Driving factors of movements of the African savannah elephant (*Loxodonta africana*) in Kenya

- a camera trap study

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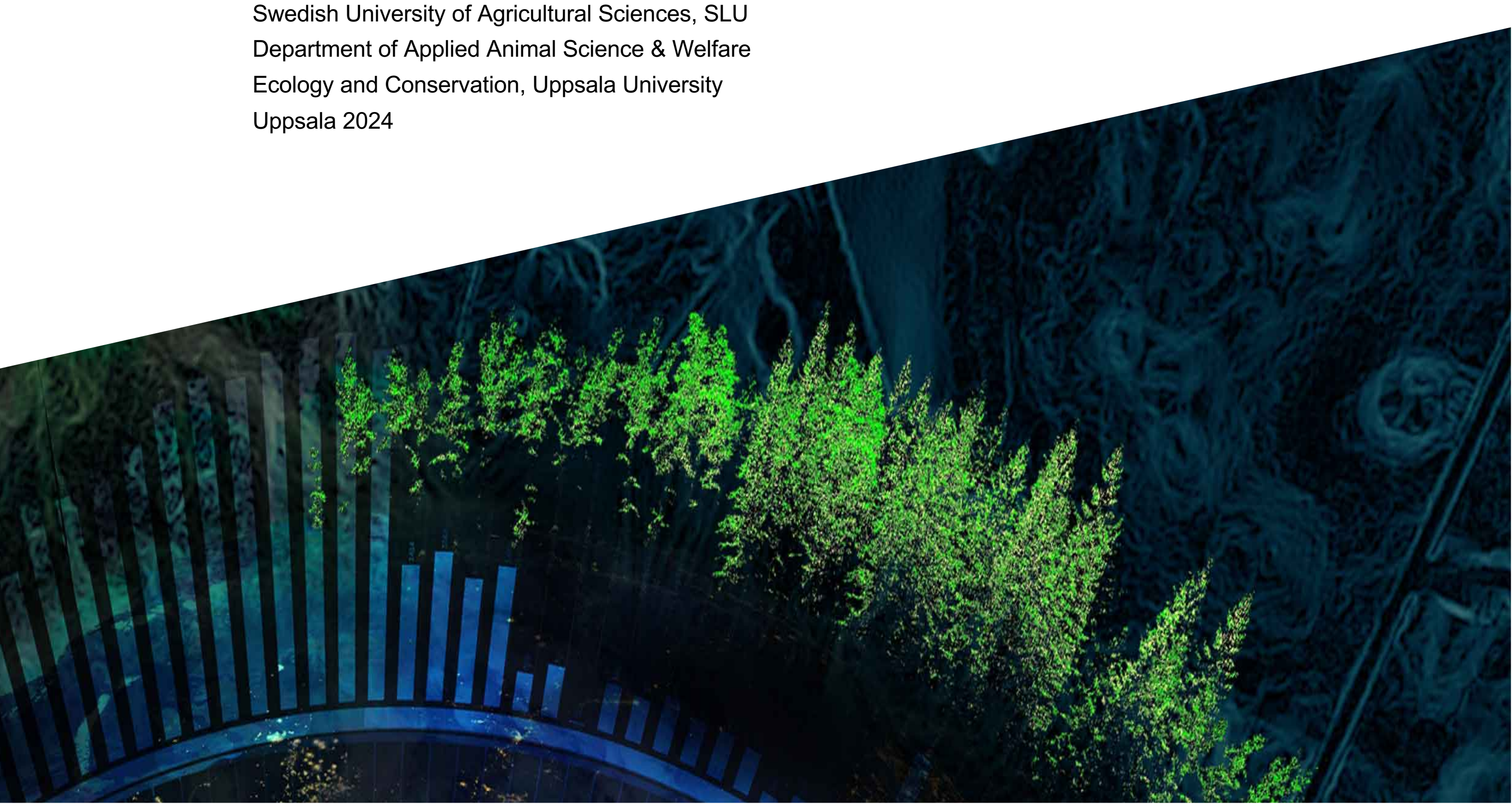

Driving factors of movements of the African savannah elephant (*Loxodonta africana*) in Kenya – a camera trap study

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Abstract

This thesis aims to identify the driving factors of the movements and the direction of movements of the African savannah elephant (LA) based on data obtained from camera traps. Thereto, the methodology involves two main steps: In a first step, the pictures of the camera traps taken between the years 2015 and 2019 were analysed. Demographic data such as age and sex as well as information on movement direction were collected. In a second step, a multivariate generalized linear model (GLM) is estimated to examine the relationship between the response variables movement and direction and the explanatory variables temperature, precipitation, mean rainfall over the last 30, 60 and 90 days, vegetation index as well as group constellation.

This thesis has three main findings: Firstly, temperature, precipitation, mean rainfall over the last 30 days (X30) and 90 days (X90), and group constellation have a significant influence on the movement activity of LA. The likelihood of movement events happening increases on average with a rise in temperature as well as a rise in X30 and X90. Contrariwise, movement activity decreases on average with higher precipitation. The importance of the temperature and precipitation variables suggests that there is an immediate response of LA´s movement activity to daily environmental conditions. Furthermore, the importance of the variables X30 and X90 indicate that there is also a seasonal component, influencing the LA activity. Moreover, variation in the likelihood of LA movements can be explained by variation in the group constellation. Male groups occur to have the highest likelihood to move, whereas female groups were least likely to cross the corridor. This suggest that sex is one of the driving factors of movement activity. Secondly, the direction of the movement of LA is determined by the following variables: temperature, group constellation and vegetation index. Higher temperature increases the likelihood of movement inside the conservancy. Male and female groups have the highest likelihood to move inside the park and single females and males the highest to move outside. When the vegetation shows a negative growth rate, LA are more likely to move inside the park. This controversial behaviour can be explained by, among other things, man-made water resources and the availability of alternative food sources within the park.

Overall, this thesis illustrates that camera traps are an effective method to determine driving factors of the LA movements and their direction of movements in Kenya. The results of this study underline the correlation between the movement activity and direction of LA and various demographic and environmental variables. Therefore, in times of changing environmental conditions and increasing human-wildlife conflicts it is of utmost importance to understand these dynamics for effective wildlife conservation and management strategies.

Keywords: African savannah elephant, movement behaviour, movement direction, Kenya, conservation, camera traps, temperature, precipitation, vegetation index, group constellation, GLM

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Abbreviations

GLM	Multivariate generalized linear model
GPS	Geographic Information System
HWC	Human-wildlife conflict
LA	*Loxodonta africana*
MSAVI2	Modified soil adjusted vegetation index
OPC	Ol Pejeta Conservancy
SD	Standard deviation
SLU	Swedish University of Agricultural Sciences
UAV	Unmanned aerial vehicle
X30	Mean precipitation over the last 30 days
X60	Mean precipitation over the last 60 days
X90	Mean precipitation over the last 90 days

1. Introduction

1.1 Species movements

Since species are able to modify and influence their environment in many different ways (Holtmeier 2015), the distribution of species in the landscape plays an important role in the ecosystem. Even more, with some species migrating their impact on the ecosystems stretches across vast areas. Migration can be defined as "repeated seasonal movement between two non-overlapping regions" (Dingle & Drake 2007, Purdon et al. 2018). These movement represent complex behaviour and involve effects in the individual fitness as well as the population demography (Rolandsen et al. 2017). Driven by "spatiotemporal variation in resources and predation" (Bolger et al. 2008) these movements also entail a trade-off, as they can lead to an increased risk of mortality (Miller & Gunn 1986) and physical costs (Guy Morrison et al. 2007). However, over the last decades increased anthropogenic threats such as barriers, habitat loss (Bolger et al. 2008), and habitat fragmentation destroyed numerous migration routes whilst minimising the area in which the animals can move freely. Overall, a sharp decline in movements was observed which in turn can be considered as "a globally threatened phenomenon, particularly for large mammals" (Bolger et al. 2008, Harris et al. 2009, Tshipa et al. 2017). Since the loss of large functionally coherent areas can lead to a very rapid reduction in populations (Bolger et al. 2008), ecologists and people working in conservation require an understanding of when, where and why movements occur (Purdon et al. 2018).

1.2 Movements of the African savannah elephant

The home range of the African savannah elephant (LA) varies from 102 to 5527 km^2 (Thouless 1996). LA can be considered partial and facultative migrators (Purdon et al. 2018). Between the years 1990 and 1992 an estimated 800 individuals of the Samburu/Laikipia elephants were documented to move up to 140 km north, from the Laikipia area to Samburu. Regularly twice a year during rainy season, LA were moving north to Samburu, where there was more precipitation, and moving back south, when the water sources started to dry up. Therefore, in 1995 Thouless assumed an association of their movements and the water availability. He also suggested that the competition of water with the increased local human population was another factor influencing these behaviours. Compared to Samburu, the Laikipia area has less human disturbances and less permanent water sources (Thouless 1995). Apart from environmental factors, age and sex also influence the movement behaviour of LA. Spending the first 10-20 years of their lives with their natal herd, young males leave their families during puberty and expand their range size (Evans & Harris 2008). The range size increases both with age and during musth period, which peaks in November–February and April–June (Taylor et al. 2020). In 2005, Douglas-Hamilton pointed out that a "large proportion of elephant range lying outside the reserves" which underlines that it is necessary for conservation actions to also focus on the unprotected areas. Being habitat engineers, LA act as a keystone species, promoting habitat heterogeneity by redistributing biomass and facilitating the access of food resources to other species (Kohi et al. 2011).

Over the last decades, the LA have suffered from many threats which has resulted in a severe decline of the entire population size. Despite this decline, there has been an increase in human-wildlife conflicts involving LA over the last decades. These conflicts resulted in adverse consequences both for humans and animals due to a negative local perception of elephants (Attia et al. 2018). Fences were often installed to avoid human-wildlife conflicts and to prevent poaching. However, this can lead to unwanted behaviour, such as increased habitat destruction by the LA (Douglas-Hamilton et al. 2005, Loarie et al. 2009). Indeed, LA have a strong influence on their habitat and can cause long-term changes in vegetation (Clegg & O'Connor 2017). This can both be positive as they can "have positive feedback effects on grassland forage and indirect effects on ecosystem processes (e.g. increasing grassland production and raising nitrogen mineralization)" (Harris et al. 2009) and negative as they could contribute to "jeopardising the persistence of impacted species and the biota that are dependent on the original complexity" (Clegg & O'Connor 2017). As this destructive behaviour is mostly found during time of food scarcity (Bax & Sheldrick 1963, Ihwagi et al. 2010) it is important to enable LA to move freely in between different areas. Thus, understanding the timing and reasons of the movements of the African savannah elephant is of vital importance (Loarie et al. 2009).

1.3 Main objective

So far, most studies on the movement of large mammals in Africa have used GPS collars as it provides a lot of easily accessible information on species' movement patterns. As GPS collars are a very costly and invasive method, camera traps, as an alternative approach, are gaining more popularity. Compared to GPS collars, camera traps cannot provide detailed information of the spatial movements yet can provide additional data such as sex, age and number of individuals. Therefrom, the aim of this study is to use camera traps to give answers to the questions of why, when and in which direction LA move. This is done by identifying which environmental or demographic variables affect their movement activities. In addition, it is examined whether the variables temperature, precipitation, mean rainfall over the last 30 (X30), 60 (X60) and 90 (X90) days as well as group constellation and vegetation influence the direction in which the animals move. Accordingly, this thesis aims to answer the following research questions:

1. Do the variables temperature, precipitation, X30, X60, X90, group constellation, and vegetation index influence the movement activity of LA?

2. Do the variables temperature, precipitation, X30, X60, X90, group constellation, and vegetation index influence the movement direction of LA?

2. Material and Methods

2.1 Study site

This study was conducted in the Ol Pejeta Conservancy (OPC) in central Kenya, located directly on the equator (0°00'N) at a Longitude of 3°86'E (Figure 1). Situated on the base of Mount Kenya in the Laikipia plateau (Muhati & Abdillahi 2018) the OPC covers an area of 36,000 ha (360 km^2) of African savannah (OPC 2023a). In fact, the major vegetation types found in this area are dense bushlands (49%), open bushlands (25%) as well as open grasslands (24%) and riverine (2%). Common species found are *Themeda triandra*, *Penisetum stramineumand, Penisetum mezianum, Acacia drepanolobium, Acacia xanthopleae,* and *Euclea divinorum* (Kavwele et al. 2017, OPC 2023a). At an altitude of 1810 m above the sea level (Kavwele et al. 2017) the daily temperature ranges between 8.2°C and 30.6°C with a yearly average of 17.8°C. The mean annual rainfall lies around 900 mm per year with a biomodal rainfall pattern (Wahungu et al. 2011). During the study period the amount of precipitation in OPC is strongly influenced by season and lies around the 0.639 mm average per day in the dry months and 4.771 mm in the wet months. In the main rainy season rainfall can reach up to 110.700 mm per day whereas in the dry season it can be down to 0 mm per day.
Founded in 2004, the former cattle range was converted into today’s conservancy. Still working as a cattle ranch, OPC holds around 6,000 cattle inside the conservancy (OPC 2023a). OPC functions as one of the largest black rhino sanctuaries in Africa and holds the last two individuals of the northern white rhino. Amongst others, the following species can also be found in OPC: *Aepyceros melampus, Equus quagga, Syncerus caffer, Loxodonta africana, Giraffa camelopardalis, Panthera leo* and *Canis aureus* (OPC 2023b). OPC is enclosed by a wildlife electric fence, yet it comprises three designated corridors allowing all species to move freely, except for rhinos (OPC 2023a). Two major management actions have taken place since the foundation: In 2001, 56 elephants were translocated from the reserve, followed by the expansion of the reserve through the establishment of corridors in 2007 (Wahungu et al. 2011). Surrounded by agropastoral communities the three corridors are placed in the north, where OPC boarders other protected areas (Kavwele et al. 2017).

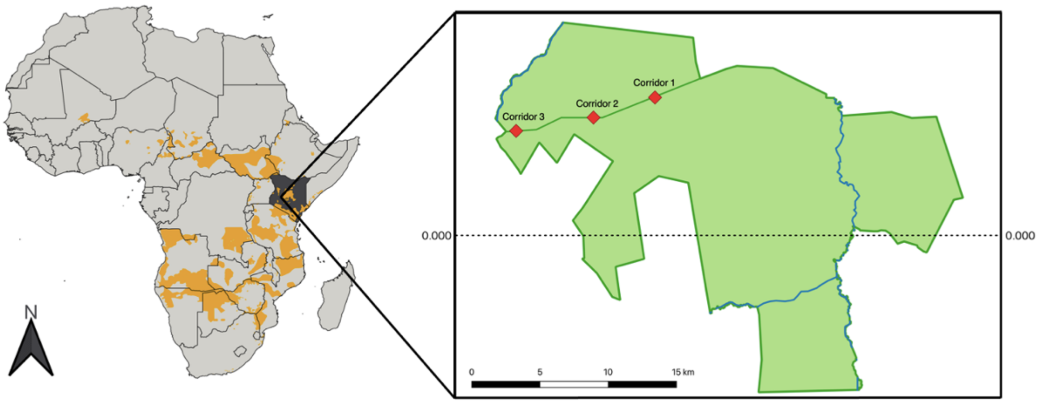


Figure 1: Map of Africa, highlighting Kenya with the species distribution of *Loxodonta africana* across Africa. Additionally, a map of Ol Pejeta conservancy in the Laikipia district, Kenya with corridor 1,2 and 3 marked on the northern border (created by the author in QGIS).

2.2 Study organism

The African savannah elephant (LA), *Loxodonta africana* (Blumenbach, 1797) is distributed across 24 countries, mainly in South and East Africa with a total population size of 415,000 (Ritchie & Roser 2022) and is considered endangered (IUCN 2021). A dramatic increase of threats across Kenya led to a population decline from 167,000 in the 1970s to 16,000 in 1989 (Mukeka et al. 2022). Due to many conservation efforts the population in Kenya is now rising again around 5% annually and has reached a population size of 36,280 individuals in 2021 (African Wildlife Foundation 2022). According to the last aerial census in 2022, OPC holds a total of 551 individuals (OPC 2023b). LA act as important keystone species in the African savannah (Pringle 2008) as they have a major impact on their environment “manipulat[ing] resources to cause cascading effects on other trophic levels” (Kohi et al. 2011). As a wide-ranging species, the movements of LA are largely dependent on the spatial and temporal availability of food and water (Wato et al. 2018, Troup et al. 2022). Their herbivorous diet contains mainly grasses and herbs, but also includes bark, leaves, and shrubs with preferences varying across areas. Living in complex social matriarchal groups, females usually stay in their group throughout their life whereas males leave the group around the age of 12-15. The majority of male elephants lives solitary, occasionally spending their time in weakly tied groups consisting of males only (Evans & Harris 2008).

2.3 Data

2.3.1 Demographic data

2.3.1.1 Data collection - Camera traps

This study contributes to the evolving literature on assessing species movements using camera traps. Specifically, the analysis builds upon camera trap pictures taken between 1-06-2015 and 31-10-2019. A total of 12 camera traps (1A-F, 2A-C, 3A-C) were set up along all three corridors in OPC to record images of animals moving in and out of the protected area, 24 hours a day. Camera 1E and 1F were installed later during the study period, with their first pictures of elephants recorded on 02-07-2018 (1E) and 19-06-2018 (1F). Due to conflicts with pasturalists searching for grazing areas during the drought, all corridors were closed between the 21-04-2017 and the 09-05-2017. Corridor 3 has been permanently closed from 21-04-2017. The purpose of the camera trap instalment was to gather information on the movement directions in and out of the conservancy. As these corridors are the only way for LA to exit and enter the conservancy, all in and out movements are covered by these cameras. The cameras are activated by infrared motion of the type Reconyx HC600 Hyperfire. Attached to a pole at a height of 0.8 metres, each camera was positioned 10 metres from the corridor within the protected area. They were strategically oriented in different directions to maximise coverage of the area. Triggered by infrared sensors, three images per trigger were taken from 1-06-2015 to 12-08-2016. To enhance species identification accuracy, this number was later increased to five images per trigger event. Batteries were replaced on a weekly basis alongside the camera SD cards so the images could be stored and subsequently sorted by species. Overall, over the study period, 249,157 images of LA were captured by the camera traps.

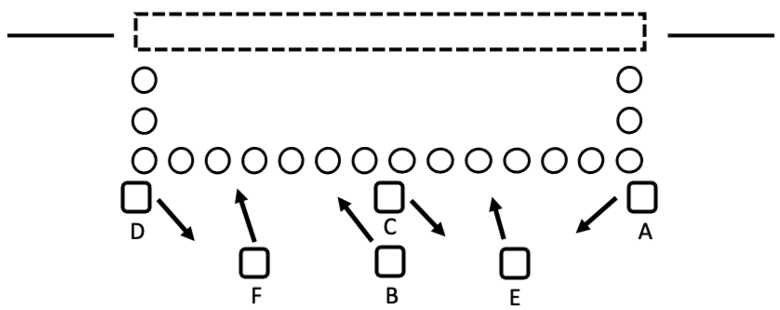


Figure 2: Illustration of corridor 1 including cameras 1A-F inside the conservancy. The corridor has a length of 183m. The circles represent the poles located within the conservancy that prevent the rhinos from leaving the protected area. The dotted line represents the opened section of the fence allowing species movement.

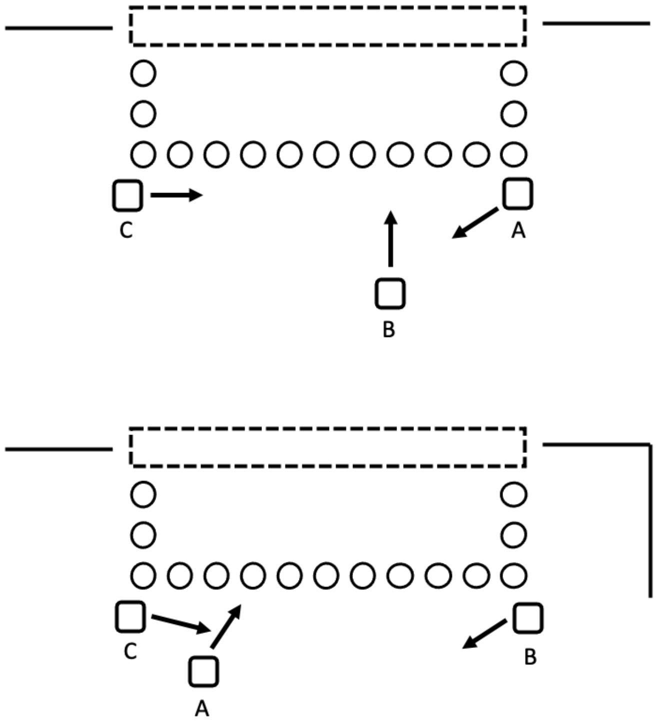


Figure 3: Illustration of corridors 2 (top) and 3 (bottom) including cameras 2A-C und 3A-C inside the conservancy. The corridors have a length of 34m. The circles represent the poles located within the conservancy that prevent the rhinos from leaving the protected area. The dotted line represents the opened section of the fence allowing species movement.

2.3.1.2 Data analysis - Software Camelot

Subsequent to the data collection, the images were analysed using the Camelot software, an open-source cross-platform software providing various features to handle camera trap pictures (Hendry & Mann 2017). The resulting database contains the factors date, time, camera name, direction, additional species sighted along with LA, and demographic parameters, such as age categories and sex. The last image per observation was always marked and these factors were saved. Observations were considered independent if they were more than 10 minutes apart. Sex identification was primarily based upon reproductive organs. When an accurate categorisation of adults was not possible, the category adult was used. The distinction between subadult and adult was determined based on size, with consideration of sexual dimorphism when possible. No sex identification was undertaken for subadult and calves, as this was not feasible in most cases. As several individuals could be visible per observation, the number of individuals sighted was given for the categories adult, female, male, subadult and calf. The direction was divided into four categories: In (species walking into the conservancy), Out (species walking out of the conservancy), Inside (species remaining inside the conservancy) and Outside (species remaining outside the conservancy). Therefrom, the demographic data of sex and age is summarised in the group constellation variable (Chapter 2.3.3). In relation to the research question "Do the variables temperature, precipitation, X30, X60, X90, group constellation, and vegetation index influence the movement activity of LA?", this leads to the following positively formulated hypothesis:

H1: Group constellation: The group constellation will influence the movement activity of LA.

Subsequently, the positively formulated hypothesis for the second research question "Do the variables temperature, precipitation, X30, X60, X90, group constellation, and vegetation index influence the movement direction of LA?" is as follows:

H2: Group constellation: The group constellation will influence the movement direction of LA.

2.3.2 Environmental data

The environmental variables used in this study are as follows: temperature (°C), precipitation (mm), vegetation index and moon phases. Temperature and precipitation were provided by Visual Crossing (Visual Crossing, https://www.visualcrossing.com). Precipitation was measured on a daily basis. To assess the vegetation and hence food availability, the modified soil adjusted vegetation index (MSAVI2) was used. The MSAVI2 was generated from multispectral unmanned aerial vehicle (UAV) satellite images for chlorophyll estimation (Tahir et al. 2018). The average vegetation index was calculated of 10 different areas inside the conservancy (see Appendix 3). Three of these areas are located directly on the northern border where all three corridors can be found. The other areas are located in the northern and central parts of the conservancy. The calculation is based on Qi et al. 1994. The calculation of the MSAVI2 index was performed by Mats Söderström, researcher at SLU. Due to vegetation data inavailability at the beginning of the study period, the vegetation data used in this study only spans between 13-02-2017 and 31-10-2019. The data for the calculation of the moon phases was taken from TimeandDate (Time and Date, timeanddate.com). Therefrom, the calculation of the moonlight intensity was based on the calculation of Śmielak (2023). According to the percentage of moonlight intensity in relation to its highest value and whether the illumination was growing or not, this was then divided into 8 phases (Table 1).

Table 1: Classification of moon phases (1-8) based on moonlight intensity and illumination growth rate.

Moon Phase	Moonlight intensity [%]	Growth rate
1	0-12,49	declining and growing
2	12,5-37,49	growing
3	37,5-62,49	growing
4	62,5-87,49	growing
5	87,5-100	declining and growing
6	62,5-87,49	declining
7	37,5-62,49	declining
8	12,5-37,49	declining

As the moon phases have proven to be a significant factor influencing the movement behaviour (Nystedt 2024), this variable was also included in the statistical analysis. This was done to increase the statistical power of the models but is not discussed further in this thesis. For further information on the impact of moon phases, the interested reader is referred to the thesis by Nystedt, 2024 also completed at SLU, Uppsala.

Referring to the research question "Do the variables temperature, precipitation, X30, X60, X90, group constellation, and vegetation index influence the movement activity of LA?", the positively formulated hypotheses are as follows:

H3: Temperature: Higher temperature leads to an increased movement activity of LA.
H4: Precipitation: Higher precipitation leads to an increased movement activity of LA.
H5: X30: Higher amounts of the mean precipitation within the last 30 days lead to an increased movement activity of LA.
H6: X60: Higher amounts of the mean precipitation within the last 60 days lead to an increased movement activity of LA.
H7: X90: Higher amounts of the mean precipitation within the last 90 days lead to an increased movement activity of LA.
H8: Vegetation: Vegetation will influence the movement activity of LA.

Referring to the research question "Do the variables temperature, precipitation, X30, X60, X90, group constellation, and vegetation index influence the movement direction of LA?", the positively formulated hypotheses are as follows:

H9: Temperature: Higher temperature leads to an increased movement of LA *into* the conservancy.

H10: Precipitation: Higher precipitation leads to an increased movement of LA *into* the conservancy.

H11: X30: Higher amounts of the mean precipitation within the last 30 days lead to an increased movement of LA *into* the conservancy.

H12: X60: Higher amounts of the mean precipitation within the last 60 days lead to an increased movement of LA *into* the conservancy.

H13: X90: Higher amounts of the mean precipitation within the last 90 days lead to an increased movement of LA *into* the conservancy.

H14: Vegetation: Vegetation will influence the movement direction of LA.

2.3.3 Processing the dataset

A total of 155 days were recorded on which none of the following species were detected by any camera within in 24 hours: *Equus quagga, Taurotragus oryx, Loxodonta africana, Crocuta crocuta, Hyaena hyaena, Lycaon pictus, Chlorocebus pygerythrus, Papio anubis* as well as three species of Antilopinae - *Aepyceros melampus, Eudorcas thomsonii,* and *Nanger granti.* We decided that it is possible for up to 4 days that none of those animals have been recorded. Hence, if there were 5 or more days without any recordings, it is very likely that those pictures were lost and those days were removed from the dataset. In most cases recordings from the weekdays Saturday to Thursday were missing which aligns with the weekly battery and memory change on Fridays. Considering deviations from this schedule for the replacements, any subsequent missing dates following missing “weeks” were also removed. In addition, the previous day and the day of the battery change were entered as missing dates, as these are considered to be incomplete. In total 136 days were excluded from the analysis.

Data preparation further involved the creation of a summary demographic variable, named group constellation. Therein, each observation was sorted into one of the following categories: Single males, single females, group of males only (>1), group of females only (>1), and mixed groups, which included at least one calf or subadult. Additionally, the environmental variables “X30”, “X60” and “X90” were created respectively representing the average precipitation of the last 30, 60 and 90 days for each day.

Furthermore, the daily growth of vegetation was calculated following the equation of MSAVI2 in Qi et al. 1994. Then, the growth of vegetation was divided into three categories: shrinking (1), stagnant (2) and growing (3). Moreover, the MSAVI2 index was divided into three categories: low (1), medium (2), high (3). Finally, these ranks were then merged into one column resulting in the Rank index comprising nine categories as follows: “11”, “12”, “13”, “21”, “22”, “23”, “31”, “32” and “33”. Additionally, the analysis considered only the Direction “In” and “Out”, as these represent the actual movements of LA. Therefrom, this processed dataset was used for statistical analysis.

2.4 Statistical analysis

2.4.1 Preliminary analysis

The preliminary data analysis included a check for normality and a correlation assessment. Therefrom, to preclude a multicollinearity problem, the variables maximal temperature, minimal temperature, season (Wet/Dry), and mean precipitation of the last 7 days were excluded from the analysis.

A first model (Model 1) examined the relationship between the movement activity (Yes/ No) and the chosen demographic and environmental explanatory variables. To do so, a multivariate generalized linear model (GLM) was fitted. This GLM models the probability of the response variable as a binary outcome based on a set of predictor variables. Using a binomial family and a logit Link function, the model was specified to reflect the binary character of the response variable. Indeed, such a specification is suitable for modelling binary results where the response variable follows a binomial distribution. A second model (Model 2) was carried out similar to the first model, however used a different response variable and therefore examined the relationship of the explanatory variables to the direction of movement (In/Out). As indicated in Table 2, the number of observations for "movement " is lower compared to "direction." This discrepancy arises because for the "movement" category, only the first observation per day was considered. This approach was taken to avoid double recordings in the movement variable for days where there was more than one observation. In the models the following variables were used as explanatory variables: temperature, precipitation, X30, X60, X90, group constellation, and moon phases. Table 2 summarises the descriptive statistics of all non-categorical variables used in this study. Furthermore, their boxplots are shown in Figure 4.

Table 2: Descriptive statistics including the mean, median, standard deviation (SD), and variance values of all non-categorical variables. N represents the number of corridor crossings. Temperature is given in Degrees Celcius and precipitation, X30, X60 and X90 in mm per day. (A) shows the descriptive statistics of the explanatory variables of the direction dataset over the entire study period. (B) shows the descriptive statistics of the explanatory variables of the movement dataset over the entire study period. (C) shows the descriptive statistics of the explanatory variables of the direction dataset over the limited period from 13-02-2017 to 31-10-2019. (D) shows the descriptive statistics of the explanatory variables of the movement dataset over the limited period from 13-02-2017 to 31-10-2019.

	N	Mean	Median	SD	Variance	Minimum	Maximum
Temp	4434	17.84	17.8	1.107	1.226	14.9	21.3
Precip	4434	3.248	0.5	6.671	44.505	0	62.013
X30	4434	3.214	1.704	3.335	11.121	0.115	16.689
X60	4434	3.437	2.386	2.672	7.14	0.432	12.364
X90	4434	3.711	3.534	2.267	5.141	0.549	10.685

(A)

	N	Mean	Median	SD	Variance	Minimum	Maximum
Temp	1452	17.817	17.8	1.114	1.242	14.9	21.3
Precip	1452	3.530	0.6	7.759	60.196	0	110.7
X30	1452	3.482	1.737	3.501	12.256	0.092	16.689
X60	1452	3.522	2.472	2.747	7.547	0.4322	12.364
X90	1452	3.585	3.46	2.187	4.782	0.549	10.692

(B)

	N	Mean	Median	SD	Variance	Minimum	Maximum
Temp	2984	17.875	17.9	1.115	1.243	15.3	21.3
Precip	2984	3.698	0.6	7.203	51.877	0	51.758
X30	2984	3.723	1.996	3.655	13.362	0.115	16.689
X60	2984	3.724	2.756	2.770	7.676	0.569	12.364
X90	2984	3.794	3.471	2.35	5.522	0.836	10.685

(C)

	N	Mean	Median	SD	Variance	Minimum	Maximum
Temp	900	17.83	17.8	1.121	1.256	15.3	21.3
Precip	900	3.831	0.782	7.578	57.42	0	51.758
X30	900	3.712	2.001	3.643	13.273	0.092	16.689
X60	900	3.641	2.482	2.84	8.063	0.569	12.364
X90	900	3.606	3.302	2.28	5.2	0.836	10.692

(D)

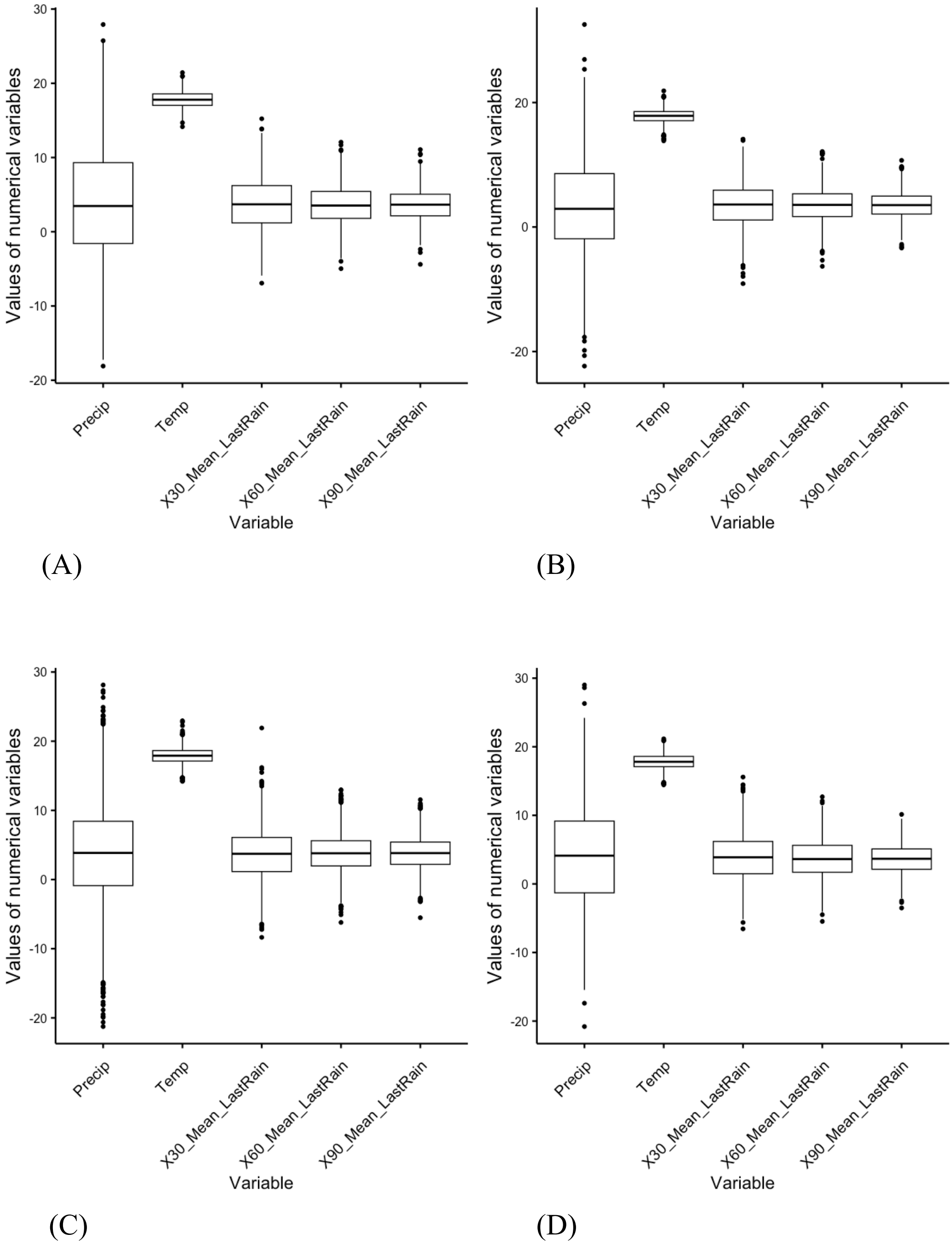


Figure 4: Visualization of the distribution of all non-categorical variables in boxplots. (A) presents the distributon of the values of the explanatory variables of the direction dataset over the entire study period. (B) illustrates the distributon of the values of the explanatory variables of the movement dataset over the entire study period. (C) displays the distributon of the values of the explanatory variables of the direction dataset over the limited period from 13-02-2017 to 31-10-2019. (D) depicts the distributon of the values of the explanatory variables of the movement dataset over the limited period from 13-02-2017 to 31-10-2019.

2.4.2 Model analysis

The estimated models were evaluated using a series of statistical test: To assess the significance of individual predictors, a likelihood ratio tests (chi-square tests) for each predictor was performed. Additionally, a chi-square test was performed to assess the overall fit of the model. Finally, the exponential function of the coefficients was calculated in order to interpret the effect of the individual predictors on the odds of the response variable.

In terms of modelling, this thesis estimated two original and two amended GLMs. The two original models (Models 1 and 2) involved a comprehensive set of explanatory variables to capture the primary effects of interest over the maximum time horizon. Meanwhile, the estimation of the two amended GLMs fulfilled a twofold purpose: On the one hand, the latter GLMs were performed on a dataset with a reduced time horizon, incorporating an additional explanatory variable "vegetation index", that was not included in the original model but only available for the reduced time horizon. Contrary, to the previous analysis, which included the entire data set, this dataset only used data between the 13-02-2017 and 31-10-2019. On the other hand, the latter two GLMs acted as robustness tests. By comparing the results of the original GLM with those of the additional models, the stability and reliability of the results was assessed. If the inclusion of the additional variable did not significantly alter the main effects or the overall fit of the model, this would have indicated that the original model is robust and that the main conclusions were not overly sensitive to changes in the predictors. This approach helped to strengthen the validity of the results and provided a more comprehensive understanding of the underlying relationships between the explanatory and response variables. All analysis were performed in R version 2023.03.1+446.

3. Results

3.1 General results

During the observational period spanning from June 1, 2015, to October 31, 2019, there were a total of 4434 individual observations of LA at all three corridors. Within this period, 892 days were recorded on which LA entered or exited the conservancy (movement “In” or “Out”), which corresponds to 61.14% of the total 1452 days included in this study. The total abundance of LA recorded daily ranged between 1 and 97 individuals. A total of 445 observations were made of single males, 16 of single females, 61 of groups of only males (>1), 3 of groups of only females (>1) and 1709 of mixed groups which included at least one calf or subadult. In sum, 1695 single adults and 505 groups of only adult could not be sexed. Of 11,423 adult observations 36.73% could be sexed. 3406 of them were female and 789 males. In 47 observations, the following other animals were recorded that were present alongside LA: *Equus quagga* (26/ 55.32%), *Bubalus arnee* (9/ 19,15%), *Eudorcas thomsonii* (6/ 12.77%), *Nanger granti* (3/ 6.38%), *Giraffa camelopardalis reticulata* (2/ 4.26%), *Panthera leo* (1/ 2.13%).

3.2 Effects of predictors on movements

Pursuant to the above outline of the methodology, estimating the first regression model identifies which explanatory variables significantly influence LA movement activities. The original GLM analysis indicated that temperature and precipitation were significant predictors of movement activity. In comparison, the analysis with the limited dataset shows slight differences in significance, with temperature and precipitation not being significant (see Appendix 4). Both models have been proven to be overall significant with both the entire data set and the limited data set having a p-value of 0.00. First, the movement activity of LA revealed to be strongly influenced by group constellation. The change in odds ratio compared to the reference category “Male group” is presented in Table 4 for each category. In general, the odds ratio is a common measure in the context of categorical variables and provides a statistically robust measure of association that facilitates more precise interpretation of group-specific effects. More specifically, this ratio is necessary for quantifying the likelihood of the outcome "yes" or “in” across different categories of the categorical variable relative to the reference category. Additionally, temperature has a significant effect on movement activity, with the likelihood of a movement event increasing by 14.868% per degree Celsius. Moreover, significant effects were observed for daily precipitation (p-value: 0.031), the average rainfall of the last 30 days (p-value: 0.000), and the average rainfall of the last 90 days (p-value: 0.018). The probability decreases by 1.597% per mm of daily precipitation, increases by 6.458% for X30, and increases by 17.507% for X90. Conversely, the average rainfall of the last 60 days and vegetation index showed no significant effect on movement activity (Table 3). The main results of model 1 are presented in Table 3. The results of model 1 based on the limited dataset are found in the Appendix 4. Visualisation of the likelihood of movement of all significant variables is presented in Figure 5. Visualisation of the data points of movement activity in relation to the significant numerical variables temperature, precipitation, X30 and X90 are found in Appendix 5.

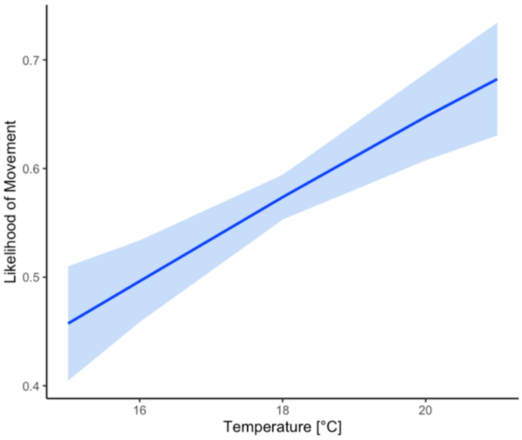
Table 3: Estimated regression results of predictor variables from Multivariate Generalized Linear Model (GLM) Analysis with the likelihood of movement activity as the response variable. More specifically, the response variable is defined as the likelihood of movement activity of LA across the corridor. P-values below the significant level of 0.05 have been highlighted.

Variable	Coefficient	Std. Error	p-value	Df
temp	0.342	0.228	**0.033**	1
precip	0.015	0.208	**0.031**	1
X30	-0.778	0.502	**0.000**	1
X60	0.892	0.858	0.197	1
X90	-0.576	0.702	**0.018**	1
Group constellation	-3.972	14.390	**0.000**	7

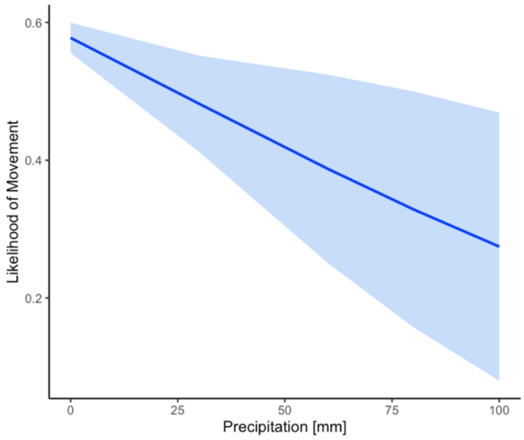
p-value < 0.05: significant

Table 4: Odds Ratio for each category of the categorical variable group constellation, in comparison to the reference category "Male group". Higher odds ratios suggest higher likelihood of the outcome "yes", while lower odds ratios suggest higher likelihood of the outcome "no".

Group constellation	Odds Ratio
Male Single	0.849
Adult Single	0.825
Female Single	0.904
Female Group	0.431
Mixed Group	0.854
Adult Group	0.713



(A)



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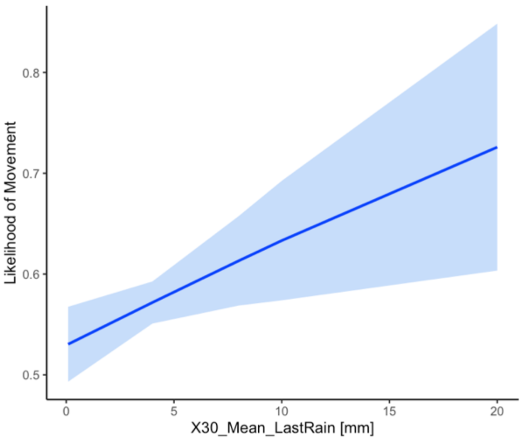

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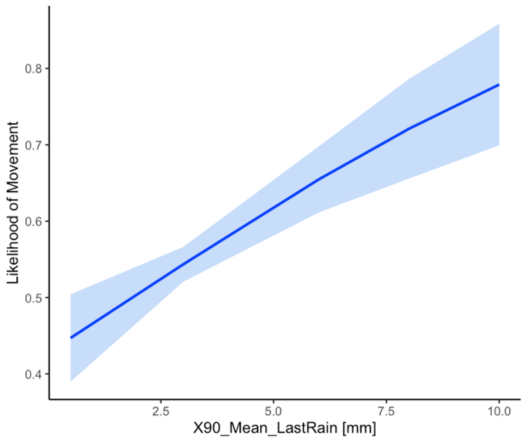

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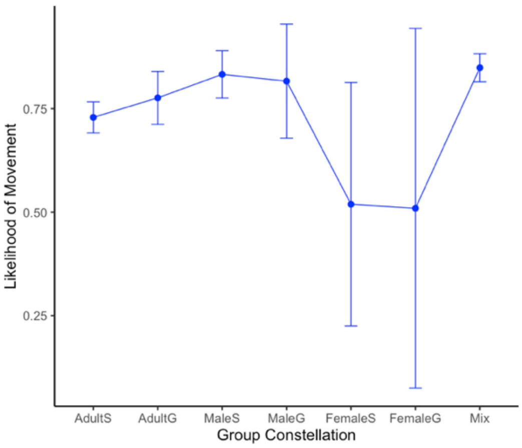


Figure 5: Visualisation of the likelihood of movement with 0 indicating "no" and 1 "yes". Each of the graphs presents the following explanatory variables (A) temperature, (B) precipitation, (C) X30, (D) X90, (E) all categories of group constellation. Additionally, graph (E) includes error bars based on the standard deviation.

(E)

3.3 Effects of predictors on direction

Following the methodology described above, the estimation of the second regression model (Model 2) demonstrates which explanatory variables exert a significant influence on LA movement direction. The direction of movement is significantly influenced by group constellation (p-value: 0.000). The extent to which the odds ratio changes in comparison to the reference category "Male groups" is shown in Table 6 for each group constellation category. Additionally, the vegetation index has a significant effect on the direction for each category (Appendix 6). Table 7 shows the extent to which the odds ratio changes relative to the reference category "11" of the vegetation index. Furthermore, temperature significantly influences the direction of movement, with a 16.865% higher probability to walk "in" per 1°C temperature increase. In contrast, daily precipitation, the average rainfall in the last 30 days, X60, and X90 do not significantly affect the movement direction (Table 5). The analysis under the limited time horizon shows similar findings and thus underlines the validity of the results obtained from the original model (see Appendix 6). Both models have been proven to be overall significant with both the entire data set and the limited data set having a p-value of 0.00. Visualisation of the likelihood of direction of all significant variables is presented in Figure 6. Visualisation of the data points of direction in relation to the significant numerical variable temperature is found in Appendix 7.

Table 5: Estimated regression results of predictor variables from Multivariate Generalized Linear Model (GLM) Analysis with the likelihood of direction "in" as the response variable. More specifically, the response variable is defined as the likelihood of LA crossing the corridor to move in the conservancy. P-values below the significant level of 0.05 have been highlighted.

variable	coef	Std. Error	p-value	Df
temp	0.174	0.035	**0.000**	1
precip	0.043	0.034	0.286	1
X30	0.044	0.054	0.773	1
X60	0.020	0.080	0.666	1
X90	0.011	0.063	0.919	1
Group constellation	-0.436	3.486	**0.000**	6

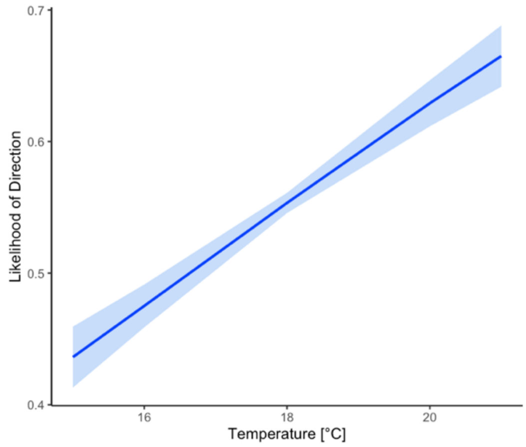
p-value < 0.05: significant

Table 6: Odds Ratio for each category of the categorical variable group constellation, indicating the change of the direction "in" or "out" relative to "Male group". Higher odds ratios suggest higher likelihood of the outcome "in", while lower odds ratios suggest higher likelihood of the outcome "out".

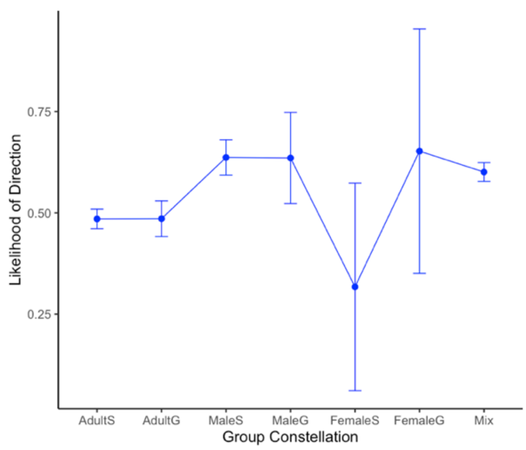
Group constellation	**Odds Ratio**
Male Single	1.005
Adult Single	0.540
Female Single	0.267
Female Group	1.076
Mixed Group	0.863
Adult Group	0.541

Table 7: Odds Ratio for each category of the categorical variable vegetation index, in comparison to the reference category "11". The odds ratios indicate the change in odds of the two directions "in" and "out" relative to "11". Higher odds ratios suggest higher likelihood of the outcome "in" relative to "11", while lower odds ratios suggest higher likelihood of the outcome "out" relative to "11".

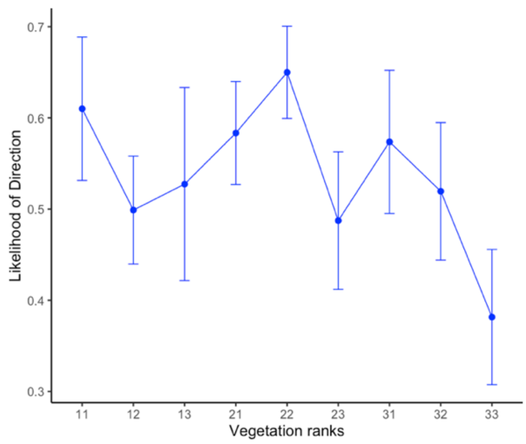
Vegetation Index	**Odds Ratio**
12	0.636
13	0.713
21	0.895
22	1.187
23	0.608
31	0.860
32	0.691
33	0.394



(A)



(B)



(C)

Figure 6: Visualisation of the likelihood of direction of each category of (A) temperature, (B) group constellation, and (C) vegetation index. Here, the value 0 stands for "out" and 1 for "in". In additon, graphs (B) and (C) includes display error bars based on the standard deviation.

4. Discussion

Anthropogenic threats with their severe consequences for the distribution of *Loxodonta africana* (LA) underline the need for protected areas and the understanding of driving factors of the movement of LA. Accordingly, this study assesses the demographic and environmental factors, influencing the movement activity as well as the direction of the movement of LA in Ol Pejeta.

4.1 Interpretation of Results

4.1.1 Movement

The results show that temperature has a significant effect on the movement tendency of elephants with an increased likelihood of 14.868% per 1°C increase. Therefore the hypothesis H3 is accepted. This is slightly surprising as Ol Pejeta does not experience drastic temperature variations. Nevertheless, with temperature being lower during rainy seasons (Isaac & Stuart 1992), the increase in movement activity with temperature might be explained by the search for water resources. Another explanation is evaporative cooling, meaning to regulate their body temperature (Hidden 2009, Mota-Rojas et al. 2021). Because elephants are missing sweat glands, they try to prevent hyperthermia by seeking the cold, flapping their ears, panting (Mota-Rojas et al. 2021), and bathing (Dunkin et al. 2013).

The results for precipitation showed great variability, with daily precipitation leading to a decline in movement activity, while X30 and X90 result in an increase in movement activity. This indicates that the hypothesis H4 on precipitation is rejected, whereas the hypotheses H5 on X30 and H7 on X90 are accepted. There are several explanations for this pattern: According to Young & van Aarde (2010), food and water are more readily available and more evenly distributed across the landscape in the rainy season than in the dry season. The availability of temporal water sources such as puddles, temporary ponds, and streams can explain the importance of precipitation on the movement activity. Higher daily precipitation seems to be slightly decreasing the movement tendencies which might be due to the availability of temporal water sources nearby. In specific, small mud puddles are not only used for drinking but are also a necessity for cooling and as protection from parasites and the sun (Vanschoenwinkel et al. 2011). Furthermore, heavier rainfall can increase the availability and quality of food resources. Subsequently increased foraging effort can increase the overall activity. The mean precipitation of the last 30 days also shows significant effects by increasing the movement tendency by 6.458% with a 1mm increase of precipitation. This again is a response to recent rainfall patterns suggesting rapid adaptation to recent environmental changes impacting the availability and spatial distribution of food and water resources. This in turn enables LA to move more freely in space since they drink daily and usually stay no further away than 15km to water sources (Ihwagi et al. 2010). The time scale of 90 days offers a comprehensive perspective encompassing a larger time span and thus allows a recognisable and lasting influence on environmental dynamics when compared to shorter time intervals. Therefore, the 90 day time span captures the seasonal variability much more effectively. In line with this, a change of movement has been documented by Birkett et al. 2012 at the end of both dry and wet season. Whilst these results provide a good indication of seasonal influence, it should be recognised that they derive from South Africa, where seasonal fluctuations are different as they have pronounced summer-winter weather patterns with just one rainy season. Given this context it is surprising that both X30 and X90 are significant, while the mean precipitation of the last 60 days appears insignificant.

The above results further underline that depending on morphological factors such as sex and age elephants have different movement behaviours (Taylor et al. 2020). Consequently, the hypothesis H1 is accepted. More specifically, the results demonstrate that especially male groups have a very high likelihood to move. The area males are moving in is generally much larger than those of females and this area tends to increase with age and musth (Hollister-Smith et al. 2007). Compared to male groups, single males and single females as well as mixed groups also have just a slightly lower likelihood to move. Males often live solitary as soon as they reached a certain age. Similar to male groups, they travel large distances in search of food and mate (Vidya & Sukumar 2005). These areas usually extend beyond protected areas, explaining their increased likelihood of movement. Single females might have to increase their movement to find food and water sources. Travelling alone they cannot rely on information of group members which might lead them to have to increase their search effort and therewith their range. Mixed groups either consist of females with a calf and/or a subadult or very large family units. The group size can be one explanation for the relatively high tendency to move as they require a higher amount of resources if they consist out of more individuals. In comparison, female groups show a much lower tendency to move. One explanation could be the social stability as these groups are close social units, providing safety. Their sharing of valuable information about resources could also reduce the distances required in the search (Langbauer Jr 2000, Payne 2003). Yet, the results do not explain whether the elephants move in and out on a daily basis or whether they cross once before possibly not returning for a longer period. The effects of X60 and vegetation on movement activity are not significant, hence the hypotheses H6 and H8 are rejected.

4.1.2 Direction

As previously discussed in the chapter 4.1.1 LA might adjust their movement behaviour towards water resources. This aligns with the results of the direction as they confirm that LA has a 16.865% higher probability to walk "In" the conservancy for a 1°C increase. This means the hypothesis H9 is accepted. In the conservancy, permanent man-made water resources are provided. In times of higher temperature, elephants tend to return to areas where necessary resources and especially water are available. Unlike streams and puddles, these man-made water tanks cannot be used for bathing, and they do not provide the protective benefits of mud. Therefore, while these water sources may not fulfil all the elephants needs, they are still frequently used in particular during periods of higher temperature and therefore water scarcity.

Next, group constellation shows to be a defining factor of the direction accepting the hypothesis H2 Between the different categories large variation could be identified in the preference to move "In" or "Out". Single male and male groups have the same likelihood to move inside the reserve. Contrary, single females are least likely to walk into the reserve. This can be explained by a higher vulnerability to predators as the density of *Panthera leo* inside the conservancy is much higher than outside the conservancy (OPC 2023). Additionally, single females may preferably feed on crops outside the reserve (Graham et al. 2010, Amwata & Mganga 2014). On the contrary, female groups tend to walk in the conservancy. Increased protection from predators provided by the group, as well as their knowledge of permanent water sources and therefore energy-saving behaviour, may contribute to this behaviour. Together with their overall low likelihood of moving, this inward movement aligns with the observation that these groups tend to stay in small areas and do not move significantly away from safe locations. Lastly, mixed groups are less likely to move into the conservancy than single male and females as well as group males yet exhibit a higher likelihood than single females. Mixed groups, including calves and subadults, are more vulnerable to predators than groups comprising only adults (Joubert 2006). Nevertheless, if water becomes less available, they are forced to move towards secure water sources as calves and subadults are even more depended on regular water supply.

Vegetation was found to be an important factor, implying that the direction of LA movements are highly influenced by ecological changes arising from seasonal variations. According to Rasmussen et al. (2006) remotely sensed vegetation data are better indicators than precipitation measurements as the latter does not "add to the overall explanatory power" of the model (Rasmussen et al. 2006). In fact, according to Rasmussen et al. (2006), vegetation data show stronger predictive power than precipitation. Even more, the relationship between precipitation and vegetation is sigmoidal, suggesting that vegetation only responds after a specific rainfall threshold is met. Beyond this threshold, further increases in precipitation do not significantly affect vegetation (Rasmussen et al. 2006). The odds ratio of each category of the vegetation index gives further insight in the specific conditions influencing the direction of movement of LA: If the vegetation growth rate is negative, the LA are more likely to move into the conservancy regardless of the current vegetation levels. This is unexpected, as a decreases in food resources is typically expected to deter movements. The vegetation data are based solely on the park, but it can be assumed that similar vegetation patterns also extend to areas in the immediate vicinity of the protected area (Muhati & Abdillahi 2018). However, the protected area has the advantage of having permanent water resources. In addition, LA can switch to alternative food resources in times of food shortage: In fact, during dry seasons a significant increase of uprooting and debarking behaviour especially of Acacia species has been documented (Ihwagi et al. 2010, Muhati & Abdillahi 2018). Extensive debarking can lead to death of those trees within 4-5 years opening up the habitat (Ihwagi et al. 2010). Trees which are more prone to this behaviour can evolve adaptive traits including a higher tolerance to debarking. These improved coping strategies with those damages are in fact observed in the Ol Pejeta conservancy (Muhati & Abdillahi 2018). This further underlines the results that LA prefer to move inside the conservancy even though the vegetation is low. Meanwhile, with a lot of vegetation present and a positive vegetation growth rate LA tend to move out of the conservancy. As vegetation is correlated to the amount of precipitation it can be assumed that in times of high vegetation not only food but also water sources are wider distributed in the landscape. Given the large number of predators in the park that can hide in its tall grass, it may be safer for the elephants to move out of the conservancy. The highest likelihood of moving into the conservancy is at constant medium vegetation abundance. As the vegetation index is likely correlated to the hight of the grass this suggests that LA prefer a medium grass hight. Therefore, the hypothesis H14 is accepted. The effects of precipitation, X30, X60 and X90 on movement direction are not significant, hence the hypotheses H10, H11, H12, H13 are rejected.

4.2 Implication and Relevance

The African savannah elephant, a mega-herbivore and the largest terrestrial mammal in Africa, is a keystone species, whose absence can lead to profound ecological changes (Western 1989, Owen-Smith 1989). Capable of transforming entire landscapes from woodland to savannah, the LA is of great ecological significance (Guldemond & Van Aarde 2008). Additionally, this species holds significant cultural (van de Water et al. 2022) and economic value (Naidoo et al. 2016).

The results of this thesis are relevant to several findings in the recent literature: For instance, the ability to transform woodlands into grasslands has led to the conclusion of LA being a major cause of biodiversity decline, especially in areas with high LA density (Western 1989, Cumming et al. 1997, Western & Maitumo 2004). In specific, the study of Clegg & O'Connor (2017) shows that the LA have their greatest impact on woody vegetation showing behaviour such as "breaking branches, debarking stems, or toppling, pollarding or uprooting whole plants" (Clegg & O'Connor 2017). In contrast, several studies demonstrated that LA actions can lead to an increase of heterogeneity and the creation of new habitats supporting other species. The occurrence of destructive behaviour during periods of grass and forb scarcity recorded by Clegg 2008 indicates a seasonal variation in such activities. This highlights the importance of further understanding elephant movement patterns and behaviour in order to develop effective management measures.

Also, both populations – humans (~ 2%) and elephants (~ 5%) –have been increasing in Kenya over the last years (African Wildlife Foundation 2022, Worldometer 2024). Further reductions in elephant range and fragmentation combined with human populations moving closer to the habitats of LA are resulting in increased human-wildlife conflicts (HWC) (Smith & Kasiki 2000). In general, LA try to avoid human population as shown by their temporal adjustment of activities often moving closer to villages more frequently at night (Cook et al. 2015, Fernando et al. 2023). However, the conversion of wildland into agricultural land contributes to the increase of HWC. Several studies have shown that LA like to feed on crops which leads to conflicts with local farmers (Graham et al. 2010, Mutahi et al. 2015). Additionally, the closure of movement routs by pastoralist communities led to an increased conflict between wildlife and farmers, due to for example crop raiding (Mutahi et al. 2015). One approach to mitigate these HWC has been the erection of an electric fence in OPC in 2006. Yet, this led to a critical increase in the local elephant population and therewith promoted biodiversity destruction. Though fencing is an effective way to reduce HWC, it poses ecological and ethical challenges by restricting elephant movements and potentially degrading habitats. Effective management must balance the ecological and socio-economic impacts with the needs of both elephants and human communities to ensure sustainable coexistence. Altogether, the investigation of movement behaviour is therewith indispensable to mitigate HWC.

Moreover, the findings of this thesis can contribute to future socio-economic planning. Tourism management is a very important generator of income in Kenya and therefore of great interest for politics and economics (Akama et al. 2011). Knowledge about elephant movements can be used not only in the planning of protected areas, but also in sustainable tourism development and sustainable social and cultural development by educating and involving local communities in decision-making processes. This applies, for example, to the sustainable resettlement of villages away from the seasonal elephant routes (Cook et al. 2015).

Socio-economic planning should carefully consider the impact on local communities and elephant populations to ensure the development of strategies that align economic growth with conservation objectives. This ethical approach aims to create sustainable solutions that benefit both locals as well as wildlife and promote long-term coexistence and ecological balance.
Finally, climate change, characterized by higher temperatures, more frequent and longer droughts, and less distinct seasons in Kenya will compel wildlife to rapidly adapt to these upcoming conditions (Marigi 2017). This thesis has shown significant correlations between environmental variables and the movement behaviour of LA. Consequently, environmental changes associated with climate change are anticipated to have an increasingly huge impact on the LA especially in the long run. For instance, extended drought periods may increase the LA's reliance on artificially provided water resources and potentially also on supplementary food resources. Furthermore, extended droughts have been shown to contribute to HWC based on resource scarcity (Mutahi et al. 2015). Therefore, careful long-term conservation planning is crucial to ensure LA can adapt to these changes.

4.3 Limitation of Data

4.3.1 Species data

The entire study is based on demographic data, which is why the accuracy of this data is of the utmost importance. This is to ensure accurate conclusions and prevent misleading results that could affect decision-making processes based on these findings. The data set comprises a total of 4434 observations, which is a sufficient sample size to obtain reliable results. However, the variable "sex" could not be used separately, as the subset of the dataset that included only single sexed adults was too small to provide reliable results.

4.3.1.2 Camera traps

Analysing the pictures taken by the camera traps, several limitations of the data emerged: Firstly, individual identification of the LA has not been carried out. Due to the amount of pictures analysed, individual identification would have exceeded the scope of this study. Although the angle and positions of the cameras covered the entire corridor section, occasionally the cameras were obstructed by animals. This then resulted in several animals not being recorded as the cameras were pointing in a different direction. Furthermore, the fixed positions and angles of the cameras constrained the ability to recognise individual morphological characteristics. In some cases, only partial views of individual elephants, such as their legs were visible, which does not allow reliable individual identification. For accurate identification, features such as tusks or ears had to be visible throughout. Additionally, the visibility of features depends on their proximity to the camera. Yet, information about distinct individuals is of considerable interest to conservation planning as it provides more detailed information on the frequency of corridor use by different animals. This problem could possibly be minimised with high-resolution cameras or videos but to date remains a general problem with camera trap pictures. Secondly, the determination of sex was often impeded by the lack of clearly distinguishable morphological features, resulting in a significant proportion of adults remaining categorically indeterminate, thus compromising the completeness of the dataset when investigating movement differences between the sexes. Furthermore, the lighting conditions influence the distance at which individuals are visible in the images and also influence the possibility of sex determination. In low light conditions the visibility of LA individuals was often limited to individuals photographed close to the camera. When only the silhouette of LA is observed, sex determination was often not possible. To enhance the accuracy of the analyses, it is recommended to use video recordings instead of still images for each observation. This potentially increases the rate of sex determination in LA and ensures more accurate counting in large groups and a better ability to identify individuals based on traits such as specific body movements (Montero-De La Torre et al. 2023). Moreover, to avoid a qualitative day and night difference, cameras which a higher image quality at night could be used. Alternatively, a maximum distance to the camera within which species are reliably recorded could be defined. Thirdly, accurate assessment of age was occasionally challenging, further complicating demographic analysis. Variation in distance between camera and subject, leading to perceived size differences, as well as different light conditions and unequal size comparisons with other individuals and sex-specific size differences may have contributed to inaccuracies in age determination of some individuals. Finally, accurate counting of individuals in particularly large groups is usually complicated by individuals photographed simultaneously by different cameras.

In addition, since several cameras record images of a particular corridor, concurrent recording at great distances and within large groups is very likely. This represents a significant bias as it leads to double counting of individuals. This problem of double recording of single individuals can be addressed in future studies by matching timestamps. For larger groups, however, the problem remains as not all individuals are likely to be captured by each camera, making it difficult to determine their exact composition. Individual identification would help to mitigate this problem.

Next, for greater accuracy of missing observation days, the following measures are recommended for future studies: Instead of examining the days on which the cameras were triggered for selected animals, a comprehensive analysis of images of all animals would be appropriate. This will give a much more accurate picture of when the cameras were not functioning. Further, this analysis should be carried out separately for each individual camera, as these work independently of each other. In addition, documentation of the days on which the cameras were changed is essential, as the exceptions to the regular battery change on Fridays, must be considered in the analysis.

Most studies on the movements of terrestrial mammals use GPS collars (Ngene SM et al. 2010, Polojärvi et al. 2011, Gunner et al. 2021), which have the advantage of providing the exact location of the animal and therefore a comprehensive overview of its movements. In recent years, however, there has been a shift towards an increase in the use of camera traps (Nichols et al. 2011, Trolliet et al. 2014). Despite these shortcomings, camera traps offer several advantages over GPS collars, such as being less expensive and non-invasive (Nichols et al. 2011). In addition, attaching GPS collars to large animals often requires sedation, an invasive procedure (Ngene et al. 2014). In contrast, camera traps can capture an unlimited number of animals and thus provide information on group sizes, age and sex ratios. In addition, the behaviour of the animals in the vicinity of the cameras can also be documented. Altogether, camera traps have been proven to be a highly useful method to conduct studies on the movement of LA but picture-taking should be improved to enable better identification and in turn increase the data reliability. For this reason and despite above shortcomings, the thesis used camera traps.

4.3.2 Environmental data

Both the movement activity and the choice of direction depend on many environmental variables. In this study, only the variables temperature, precipitation and an index of vegetation were considered. The precipitation data used in this thesis derives from Nanyuki, a town 14 km east of Ol Pejeta. Using precipitation data originating from inside as well as outside the corridors would increase the quality of the results and improve the understanding of the movement. Furthermore, an assessment of the outliers (see Appendix 5) of the precipitation data set should be conducted to ensure the reliability on the data set.

Additionally, also the vegetation index should be calculated for both inside and outside the conservancy which however exceeded the scope of this thesis. Moreover, due to temporal constraints within the dataset, the data availability for the vegetation index was limited. As the second analysis of the movement deviated in part from the results of the first, it is important to expand the vegetation index dataset in order to improve the robustness analysis of this thesis. Furthermore, the MSAVI2 data can only be calculated if cloud-free satellite images are available. Consequently, the amount of missing data increases with high cloud coverage, occurring especially during the rainy season. As a result, MSAVI2 data from this

period is lacking, and gaps are filled by interpolating the data using the known values before and after the missing days.
Further, it has been observed that LA tend to resort to alternative food sources such as bark and roots during periods of food scarcity. In specific, increased debarking behaviour has been documented during dry periods (Ihwagi et al. 2010). Consequently, the vegetation index may not provide a comprehensive assessment of food availability. It is therefore necessary to investigate whether behavioural patterns, such as debarking, are common in the study region. Moreover, all possible alternative food resources should be included in future analyses.
The extent of water resources inside and outside the protected area also remains uncertain. Knowledge of the presence of permanent water sources can significantly influence LA movement patterns (Loarie et al. 2009, Fox 2015). Therefore, it is critical to document the timing and locations of both permanent and temporary water sources. The availability of permanent water sources can be another decisive factor.

4.3.3 Limitation and specification

In addition to the variables used in this study, there are numerous other factors that could predict the movement of LA. One such factor could be density dependence (Morales et al. 2010). Demonstrated by many large herbivores (Hopcraft et al. 2014) density dependence is a strategy to avoid intra-specific competition. Yet, Purdon et al. 2018 states that the elephants do not move towards specifically regions with a lower elephant density. Purdon et al. (2018) also criticises that density dependency is not an accurate measure of intra-specific competition as it also depends on the availability of water resources. In addition, it is not known how many LA are in Ol Pejeta at any given time, as a census is only conducted annually. Accordingly, density dependence is excluded from the analysis.
Furthermore, next to sex and age also phenotypic characteristics, such as body size and personalities can influence the movement behaviour as they determine the intra- and inter-specific competition ability (Purdon et al. 2018). Next, LA react strongly on olfactory signals of predators leading them to avoid specific areas of risk (Valenta et al. 2021). Predation events are proven to have long lasting effects on habitat use, demography and behaviour (Lima 1998, Creel & Christianson 2008). Elephants aged 4-15 years old are at major risk to be preyed on by lions (Joubert 2006, John Power & Shem Compion 2009). Whereas it is not very likely that predation has a lasting effect on the elephants population size, the fear and predator avoidance no matter the age, is most likely to be a lasting factor influencing their behaviour. With Ol Pejeta having a very high concentration of lions (OPC 2023) it is possible that predator avoidance is a further variable that explains the direction and movement behaviour of LA. Seasonal interactions could also be considered, as predation success is also dependent on body condition. Similar, grass

height may also play a role in the variation in direction of movements and movement behaviour of LA, as lions can make themselves more invisible in higher grass. Additionally, it is most likely that all morphological as well as environmental variables interact with each other influencing the individual requirements and competitive ability (Purdon et al. 2018). Yet, the model specification concentrated on the analysed predictors due to data inavailability and parsimony and the analysis of additional or alternative explanatory variables remains for future studies.

5. Conclusion

In conclusion, the results of this thesis indicate that both environmental and demographic variables are significantly influencing the movement behaviour of LA. Firstly, this thesis reveals that temperature, precipitation, and mean rainfall over varying time spans significantly affect movement activity, with higher temperatures and longer-term wet conditions promoting increased movement activity. Group constellation also plays a crucial role in explaining variation in LA movement in Kenya, with male groups showing a higher likelihood to move compared to female groups. Secondly, the direction of LA movement is influenced by temperature, group constellation, and vegetation index. Specifically, higher temperatures, both male and female groups, and medium vegetation density increase the likelihood of LA moving into the conservancy. These results suggest both immediate responses of LA movement behaviour to daily environmental conditions and seasonal variations, which in turn are influenced by longer-term climate patterns. Understanding these movement behaviours and dynamics is essential for effective wildlife conservation and management strategies amidst changing environmental conditions.

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Popular science summary

The African savannah elephant is distributed across 24 countries, mainly in South and East Africa and is considered endangered. Having a large impact on their local environment, they play a very important role in the ecosystem. In addition, as they move very large distances they are especially vulnerable to loosing their habitat and the destruction of their migration routes. Accordingly, over the last decades the population has drastically decreased and effort is now concentrated on maintaing these population sizes. Nevertheless, there has been a rise in human-wildlife conflicts. In order to mitigate these conflicts and to improve the conservation of the African savannah elephant it is important when, where and why elephants move.

In this thesis, the movement activity and the direction of movement of the African savannah elephant was investigated in central Kenya. In specific, movement behaviour and direction was assessed with respect to temperature, precipitation, the mean precipitation of the last 30, 60 and 90 days, group constellation, and vegetation. For this purpose, pictures of camera traps located at corridors of a conservancy were used. This thesis discovers two main findings: Firstly, the elephants are moving more whith an increase in temperature as well as a rise in the mean precipitation of the last 30 and 90 days. Meanwhile, movement activity decreases on average with higher precipitation. Male groups are moving the most, whereas female groups are least likely to cross the corridor. Secondly, the direction of the movement is influenced by temperature, group constellation and vegetation. Male and female groups are most likely to move inside and single females and males are most likely to move outside. Elephants are reported to move inside the conservancy with higher temperature as well as shrinking vegetation availability.

Even though further studies should assess additional factors influencing the movement behaviour, this thesis gives a strong indication of the driving factors of the movement behaviour and the direction of movement African savannah elephant in central Kenya. Furthermore, this thesis illustrates that camera traps are a cheap alternative method to GPS collars when stuyding animal movements. In particular in times of increased human-wildlife conflicts and climate change it is very important to understand the movement dynamics of the African savannah elephant for effective long-term wildlife conservation and management strategies.

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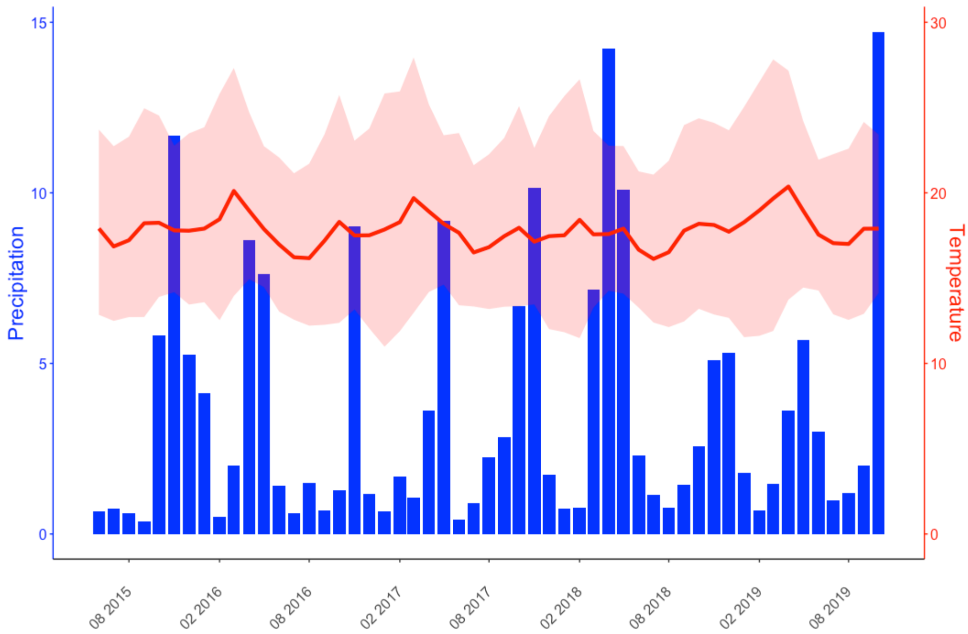
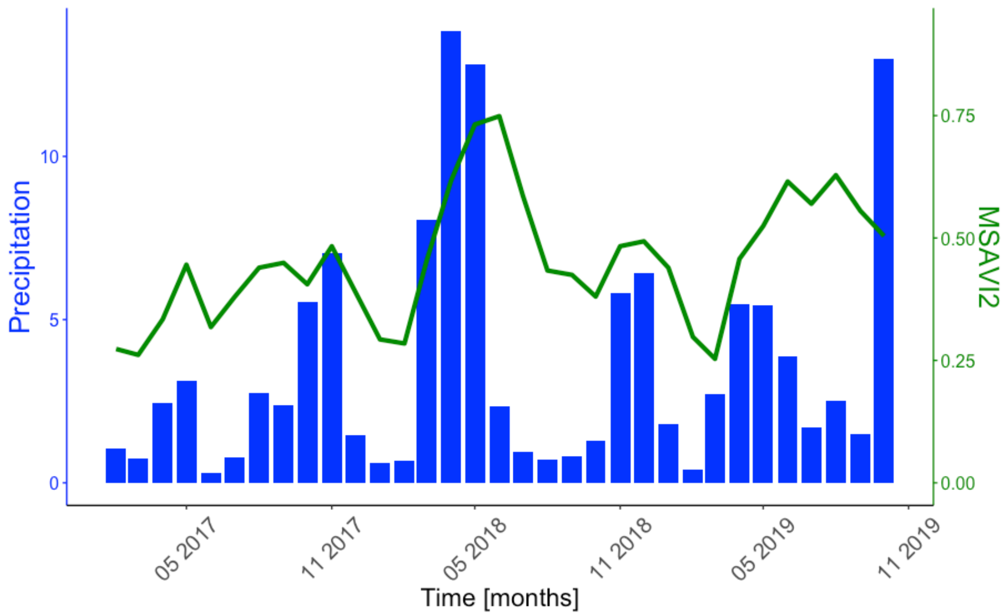
Appendix 1



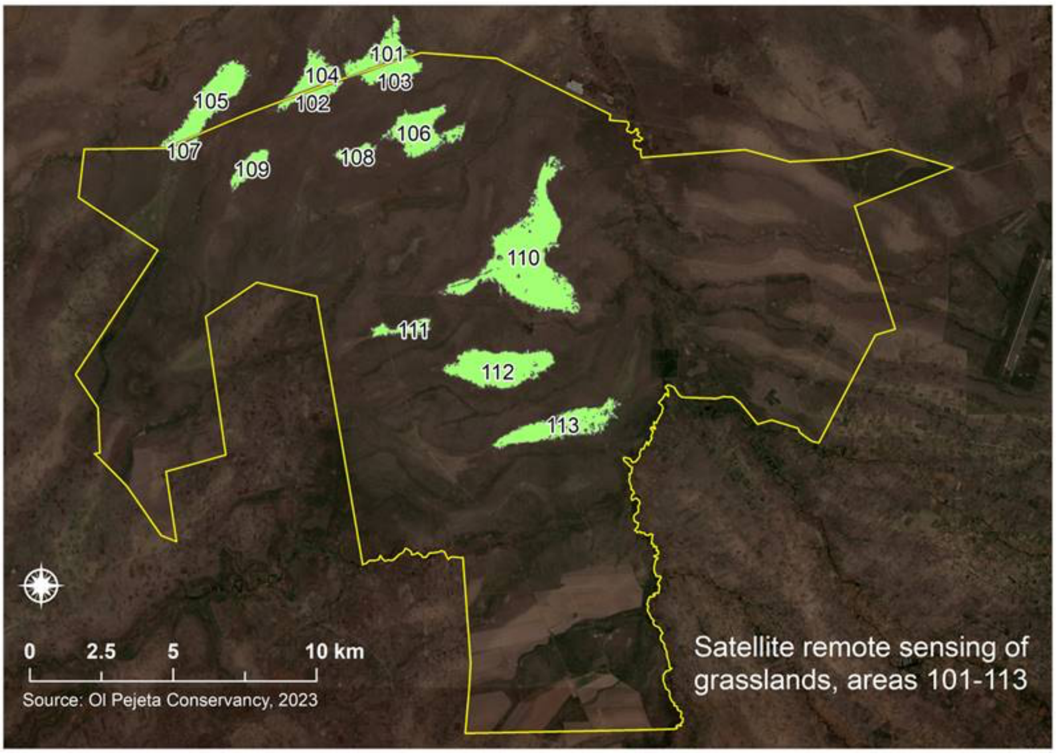
This graph shows the mean monthly precipitation and the mean monthly temperature over the time period 06-2015 and 10-2019. Both temperature and precipitation data originate from the nearby town of Nanyuki.

Appendix 2



This graph shows the mean monthly precipitation and the mean monthly MSAVI2 over the time period 02-2017 and 10-2019. The precipitation data originates from the nearby town of Nanyuki whereas the MSAVI2 data originates directly from inside the conservancy.

Appendix 3



This graph shows the patches used for the satellite remote sensing of the grassland to calculate the MSAVI2. Patches 105, 104, 101 have not been used in this study as their MSAVI2 has not yet been calculated. (Picture originates from Mats Söderström)

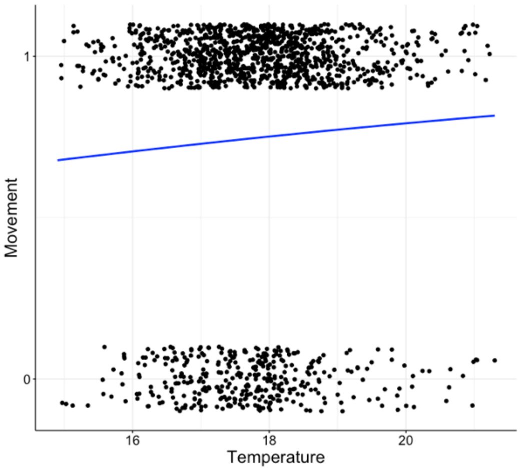
Appendix 4

Estimated regression results of predictor variables from Multivariate Generalized Linear Model (GLM) Analysis (Model 1) with movement as the response variable. Here the limited data set was used in order to use the vegetation index. P-values below the significant level of 0.05 have been highlighted.

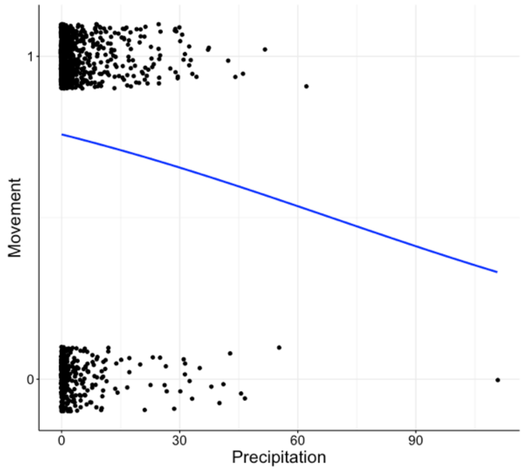
variable	coef	Std. Error	p-value	Df
temp	0.192	0.119	0.105	1
precip	-0.148	0.098	0.219	1
X30	0.465	0.200	**0.029**	1
X60	-0.434	0.289	0.811	1
X90	0.323	0.246	**0.013**	1
Group constellation	-1.955	1.429	**0.002**	6
Vegetation Index	0.400	1.140	0.238	8

p-value < 0.05: significant

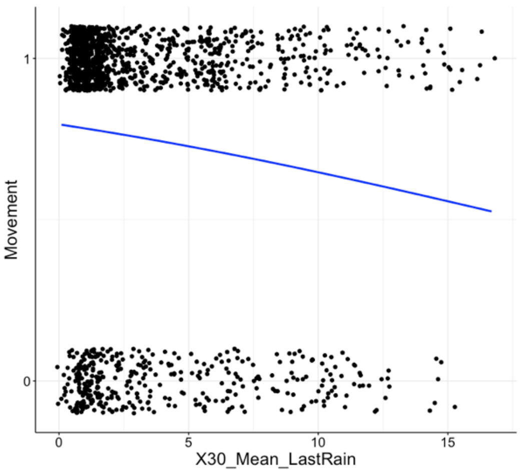
Appendix 5



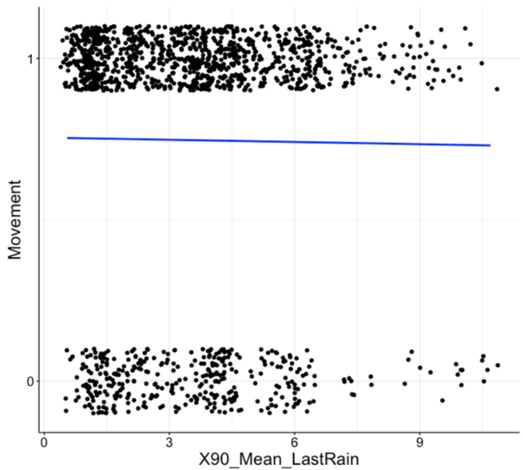
(A)



(B)



(C)



(D)

Visualisation of the data points of movement activity with 0 indicating "no" and 1 "yes" in relation to following significant numerical variables: (A) temperature (B) precipitation, (C) X30 and (D) X90. The blue line represents the logistic regression, illustrating the probability of movement as a function of the respective variable.

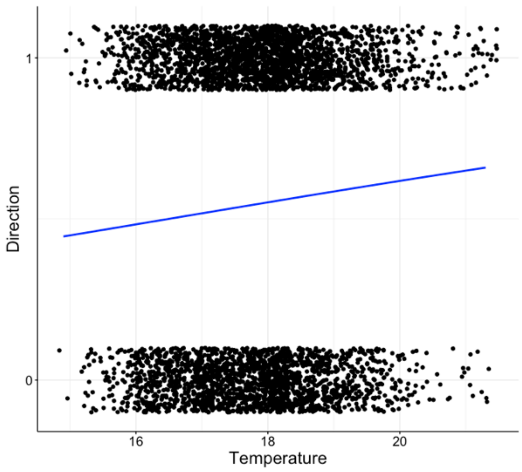
Appendix 6

Estimated regression results of predictor variables from Multivariate Generalized Linear Model (GLM) Analysis (Model 2) with direction as the response variable. Here the limited data set was used in order to use the vegetation index. P-values below the significant level of 0.05 have been highlighted.

variable	coef	Std. Error	p-value	Df
temp	0.324	0.054	**0.00**	1
precip	0.106	0.044	0.295	1
X30	0.045	0.079	0.353	1
X60	-0.060	0.1205	0.324	1
X90	0.118	0.101	0.612	1
Group constellation	-1.963	3.039107	**0.00**	6
Vegetation Index	-0.334	2.897	**0.00**	8

p-value < 0.05: significant

Appendix 7



(A)

Visualisation of the data points of direction with 0 indicating "out" and 1 "in" in relation to the significant numerical variable temperature. The blue line represents the logistic regression, illustrating the probability of direction as a function of the respective variable.

Publishing and archiving

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