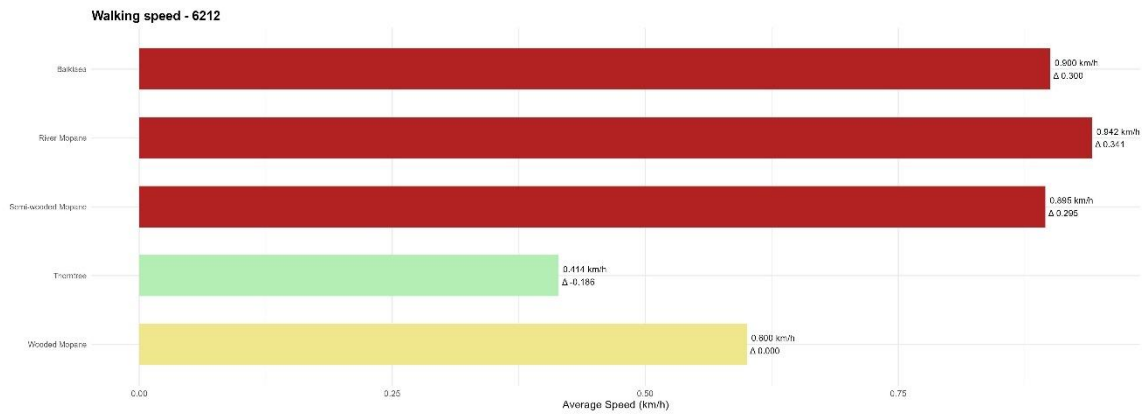
Attachment 25.



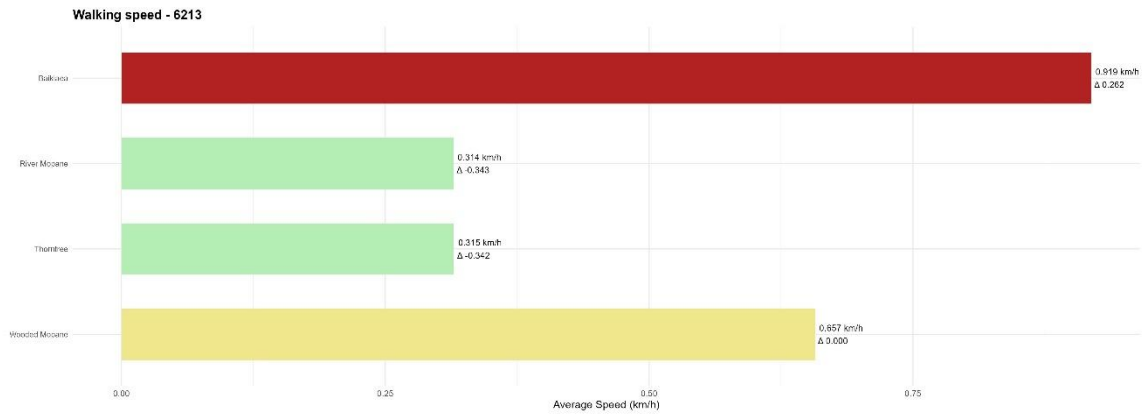
Attachment 26.



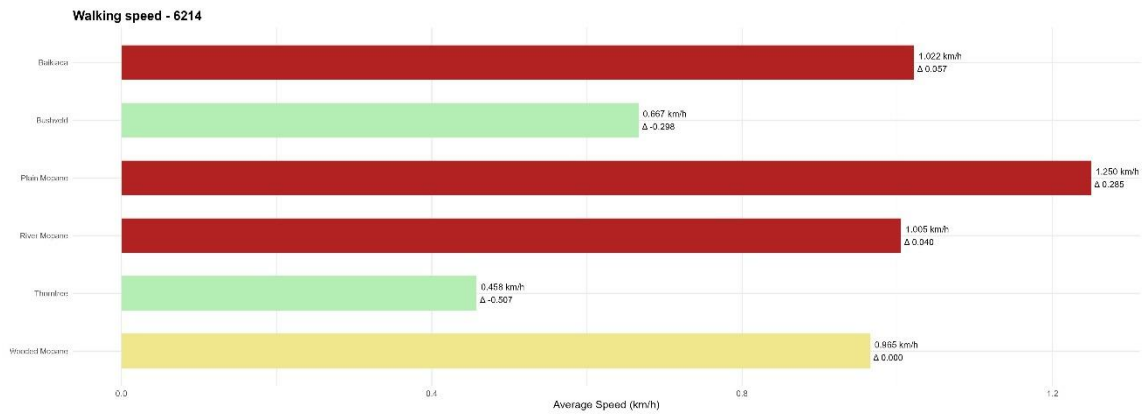
Attachment 27.



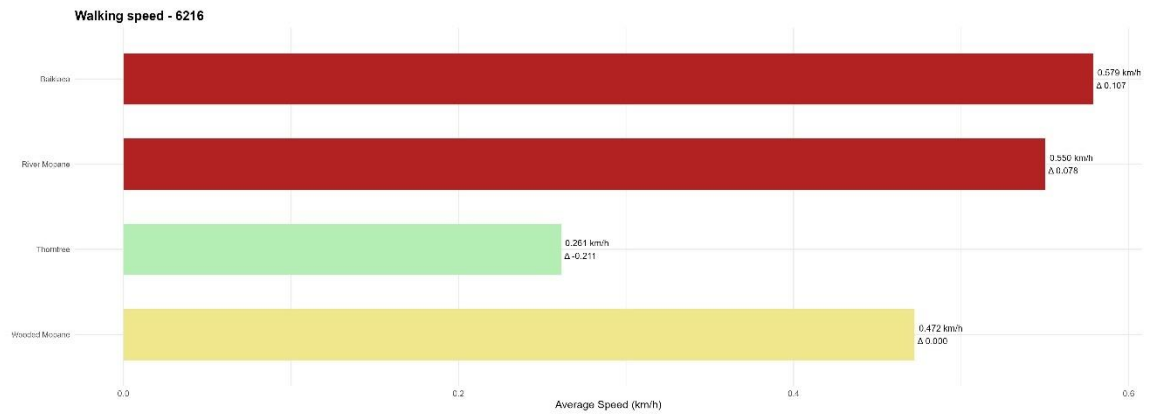
Attachment 28.



Attachment 29.



Attachment 30.



Attachment 31.