



UNIVERSITY OF
GOTHENBURG

DEPARTMENT OF BIOLOGICAL AND
ENVIRONMENTAL SCIENCES

ENVIRONMENTAL AND SOCIAL DETERMINANTS OF ELEPHANT WALKING SPEED IN CONFLICT- PRONE AREAS

Makgadikgadi Pans National Park



Lynn Kleinjan

Degree project for Master of Science (120 hec) with a major in Biology

BIO797, Conservation Biology, 60 hec

Second cycle

Semester/year: Autumn 2024 – Spring 2025

Supervisor: Søren Faurby, Department of Biological and Environmental Sciences
Kate Evans, Elephants for Africa

Examiner: Luc Bussière

Index

Abstract	2
Abstract (SE)	3
Introduction	4
The elephant as a keystone species	4
Threats	4
Environmental conditions	5
Social dynamics	6
Human-elephant conflict	6
Aim and research question	7
Material and method	7
Study area	7
Camera trap data	8
Statistical analysis	9
Data preparation and transformation	9
Modelling approach	11
Results	11
General overview of data	11
Key predictors	15
Walking direction	15
Time of day	16
Temperature	18
Weak or non-significant predictors	18
Rainfall	18
Sex and age	19
Interactions	19
Time of day x temperature	19
Time of day x walking direction	20
Temperature x walking direction	21
Discussion	22
Overview key results	22
Conservation implications	23
Limitations and future research	24
Conclusion	26
Acknowledgements	26
References	26
Appendix 1 Popular science summary	33
Appendix 2 Tables	34
Appendix 3 Residuals	37

Abstract

African savannah elephants (*Loxodonta africana*) are keystone species whose movements play a crucial role in shaping ecosystems. Yet, their populations are under increasing pressure from poaching, habitat loss, and rising levels of human-elephant conflict (HEC). Gaining a better understanding of how elephants move, particularly their walking speed, can help improve conservation efforts and reduce conflict. This study explores how time of day, environmental conditions (temperature, rainfall, water availability), and social factors (sex and age class) influence walking speed in elephants living in the Makgadikgadi Pans National Park in Botswana, a high-conflict area known for its large number of male elephants, called bulls. Between June 2014 and April 2017, camera traps were placed along established elephant paths to monitor movement. The data were analysed using linear models and generalized additive models (GAMs). The direction of travel turned out to be the strongest predictor of speed: elephants moved significantly faster when heading toward water or food. Time of day also had a clear influence, with a 24-hour rhythm showing higher speeds at night, likely reflecting both thermoregulatory needs and possible crop-raiding behaviour. Temperature had a non-linear relationship with speed: elephants moved faster as temperatures rose, up to a point, after which their speed dropped, suggesting an optimal temperature range for activity. Interactions between time of day and temperature, as well as between time and direction, pointed to a complex mix of behavioural drivers. Other factors like rainfall, sex, and age had only weak or inconsistent effects. Taken together, these findings, based on a unique ecological and social context, shed light on the movement patterns of elephants and point to the importance of considering time, environment, and social structure when developing conservation strategies and managing coexistence in human-altered landscapes.

Keywords: African savannah elephant - walking speed – movement patterns - conflict mitigation - elephant pathways - human elephant conflict

Abstract (SE)

Afrikanska savannelefanter (*Loxodonta africana*) är en nyckelart som har stor påverkan på ekosystemens funktion. Samtidigt hotas deras populationer allvarligt av tjuvjakt och ökande konflikter mellan människor och elefanter (HEC), vilket förvärras ytterligare av habitatförlust. För att kunna bevara elefanterna på ett effektivt sätt och minska konflikterna krävs en bättre förståelse för deras rörelsemönster, särskilt gånghastigheten. I denna studie analyseras hur gånghastigheten hos savannelefanter påverkas av tid på dygnet, miljöfaktorer som temperatur, nederbörd och vattentillgång, samt sociala faktorer som kön och ålder. Studien genomfördes i Makgadikgadi Pans nationalpark i Botswana, ett konfliktutsatt område med hög andel tjurar. Data samlades in med kamerafällor längs etablerade elefantstigar mellan juni 2014 och april 2017, och analyserades med linjära modeller och generaliserade additiva modeller (GAM). Den starkaste faktorn som påverkade gånghastigheten var riktningen, elefanterna rörde sig snabbare när de var på väg mot vatten eller föda. Även tid på dygnet hade tydlig betydelse, med en dygnsrytm där hastigheten var högre nattetid, vilket sannolikt speglar både behov av temperaturreglering och eventuellt rörelsemönster kopplade till grödförstörelse. Temperaturen visade ett icke-linjärt samband med hastigheten: elefanterna rörde sig snabbare vid ökande temperaturer upp till en viss gräns, men minskade sedan takten, vilket tyder på ett optimalt temperaturområde för aktivitet. Interaktioner mellan tid på dygnet och både temperatur och gångriktning visade att rörelsemönstret styrs av flera samverkande faktorer. Nederbörd, kön och ålder hade svaga eller inga signifikanta effekter. Trots detta ger studiens resultat, i ett unikt ekologiskt och socialt sammanhang, viktiga insikter i elefanter rörelsebeteende. De understryker vikten av att väga in både tidsmässiga, miljömässiga och sociala aspekter i arbetet med att ta fram effektiva bevarandestrategier och främja fredlig samexistens i landskap som påverkas av människor.

Introduction

The elephant as a keystone species

African savannah elephants (*Loxodonta africana*), the largest known terrestrial mammals, are known for their complex social structures, high intelligence, and wide-ranging movements. As megaherbivores, they require vast areas to meet their dietary and water needs, shaping landscapes and influencing ecological processes in the ecosystems they inhabit (Haynes, 2012; White, 1994). As they move across vast areas, elephants unintentionally perform vital ecological tasks like spreading nutrients, dispersing seeds, and opening up water sources, roles that become especially crucial in dry environments (Wato et al., 2018). Elephants are, therefore, not only ecological engineers but also keystone species whose presence, or absence, has cascading effects on biodiversity and ecosystem functioning (Campos-Arceiz & Blake, 2011; Wall et al., 2013).

The ecological significance of elephants is evident in the ways they alter vegetation structure. Elephants are large, generalist herbivores that function as highly effective seed dispersers. Their substantial body size, broad and often frugivorous diet, and major contribution to vertebrate biomass within ecosystems underpin their ecological impact (White, 1994). Additionally, through browsing and uprooting trees, they can convert woodland to grassland (Ferry et al., 2021), which may favour some species while disadvantaging others. This dynamic role in shaping habitats allows for greater habitat heterogeneity and biodiversity (Zyambo, 2016). Additionally, elephants frequently use and maintain waterholes and pathways to water sources, benefitting numerous other animals (Grainger et al., 2005).

Understanding the movement ecology of elephants is central to grasping their role as keystone species. Their walking speed and directionality reflect underlying behavioural decisions tied to resource availability (Chamaillé-Jammes et al., 2013), social dynamics (Wittemyer et al., 2007), and risk perception (Ihwagi et al., 2018). Movement patterns are not random; they are shaped by cognitive mapping, experience, and environmental cues. How elephants move, how fast they walk and in which direction, often says something about what they're doing and why, and that has direct ecological consequences. For instance, "streaking" behaviour, characterised by rapid, straight-line movement, can indicate goal-directed travel, often toward predictable resources such as waterholes, fruiting trees or agricultural crops, especially in dry or fragmented landscapes (Wall et al., 2013). In contrast, slower and less directional movement is typically associated with foraging, socialising, or exploratory behaviour, often within resource-rich or familiar areas (Wato et al., 2018).

These behavioural distinctions are ecologically significant as they reveal how elephants navigate through landscapes. Movement behaviour to the detail of walking speed and local directionality is poorly mapped in science. This is not only crucial for comprehending the ecological role of elephants, but also for conservation strategies that will indirectly influence general wildlife biodiversity. In recent decades, elephant populations have suffered drastic declines due to poaching, habitat loss, and conflict with humans. It is estimated that African savannah elephant populations have declined by more than 50% in the last 75 years (Gobush et al., 2022). The loss of such a pivotal species presents not only an ethical crisis but also an ecological one, threatening the integrity of entire ecosystems.

Threats

The African savannah elephant has seen a dramatic reduction in population size, particularly in regions where law enforcement and conservation measures are weak. According to the IUCN Red List, the African savannah elephant is currently classified as "Endangered", with an estimated

population of fewer than 350,000 individuals. Conservation efforts have had mixed results, with some regions seeing stabilisation or slight increases in populations, while others continue to experience sharp declines. The elephant's steep population decline is mainly a consequence of poaching and human-elephant conflict due to anthropogenic influences (Gobush et al., 2022).

One of the primary drivers of population decline in African elephants is poaching for ivory. Despite the international ban on ivory trade implemented by CITES in 1989, the illegal trade continues to thrive, driven by persistent demand, particularly in European, American and Asian markets (Nishihara, 2003; Nishihara, 2012; Stiles, 2004). This trade not only depletes elephant numbers but also disrupts social structures, particularly when key individuals such as matriarchs or large bulls are targeted. The loss of these individuals destabilizes group cohesion and can alter movement patterns, making herds more vulnerable to other threats, including human-elephant conflict (Chase et al., 2016; Thouless et al., 2016; Wittemyer et al., 2014). Poaching often occurs in remote areas where law enforcement is limited, exacerbating the challenges in protecting elephant populations, even in protected zones (Thouless et al., 2016).

Human-elephant conflict arises when elephants encounter human settlements and agricultural areas. Urban expansion, agriculture, and infrastructure development have drastically reduced the amount of viable habitat for elephants (Graham et al., 2009). Fragmented landscapes force elephants to cross human-dominated areas, increasing the risk of conflict and injury. The most prominent form of conflict is crop raiding, damaging livelihoods and causing food insecurity for rural communities (Goswami et al., 2015; Graham et al., 2010; Sitienei et al., 2014). Retaliatory killings, defensive fencing, and habitat fragmentation further exacerbate the threats elephants face (Enukwa, 2017; Graham et al., 2010; Webber et al., 2011). This conflict is particularly intense in areas where wildlife corridors intersect with farmlands or where natural resources like water are shared. Additionally, crop raiding conflicts cause harm to humans, high crop losses and additional hidden problems of psychosocial well-being (Gontse et al., 2018; Hoare, 2015; Mayberry et al., 2017).

Environmental conditions

Elephant movement is strongly shaped by dynamic environmental conditions, particularly those that affect water availability and thermal stress (Kinahan et al., 2007; Young et al., 2009). In semi-arid ecosystems, elephants often travel longer distances during dry periods and hotter parts of the day to reach water sources (Young et al., 2009). Additionally, elephants typically need to drink every 1–3 days (Pontzer et al., 2020). Rainfall plays a central role in this: not only does it replenish surface water, but it also stimulates vegetation growth, both of which can trigger shifts in elephant movement patterns (Garstang et al., 2014).

Another major factor is thermoregulation. Because of their massive bodies and poor heat-dissipating capacity, elephants overheat easily, especially in extreme temperatures (Wright & Luck, 1984), of up to 50°C (Baillie & Cole, 1987). As a response, elephants modify their daily activity patterns: they tend to travel or forage more actively during the cooler hours around dawn and dusk (Kinahan et al., 2007), and reduce movement during the midday heat (Graham et al., 2009). This behavioural adjustment is not limited to timing alone; high ambient temperatures have also been shown to correlate directly with a decrease in walking speed, as elephants reduce energy expenditure to avoid overheating (Chamaillé-Jammes et al., 2013; Rozen-Rechels et al., 2020; Thaker et al., 2019). Thermoregulation can therefore affect both the timing and the intensity of movement, often in combination with directional shifts towards water or shaded areas that aid in cooling.

These patterns are not just physiological responses but are also shaped by risk. Time of day, for instance, is relevant not only for temperature avoidance but also for avoiding humans. In regions with poaching pressure or human disturbance, elephants may shift their activity to more nocturnal hours (Douglas-Hamilton et al., 2005; Graham et al., 2009). The fact that thermoregulation and risk avoidance often overlap shows just how flexible elephant behaviour can be in response to environmental pressures.

Social dynamics

Elephant societies are among the most complex in the animal kingdom (Moss & Poole, 1983). Social structure in elephants is strongly influenced by age, sex, and kinship (Wittemyer et al., 2005). Female elephants, cows, live in matriarchal family units composed of related females and their offspring. These units are stable and cooperative, with the oldest female, the matriarch, leading the group (Moss & Poole, 1983). Males, on the other hand, leave the natal herd around puberty (ages 12–15) and alternate between solitary travel and participating in temporary bachelor groups, sometimes switching within a single day. As males mature, particularly into adulthood, they tend to range more widely and move more independently than younger individuals (Evans & Harris, 2008).

Age plays a crucial role in influencing elephant movement. Calves and juveniles have limited mobility and require frequent rest and feeding, which slows overall group movement (Lee & Moss, 1999). Sub-adult elephants begin to explore broader territories as they gain independence (Wittemyer et al., 2013), and this trend continues into adulthood. For adult females, who usually remain in cohesive family units with calves and juveniles, movement is constrained by the need to maintain group cohesion and accommodate the needs of the youngest members (Wittemyer et al., 2005).

Human-elephant conflict

African savannah elephants are highly dependent on permanent water sources and the surrounding vegetation, particularly in semi-arid landscapes. To access these vital resources, elephants rely on established movement routes known as elephant pathways, narrow, vegetation-free trails formed through habitual use (Allen, 2022; Presotto et al., 2019). These pathways not only facilitate access to water and forage but also reflect long-term spatial knowledge passed through generations. Frequently used elephant pathways are often located close to water (Shannon et al., 2009), making them critical corridors in dry environments.

However, humans also tend to concentrate near permanent water sources, relying on these areas for settlement, agriculture, and livestock. This overlapping dependence on limited resources frequently results in spatial conflict. In many regions, cultivated fields located near elephant pathways are at higher risk of crop raiding (Gerhardt et al., 2014), a common form of human-elephant conflict, particularly during harvest seasons when elephants are drawn to high-energy crops. Observations from areas like the Okavango Delta in Botswana confirm that crop raiding is strongly associated with proximity to established elephant routes (Songhurst & Coulson, 2014). Efforts to mitigate such conflicts, including fencing and deterrents, have had mixed results, and understanding movement patterns remains key to developing more effective strategies (Enukwa, 2017).

In Botswana, home to the world's largest population of African savannah elephants, these dynamics are particularly pronounced (Hyvarinen et al., 2021; Osborne et al., 2018; Thouless et al., 2016). The Makgadikgadi Pans National Park, hereafter Makgadikgadi, in north-central Botswana, has

seen significant ecological changes following the return of water to the Boteti River in 2009, after nearly two decades of drought (Evans, pers. comm., 2024). Since then, elephant numbers in the region have increased substantially, with a reported annual growth rate of 16% at its peak, before stabilising in more recent years (Chase, 2015). While many protected areas are dominated by family groups, Makgadikgadi is characterised by a high density of bull elephants, which may result in different patterns of movement and conflict compared to regions dominated by breeding herds (Evans, 2006; Evans & Harris, 2008; Lee et al., 2011; Redmore, 2024).

Aim and research question

The objective of this study is to estimate walking speeds and thereby analyse movement patterns of elephants across different conditions in a conflict-prone and bull dominated area. By looking at the walking speeds and possible environmental and social predictors, this research aims to identify key trends that can support conservation efforts.

The study aims to answer the following primary question:

How do time of day, environmental factors (temperature, rainfall and water resources), and social attributes (sex and age class) influence walking speed of the African savannah elephant in the Makgadikgadi Pans National Park?

By exploring how movement and speed differ based on time of day, social influences and environmental factors, this research seeks to contribute valuable insights into human-elephant coexistence strategies, enabling more effective and sustainable solutions for communities affected by HEC.

The following six hypothesis are tested:

HA: Elephants display faster walking speeds during the night, indicating crop raiding behaviour.

HB: Higher temperatures are associated with decreased walking speed.

HC: Higher rainfall is associated with increased walking speed, due to directed movement towards the river.

HD: Elephants travelling towards a water or food source are associated with increased walking speed.

HE: Solitary bulls travel faster and more directionally than cows.

HF: Older elephants are associated with increased walking speed.

Material and method

Study area

The protected area of the Makgadikgadi covers approximately 4,900 km (Chase, 2015) in north-central Botswana. The parks lie southeast of the Okavango Delta, and are bordered to the west by the Boteti River, which marks a sharp transition from protected land to surrounding communal areas. The Boteti River is of critical ecological importance, serving as the primary water source in an otherwise semi-arid region. As the river resurged it altered wildlife movement in the area, damaging the wildlife fence that zigzagged across the river and was built in 2004 to reduce livestock-wildlife conflict. During the time period the data was collected, the fence remained severely damaged and dysfunctional along the western boundary despite of maintenance efforts. Allowing animals to move freely between the park and surrounding lands (Evans, 2019).

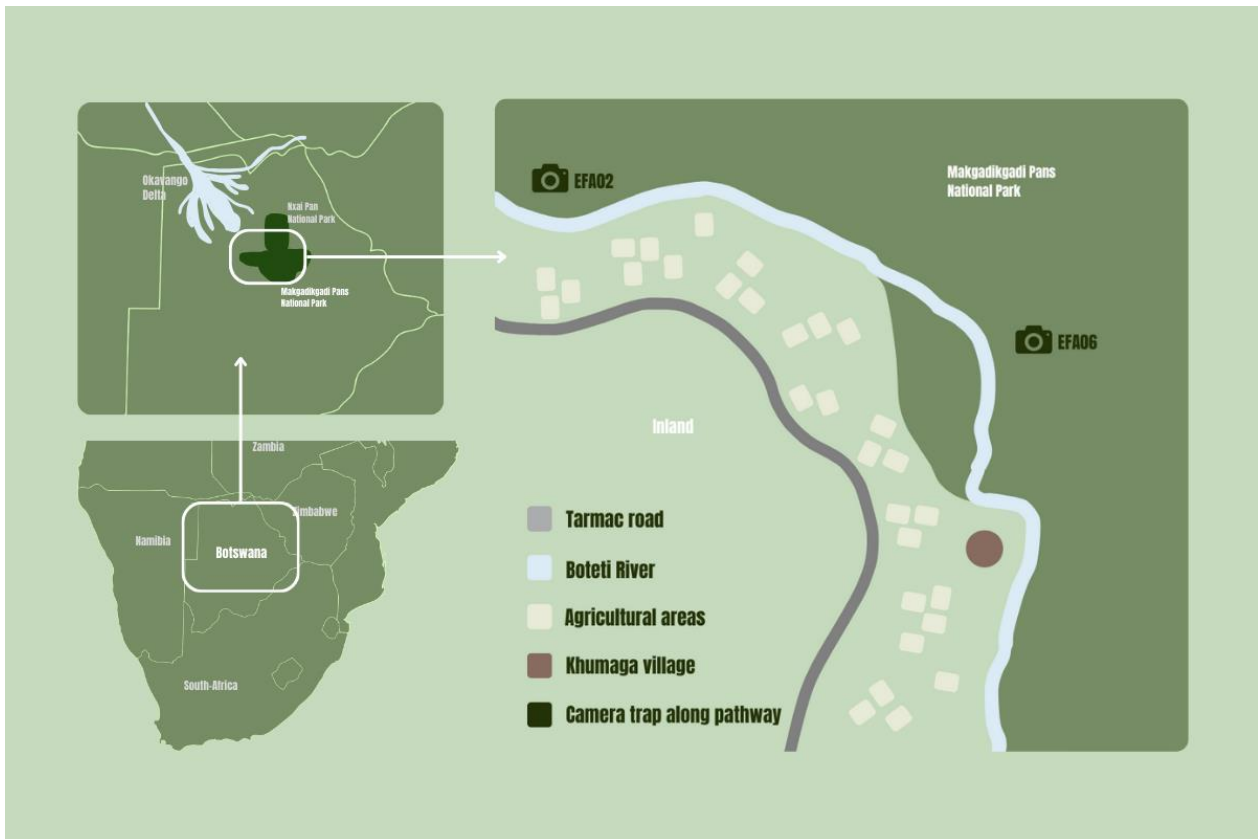


Figure 1. Map of study area. Camera positions are marked with dark green camera icons, Khumaga village is represented by a brown dot and the Boteti River by the blue line. The darker green represents Makgadikgadi, while the lighter green represents unprotected land with beige marking agricultural fields. The inlay shows the maps position within Botswana represented by a white rectangle.

The region experiences a semi-arid climate, with two distinct seasons. The wet season lasts from roughly November to April (Allen et al., 2021; Chase, 2015), during which rainfall is highly variable and often localised, with an annual average of approximately 450 mm (Meynell & Parry, 2002). Temperatures during this period can exceed 40°C during the day. The dry season extends from May to October, with cooler nights and daytime temperatures averaging around 28°C. Ground frost is occasionally recorded (Kgathi & Kalikawe, 1993; Thomas & Shaw, 1991). Vegetation in the park varies, western riparian zones characterised by dense shrubs and trees from, such as thorn trees and gum acacia, while the eastern areas consist predominantly of open grasslands and more sparsely scattered vegetation (Brooks, 2005).

Makgadikgadi hosts a predominantly male savannah elephant population, with approximately 98% of sightings consisting of bulls (Evans, 2019). Elephant density fluctuates seasonally, increasing during the dry months as individuals concentrate near permanent water sources, and dispersing during the rains when temporary pools and fresh forage become available. The park also contains a network of well-defined elephant pathways, connecting key resources across the landscape (Allen et al., 2021; Allen et al., 2020; Gerhardt et al., 2014).

Camera trap data

This study utilised camera trap data collected by Elephants for Africa (EFA) between June 2014 and April 2017. Camera traps were placed along eight established elephant highways within the Makgadikgadi. The cameras (Reconyx HC600 Hyperfire, with the exception of EFA06 using Bushnell 119435C until April 2016) were motion-triggered and captured images at one-second intervals when activated. Data collection paused between April and July 2016. However,

inconsistencies in the dataset, due to camera traps being moved along the elephant highway, when trees that the camera traps were attached to, or poles, were damaged, limited the usable data. Only two cameras, EfA02 and EfA06, were deemed reliable for this study.

Camera trap photographs used in this study were collected through the Snapshot Safaris project (SnapshotSafari), in which citizen scientists identified wildlife captured in the images. The resulting data were compiled in an Excel database, with each row representing one photo. Each entry included a link to the image, capture site (EFA02–EFA09), date and time of capture, the identified species, and a consensus probability score (p) reflecting agreement across observers. A score of $p = 1$ indicated unanimous agreement (100%), while $p = 0.5$ indicated that 50% of observers identified the same species.

For this study, the dataset was filtered to include only elephant observations at sites EFA02 and EFA06. To ensure usable speed measurements, only sequences containing at least two consecutive photographs were included. Further filtering removed individuals that were stationary or not clearly moving along elephant pathways. This was based on the ‘moving’ variable, retaining only observations with $p > 0$.

To calculate walking speed, a pixel-to-metre scaling factor was established by measuring the shoulder-to-foot height of male elephants in the images and referencing the known average adult male height of 3.5 metres. Sequential photographs were overlaid using the image processing software Fiji2 (Schindelin et al., 2012). Distances were measured between consistent anatomical marks (e.g., tip of the tusk or base of the tail), depending on visibility across frames. Speed was then calculated in R using time intervals between frames, resulting in movement speeds in metres per second, which were converted to kilometres per hour using the following formula:

Equation 1: Calculation of walking speed (in km/h) from the measured distance (in pixels), scale factor (metres per pixel), and time interval between frames (in seconds), with conversion from metres per second to kilometres per hour.

$$speed \left(\frac{km}{h} \right) = \left(\frac{d \times s}{t} \right) \times 3.6$$

d = measured distance between two points on the elephant (in pixels)

s = scale factor (metres per pixel)

t = time interval between photos (in seconds)

3.6 = conversion factor from m/s to km/h

A total of 1,176 movement observations (63 from EfA02 and 1113 from EfA06) were successfully analysed for walking speed. For cases where an elephant moved too fast to be captured on sequential images, speed was imputed as the maximum measured speed in the dataset (27.35 km/h). In addition to speed, walking direction and ambient temperature at the time of capture were recorded for each observation. To ensure that only active movement was considered in the analyses, observations with a recorded speed of 0 km/h were excluded.

Statistical analysis

Data preparation and transformation

To prepare the dataset for statistical modelling, raw camera trap data from two sites (EFA02 and EFA06) were imported, cleaned, and merged into a unified dataset. Timestamps were created by combining date and time fields. From these, the hour of the day was extracted for time-of-day analyses. Time of day was hypothesized to affect walking speed through circadian or thermal influences. Because time is circular, using raw hour values in linear models can be misleading. For example, 00:00 and 01:00 are numerically far apart from 23:00, even though they are adjacent in real time. To capture this variation, four transformations of the hour variable were created: a sine-

transformed 24-hour cycle, peaking at midday (Equation 2, Figure 2), a cosine-transformed 12-hour cycle capturing dawn/dusk activity (Equation 3, Figure 2), and two Gaussian dip functions centred at 12:00 and 15:00, respectively (Equation 4, Figure 2).

Equation 2: Sine transformation to model a 24-hour circadian cycle, peaking at hour 12:00 and reaching a minimum at hour 0 and 24.

$$24\text{h cycle} = \sin\left(\frac{2\pi \cdot \text{hour}}{24}\right)$$

Equation 3: Cosine transformation to represent a 12-hour cycle, shifted to align peaks with hour 6 and 18 (dusk and dawn), capturing sub-daily rhythmicity.

$$12\text{h cycle} = \cos\left(\frac{2\pi \cdot (\text{hour} - 6)}{12}\right)$$

Equation 4: Gaussian-shaped negative exponential function to model a dip in activity or value around midday or afternoon. The parameter μ determines the centre of the dip (12:00 or 15:00), and σ controls the width of the dip.

$$(\text{after})\text{noon dip} = -\exp\left(-\frac{(\text{t} - \mu)^2}{2\sigma^2}\right)$$

Where $\mu \in [12,15]$ and $\sigma = 1$.

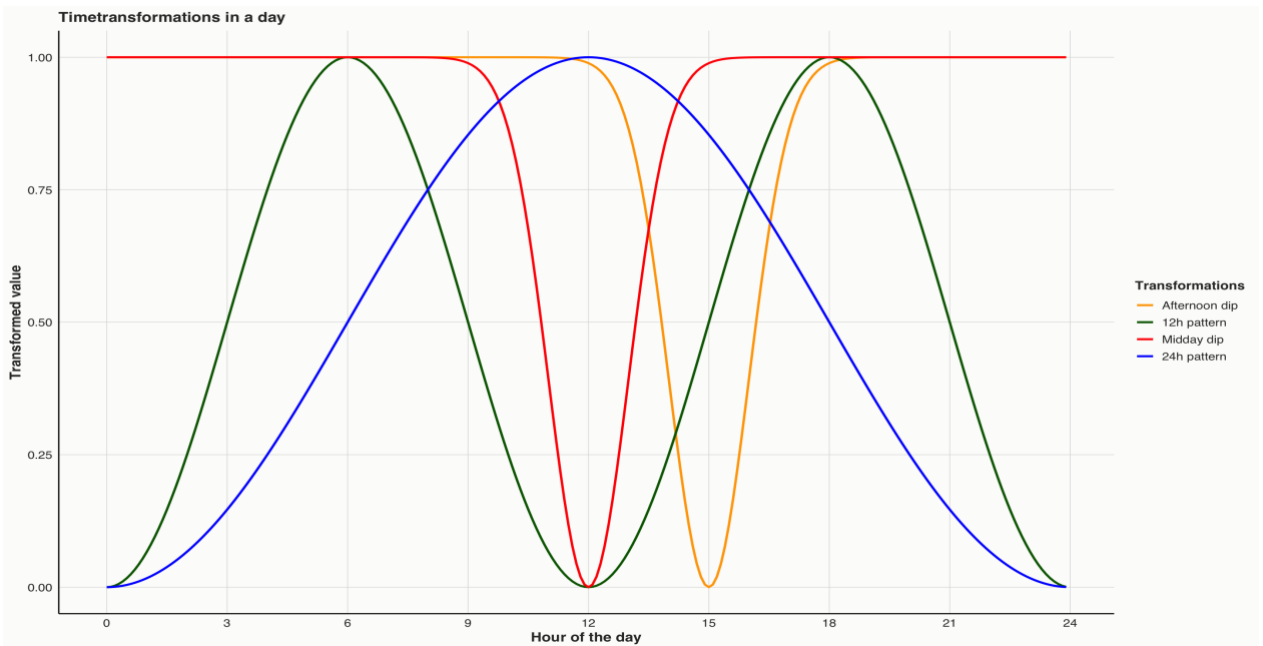


Figure 2. Visualization of different time-based transformations over a 24-hour period. The plot shows a sinusoidal 24-hour pattern (blue), a cosine-based 12-hour pattern (dark green), and two dip transformations capturing reduced values around midday (red) and afternoon (orange).

These transformations were applied to the extracted hour (0 – 23) variable to model temporal variation in walking speed. The sine and cosine transformations allowed for modelling cyclical patterns in time while maintaining compatibility with both LMs and GAMs. This method was chosen deliberately: although cyclic splines could have been used in the GAMs alone, the chosen sinusoidal transformations enabled consistent time modelling across both linear and additive modelling approaches.

Additionally, extra information was added to the unified dataset. A dataset on rainfall was joined based on date, and a 30-day rolling average was computed to represent cumulative prior rainfall using the *rollmean* function from the *zoo* R package (Zeileis & Grothendieck, 2005). To reduce skewness and stabilize variance, a square root transformation was applied. Identifying whether the observation came from a cow herd or bull group, hereafter named sex, was inferred from group composition, whereby observations with a juvenile presence probability > 0.5 were identified as ‘female’, and remaining observations as ‘male’. Age was coded numerically as juvenile (0), sub-adult (1), or adult (2). Records with unknown age were excluded from age-related analyses. All continuous predictors were visually inspected for outliers and transformed where necessary to meet

model assumptions. Data wrangling and reshaping were performed using the *dplyr* and *tidyr* packages (Wickham et al., 2023; Wickham et al., 2024).

Modelling approach

Statistical modelling focused on identifying which environmental and biological factors best explain variation in elephant walking speed. Two modelling frameworks were used: linear models (LMs), using the *lm* function in the *stats* R package (R Core Team, 2025), and generalized additive models (GAMs), using the *gam* function in the *mgcv* R package (Wood, 2017). LMs were applied to all predictors, being time of day, temperature, walking direction, sex, rainfall and age. GAMs were employed to detect and model non-linear effects of continuous predictors, being time of day, temperature and rainfall. Default dimension of knots was used for the smoother, unless exceeding the number of unique observations for a variable. In those cases, dimension was set to 7. Each model was fitted to the unified dataset as well as separately for the smaller and bigger dataset of the different sites using the *map* function in the *purrr* R package (Wickham & Henry, 2025). Additionally, interactions between predictors were explored to determine whether the effect of one variable depended on another using both LMs and GAMs.

Model assumptions were assessed using residual diagnostics, including histograms, residual plots, and Shapiro-Wilk tests. Model visualisations and diagnostic plots were produced using *autoplot* in the *ggfortify* R package (Tang et al., 2016) and *vis.gam* in the *visreg* R package (Breheny & Burchett, 2017). In all GAMs, initial models were fitted with a Gaussian error distribution. However, residuals consistently deviated from normality (Shapiro-Wilk $p < 2.2e-16$). As a result, all GAMs were refitted using a Gamma error distribution with a log link, and a small constant (0.01) was added to the response variable to ensure positivity. Model fit and explanatory power were evaluated using summary statistics, AIC values, and visualization of predicted versus observed values using the *ggplot* function in the *ggplot2* R package (Wickham, 2016).

Temperature was tested as both a linear and quadratic predictor in LMs, and as a smooth term in GAMs. The inclusion of a quadratic term in the linear models allowed for the detection of simple curvilinear (e.g., unimodal) relationships, while maintaining model interpretability. This approach served as a parsimonious alternative to GAMs when non-linearity was suspected but not complex. GAMs, in contrast, offered a more flexible, data-driven way to model potentially irregular or non-symmetric effects.

Results

General overview of data

The dataset comprises 1176 observations from two distinct locations, s and EFA06, with the coordinates for these sites as follows: EFA02 (5°58.38' N, 38°36.41' E) and EFA06 (5°58.64' N, 38°36.50' E). These observations include various environmental and behavioural variables, which include speed, temperature, direction, precipitation, sex, age, and time of day. The number of observations varied considerably between sites and months (Figure 3). For EFA02, the data were collected from November 2014 to March 2016, with observations being sparse and irregular. The number of observations varied, with a peak of 12 observations in April 2015, followed by a decrease in subsequent months. In contrast, EFA06 had a much larger dataset, with observations spanning from July 2016 to December 2016. The highest number of observations occurred in August 2016, with 345 observations, while the lowest count was in October 2016, with 26 observations. EFA06 exhibited a clear seasonal pattern, with higher numbers of observations during August and September as well as December and January, while showing less observations

in October and November. To facilitate readability, EFA02 will hereafter be referred to as the 'small site', and EFA06 as the 'big site'.

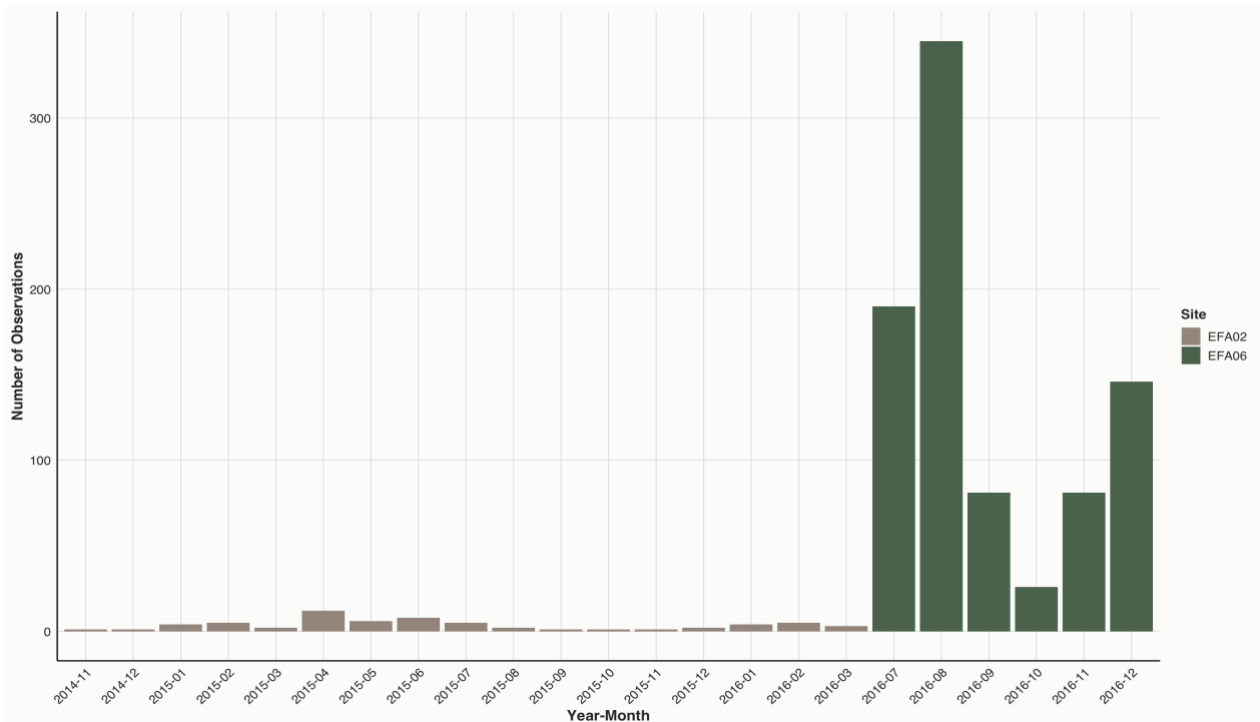


Figure 3. Number of observations per site over time, categorized by year and month. The data shows the variation in observation counts at two different sites (small EFA02 and big EFA06).

The speed of the observations ranged from a minimum of 0.07 m/s to a maximum of 27.35 m/s. The mean speed was 7.61 m/s, with a median value of 5.62 m/s, indicating a moderately skewed distribution, with a standard deviation of 5.32 m/s (Figure 4A). Temperature values varied between 5°C and 43°C, with the mean temperature being 21.51°C and the median at 20°C (Figure 4B).

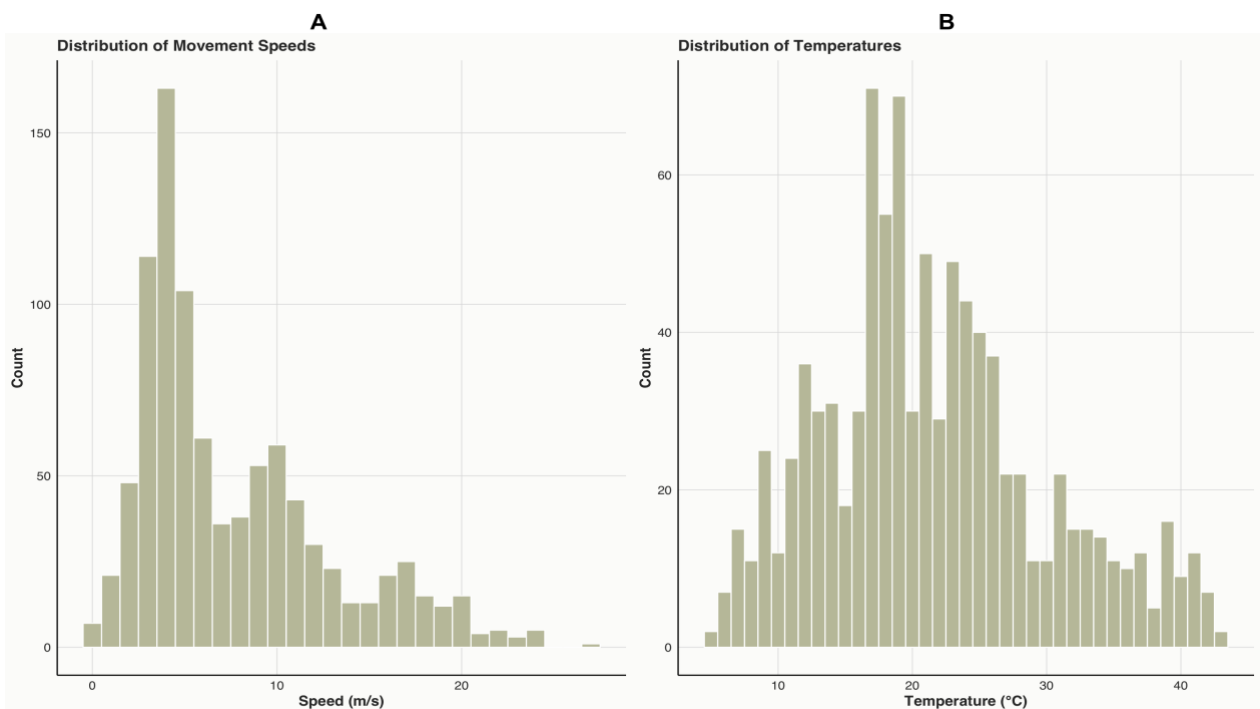


Figure 4. Range and frequency of speed and temperature across the dataset. A: Distribution of movement speeds (in meters per second) observed in the study. B: Distribution of temperatures (in °C) recorded during the study.

The direction of movement was grouped by site and classified as either left (L) or right (R) relative to the camera. At the small site, there were 42 observations of elephants moving towards the river and 21 moving inland. At the big site, the observations were more numerous, with 399 instances of leftward movement and 470 instances of rightward movement. When the counts were aggregated across both sites, the total number of leftward movements was 441, while rightward movements totalled 491. Figure 5 shows the distribution of movement directions across the two locations.

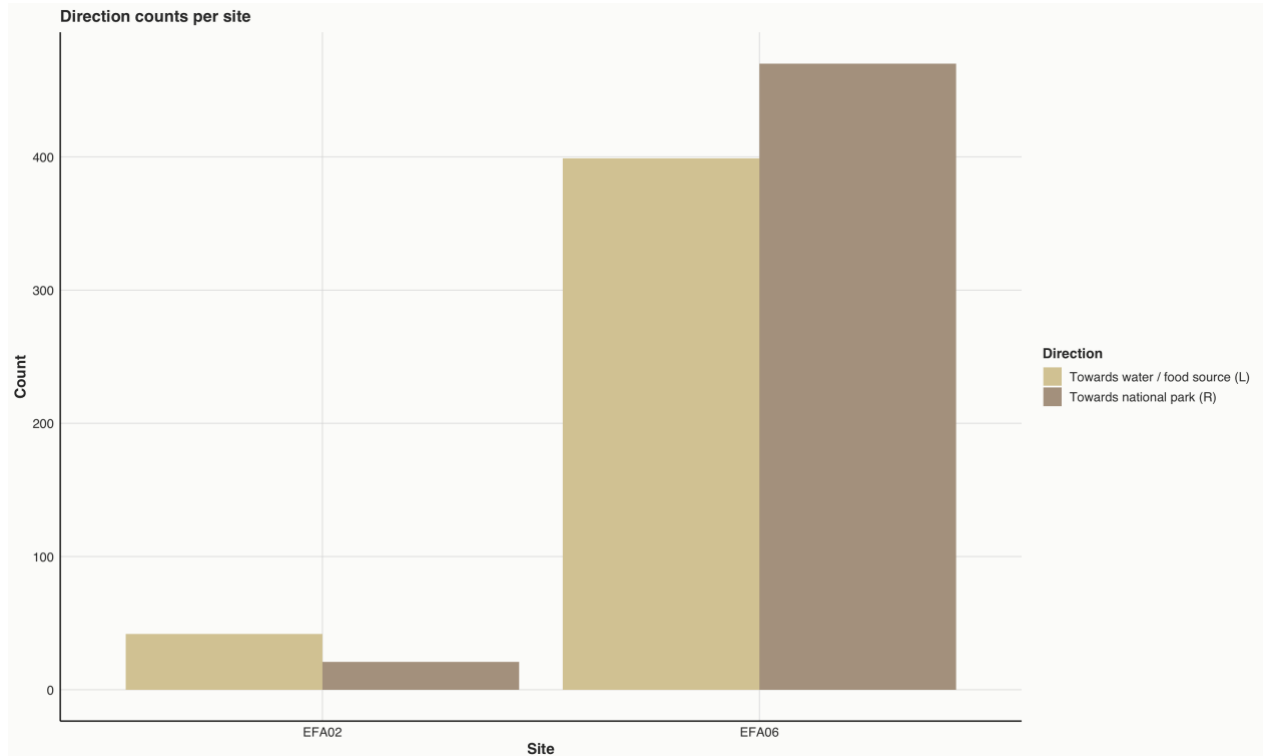


Figure 5. Counts of left (L) and right (R) directional movements for each site. The plot compares directional preferences across sites.

Precipitation data was included in the dataset, with 30-day rolling averages calculated to account for temporal trends in rainfall. The distribution of raw precipitation data showed a minimum of 0.00 mm, a median of 0.00 mm, and a mean of 0.36 mm, with a maximum of 20.00 mm. The transformed precipitation data, based on the square root of the rolling averages, showed a more normally distributed pattern, with a mean of 0.37 and a maximum value of 1.99.

The variable of sex was determined by the presence of young, as indicated in the dataset. The dataset contained observations of both male and female elephants, but the distribution of sexes varied across the two sites. At the small site, only males were present, with a total of 63 observations. At the big site, both males and females were observed. Specifically, there were 809 male observations and 60 female observations. These numbers indicate a notable difference in the representation of sexes between the two sites, with a larger number of males observed. For females, the observed speeds ranged from 1.30 m/s to 24.50 m/s, with a mean speed of 8.53 m/s and a median of 5.71 m/s. The standard deviation for females was 5.51 m/s, based on 60 observations. For males, the speed ranged from 0.0701 m/s to 27.40 m/s, with a mean of 7.55 m/s, a median of 5.61 m/s, and a standard deviation of 5.15 m/s, based on 872 observations (Figure 6).

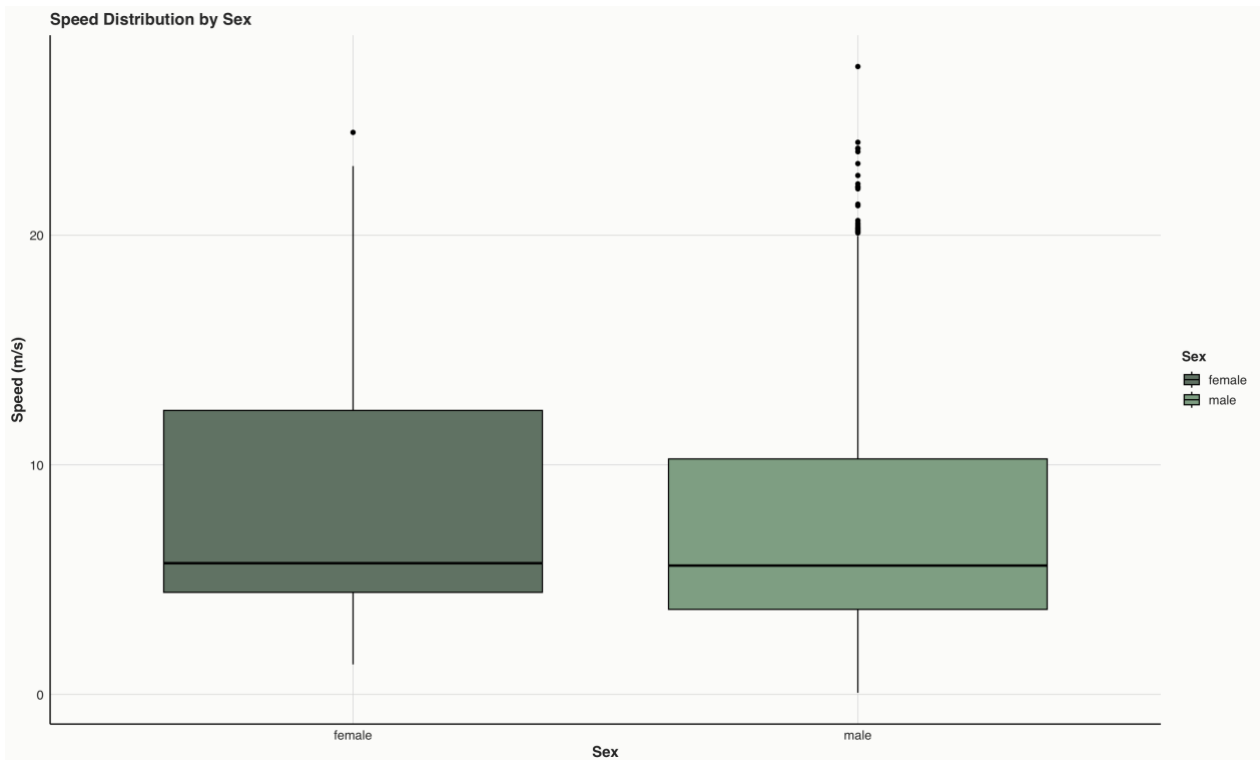


Figure 6. Boxplot illustrating the distribution of movement speeds by sex. The plot compares the median, interquartile range, and outliers between males and females.

The analysis of movement speeds across different hours of the day revealed that the minimum recorded speeds ranged from 0.07 m/s to 5.85 m/s, while the maximum speeds varied between 8.07 m/s and 24.10 m/s, reflecting the lowest and highest observed speeds at each hour of the day, respectively. The average speed across the day fluctuated, with the highest speeds generally observed during the early morning and midday hours. In contrast, the lowest average speeds were recorded later in the afternoon, particularly around 15:00 (Figure 7).

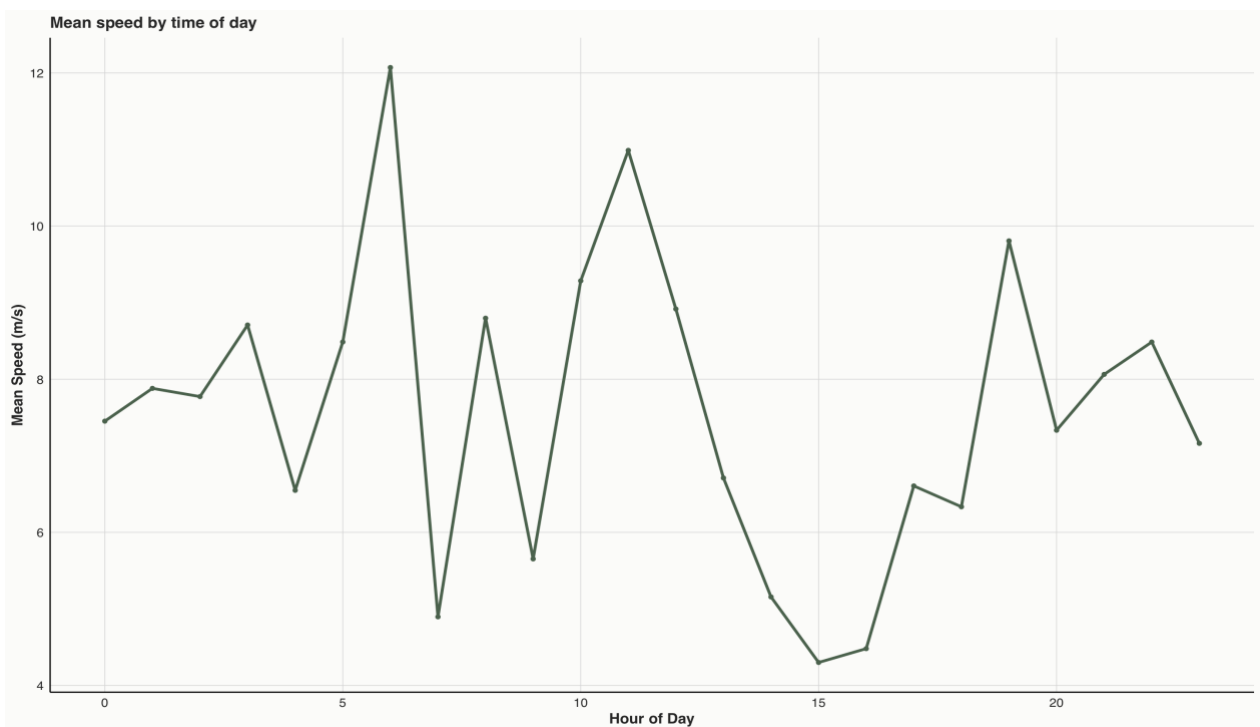


Figure 7. Line plot illustrating movement speed across the day. The plot shows the mean movement speed across different hours of the day.

The distribution of age categories for the two study sites is as follows. For the small site, the data primarily represent sub-adult and adult elephants, with 36 sub-adult elephants (10-20 years), 25 adult elephants (21-36+ years), and 1 juvenile elephant (0-9 years). Additionally, 1 observation was classified as "unknown" and removed. For the big site, juvenile elephants (0-9 years) were more frequently observed, with 84 juvenile elephants recorded, alongside 504 sub-adult elephants and 249 adults. There were also 32 observations labelled as "unknown", which were also removed. Across both sites, the data predominantly reflect the behaviour of sub-adult and adult elephants, with juvenile elephants being less frequently observed (Figure 8).

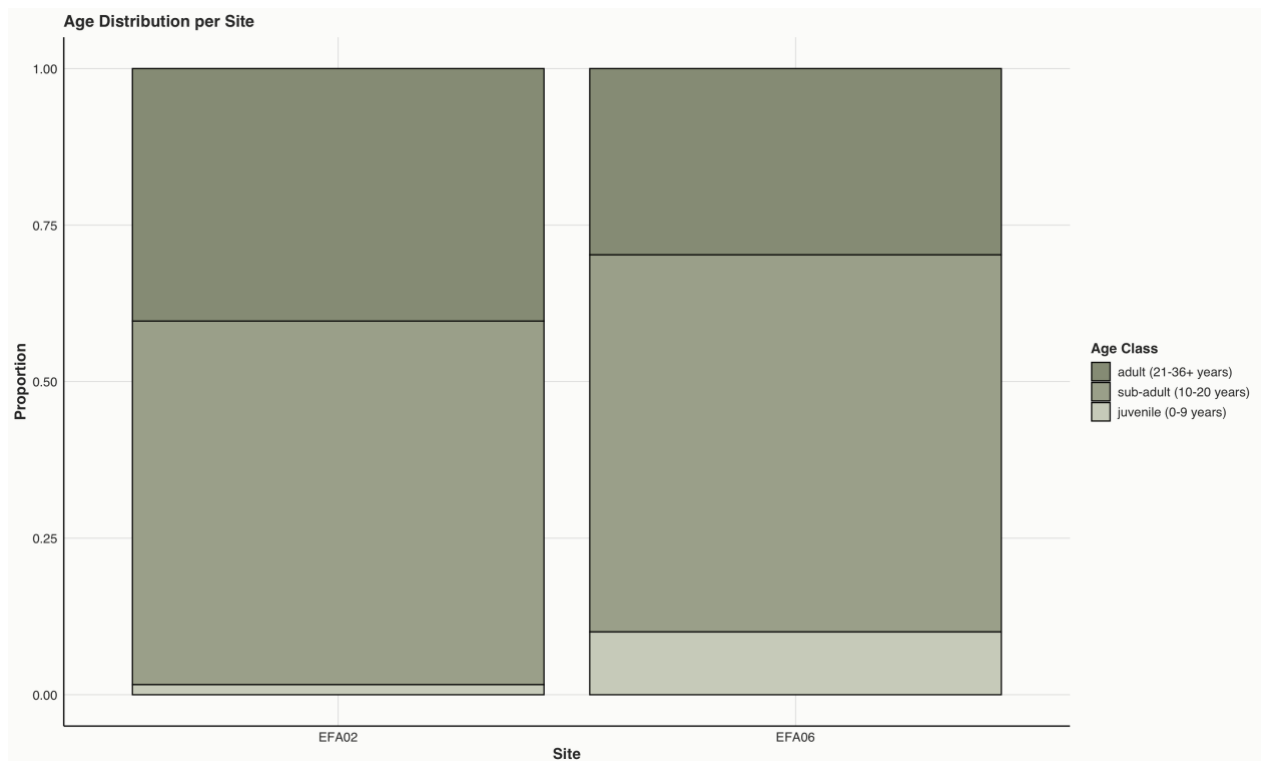


Figure 8. Proportional distribution of age classes (juvenile, sub-adult, and adult) across different sites. The fill shows the proportion of each age class at the two sites.

Key predictors

Walking direction

Walking direction emerged as the strongest and most consistent predictor of movement speed. Elephants moved significantly faster in one direction compared to the opposite direction, with this effect clearly present in both the combined dataset ($\beta = -7.44$, $p < 0.001$, $R^2 = 0.52$) and at the big site ($\beta = -7.90$, $p < 0.001$, $R^2 = 0.57$) (Figure 9). The high explained variance indicates that walking direction accounted for a substantial portion of variation in movement speed. No significant effect was found at the small site, likely due to limited sample size. This result highlights a clear and consistent directional effect on movement behaviour, where elephants move faster when walking towards the water and/or food source compared to walking inland. Other statistical outcomes are listed in Appendix 2 (Table A2.1).

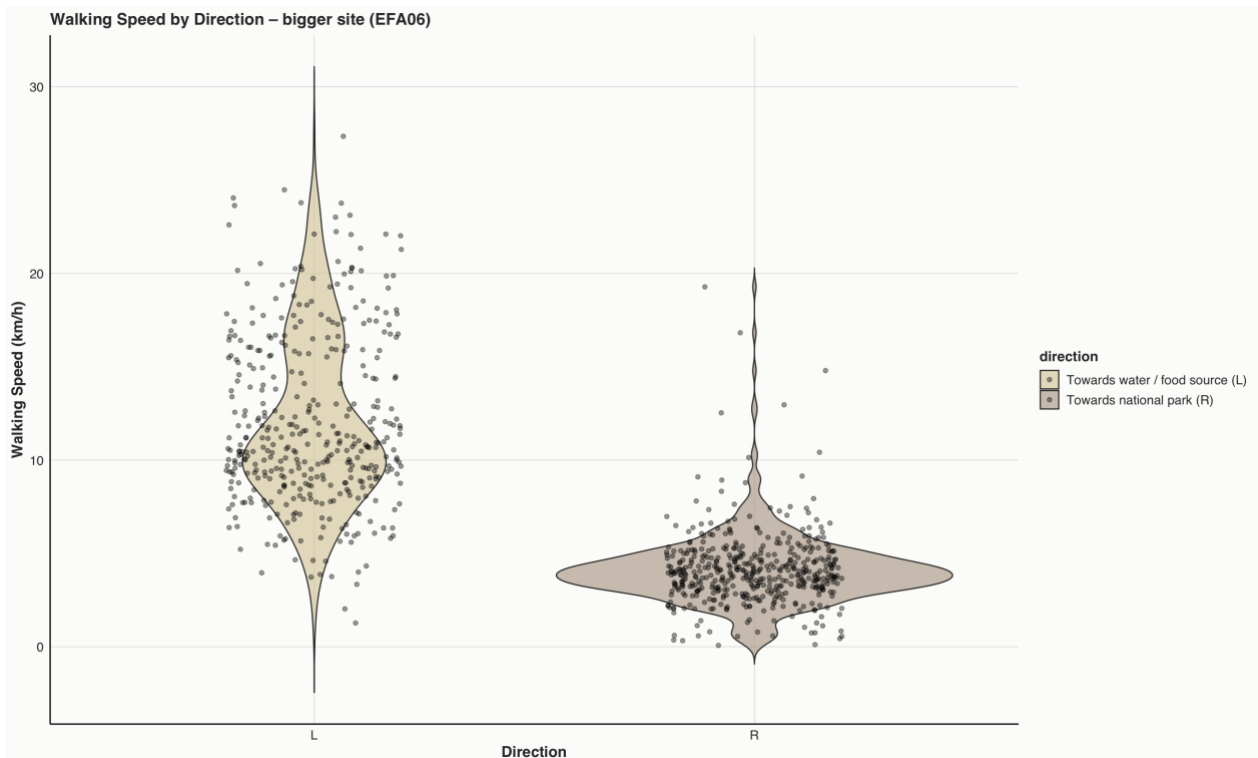


Figure 9. Distribution of walking speeds by movement direction separated for the bigger site (EFA06). The violin plot shows the full distribution of walking speeds (km/h), with individual observations overlaid as jittered points.

Time of day

Movement speed varied systematically with time of day. In linear models, a consistent afternoon dip was observed in the combined data ($\beta = 4.32$, $SE = 0.808$, $p < 0.001$, $R^2 = 0.030$) and at the big site ($\beta = 4.71$, $SE = 0.865$, $p < 0.001$, $R^2 = 0.033$), with elephants slowing down around 15:00. The model for the big site showed the best model fit (AIC = 5313) (Figure 10).

Movement speed varied systematically with time of day, with the 24H GAM for the big site emerging as the best model (lowest AIC = 5005). This GAM revealed a clear 24-hour rhythmicity (edf = 6.82, ref.df = 7.94, $p < 0.001$, $R^2 = 0.047$), suggesting that elephants exhibited a circadian rhythm in their movement patterns (Figure 11). Additionally, significant effects for the 12H (bimodal activity pattern) and noon dip transformations were found in the GAMs for both the combined dataset and EFA06, though these models had lower AIC values than the 24H GAM for the big site.

At EFA02, only a single significant effect (afternoon dip in a GAM: edf = 3.91, ref.df = 3.99, $p = 0.0023$, $R^2 = 0.213$) was found, suggesting potential site-specific variation in behavioural rhythms. Other statistical outcomes are listed in Appendix 2 (Table A2.2, A2.3). Residual plots for the figures are provided in Appendix 3 (Figure A3.1, A3.2).

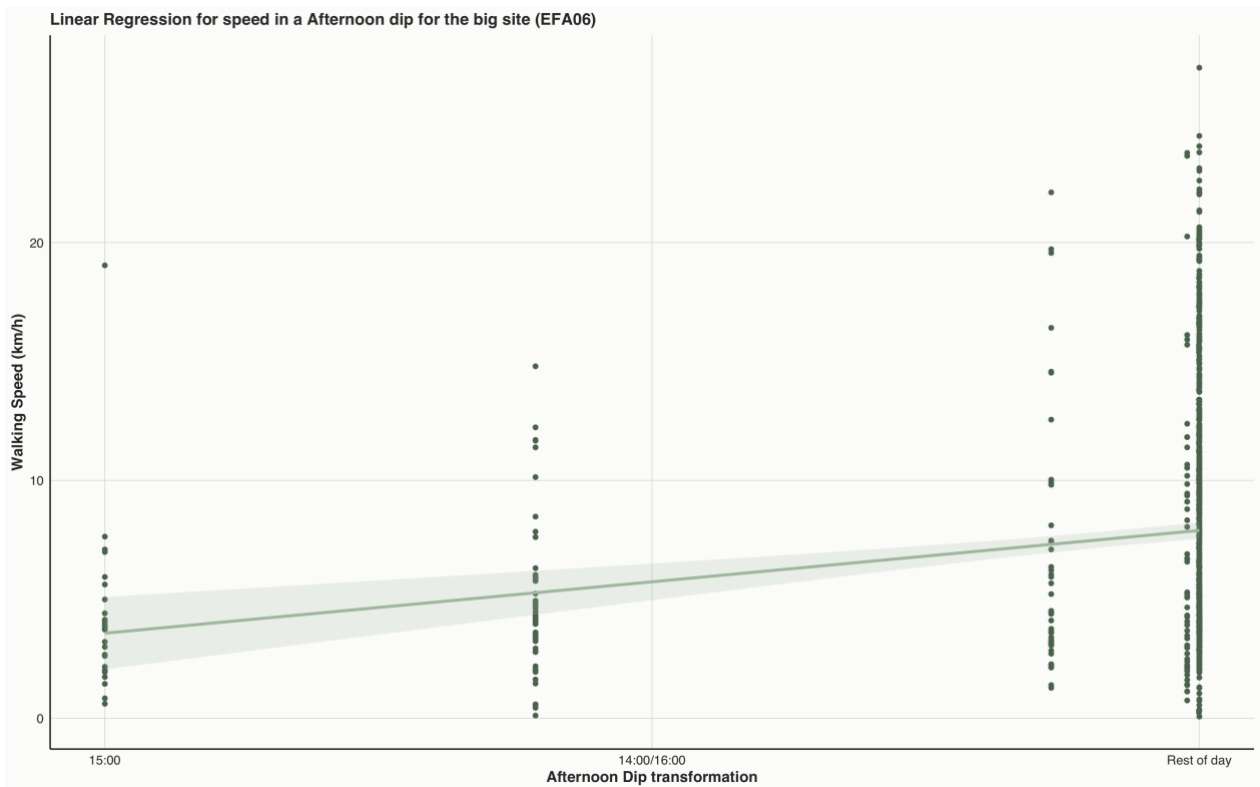


Figure 10. Linear relationship between transformed 'afternoon dip' values and walking speed at the big site (EFA06). The scatter plot displays individual observations, while the fitted regression line indicates a general trend, with shaded confidence intervals representing the 95% uncertainty range.

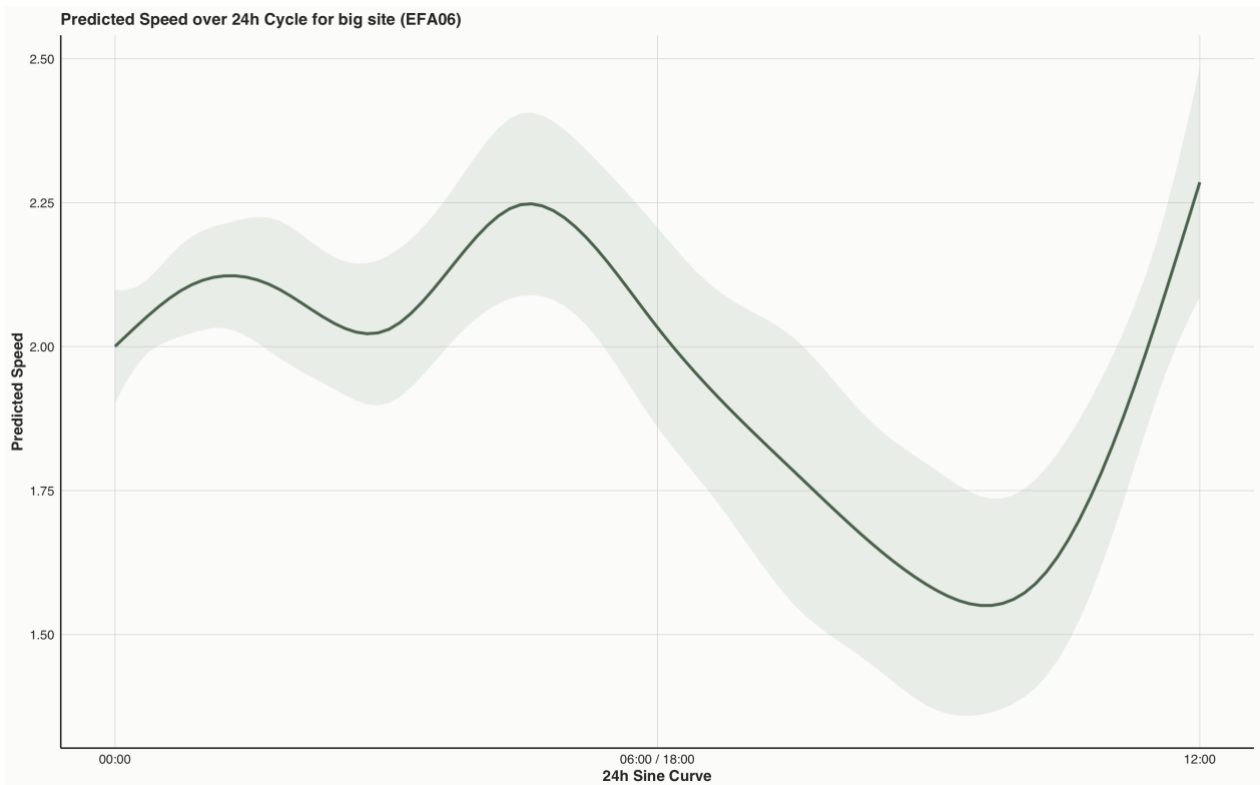


Figure 11. Predicted walking speed across a 24-hour cycle at the big site (EFA06), based on a generalized additive model (GAM) for the sine-transformed time variable. The solid line represents the model's fitted values, while the shaded ribbon denotes the 95% confidence interval.

Temperature

Temperature showed a non-linear relationship with movement speed, best captured by the GAM fitted for the big site, which yielded the lowest AIC of all temperature models (AIC = 5003) and was highly significant (edf = 6.90, ref.df = 7.95, $p < 0.001$, $R^2 = 0.0508$). This model shows a curved relationship between temperature and movement, with speed increasing up to an optimal range before declining, likely reflecting thermally constrained activity (Figure 12).

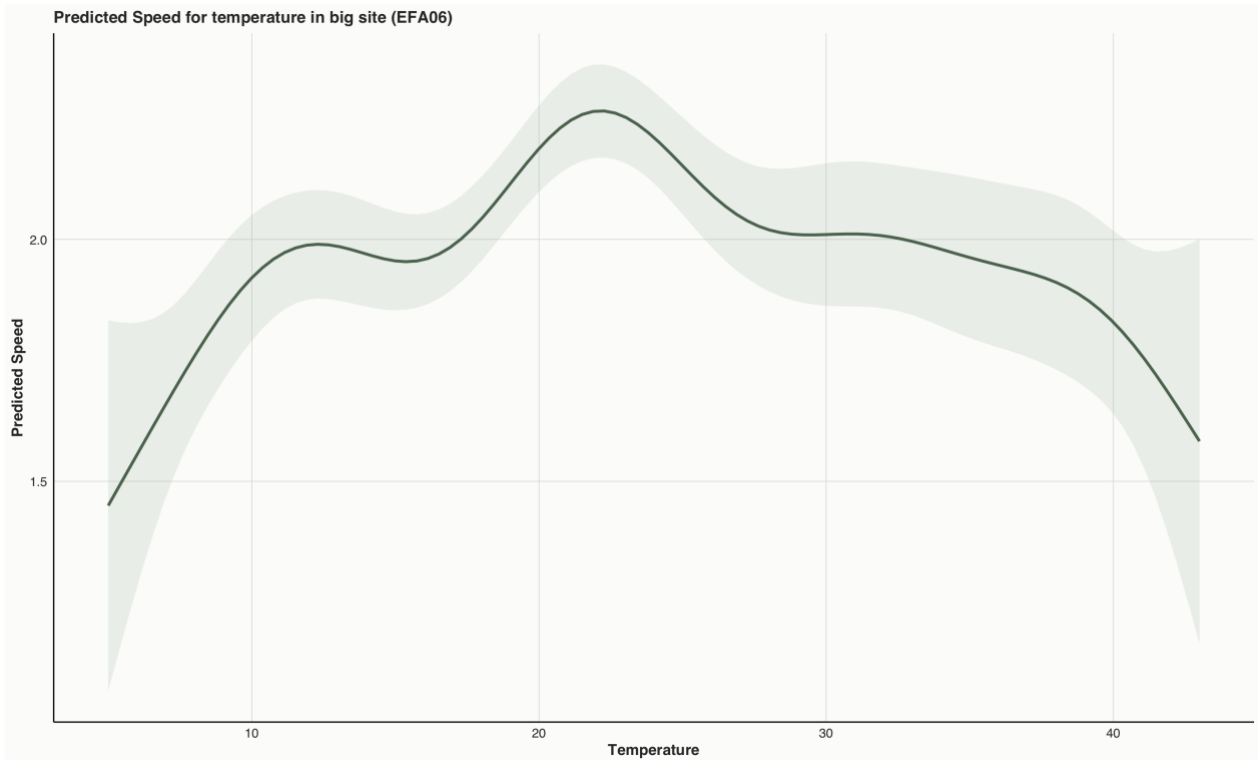


Figure 12. Predicted walking speed as a function of temperature at the big site (EFA06), based on a generalized additive model (GAM). The solid line represents the model's fitted values, while the shaded ribbon shows the 95% confidence interval.

The combined dataset also showed a significant non-linear effect of temperature in both the quadratic LM ($\beta = -0.0101$, $p < 0.001$, $R^2 = 0.0277$, AIC = 5690) and the GAM (edf = 5.26, ref.df = 6.37, $p < 0.001$, AIC = 5347), although neither outperformed the site-specific GAM for EFA06 in terms of fit.

Other statistical outcomes are listed in Appendix 2 (Table A2.4, A2.5). Residual plots for the figure are provided in Appendix 3 (Figure A3.3).

Weak or non-significant predictors

Rainfall

Rainfall had a statistically significant but biologically negligible effect on movement speed (combined LM: $\beta = 0.745$, $p = 0.045$, $R^2 = 0.0045$). A GAM at EFA06 was also significant ($p = 0.0243$), but the smoother's edf = 1 confirmed a linear effect. The low R^2 values across models indicate that rainfall contributes minimally to variation in movement speed. Other statistical outcomes are listed in Appendix 2 (Table A2.6, A2.7).

Sex and age

Neither sex nor age significantly predicted movement speed. These predictors were excluded from further analyses due to low statistical power (in the case of sex) and consistently non-significant results (for age). Full results are available in Appendix 2 (Table A2.8, A2.9).

Interactions

Time of day x temperature

To assess whether temperature effects on movement speed varied across the day, twelve interaction models were tested using four time-of-day transformations (24H, 12H, noon dip, afternoon dip) in both linear (LM) for temperature and temperature squared, and non-linear (GAM) frameworks.

Among all models, the afternoon dip GAM showed the best overall fit (edf = 9.288, ref.df = 10.330, $p < 0.001$, $R^2 = 0.098$, AIC = 5965.2), indicating a strong and time-specific non-linear effect of temperature during the afternoon period (Figure 13). The 24H, 12H, and noon dip GAMs were also significant, but had notably higher AICs, suggesting a less optimal fit.

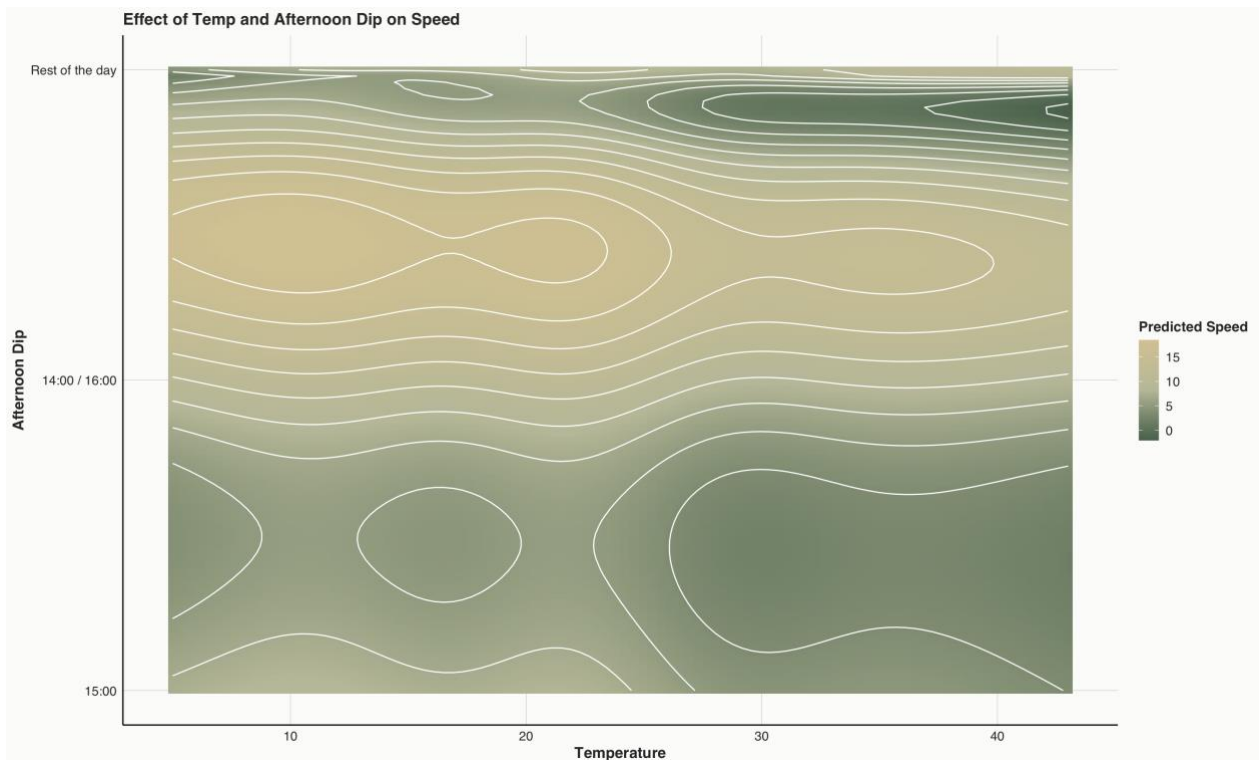


Figure 13. Predicted effect of temperature and afternoon dip time transformation on movement speed. Predicted speed is shown using a colour gradient, with lighter tones indicating higher predicted speed. Contour lines represent iso-speed levels.

While the linear models also revealed significant interactions in the 24H and 12H versions their overall explanatory power was lower, and model fit substantially weaker than in the afternoon dip GAM.

These findings suggest that the relationship between temperature and movement speed is not only non-linear but also varies across the day, with the strongest interaction emerging in the afternoon. Full results, including those of the non-significant models, are provided in Appendix 2 (Table A2.10, A2.11). Residual plots for the figure are provided in Appendix 3 (Figure A3.4).

Time of day x walking direction

To assess whether the effect of time of day on movement speed differed between walking directions, an interaction model was tested using the afternoon dip transformations from earlier.

The afternoon dip interaction GAM showed a significant effect for walking towards the water/food source (edf = 1.002, ref.df = 1.004, $p < 0.001$, $R^2 = 0.508$, AIC = 5355) indicating that the daytime fluctuation in speed was direction-dependent (Figure 14).

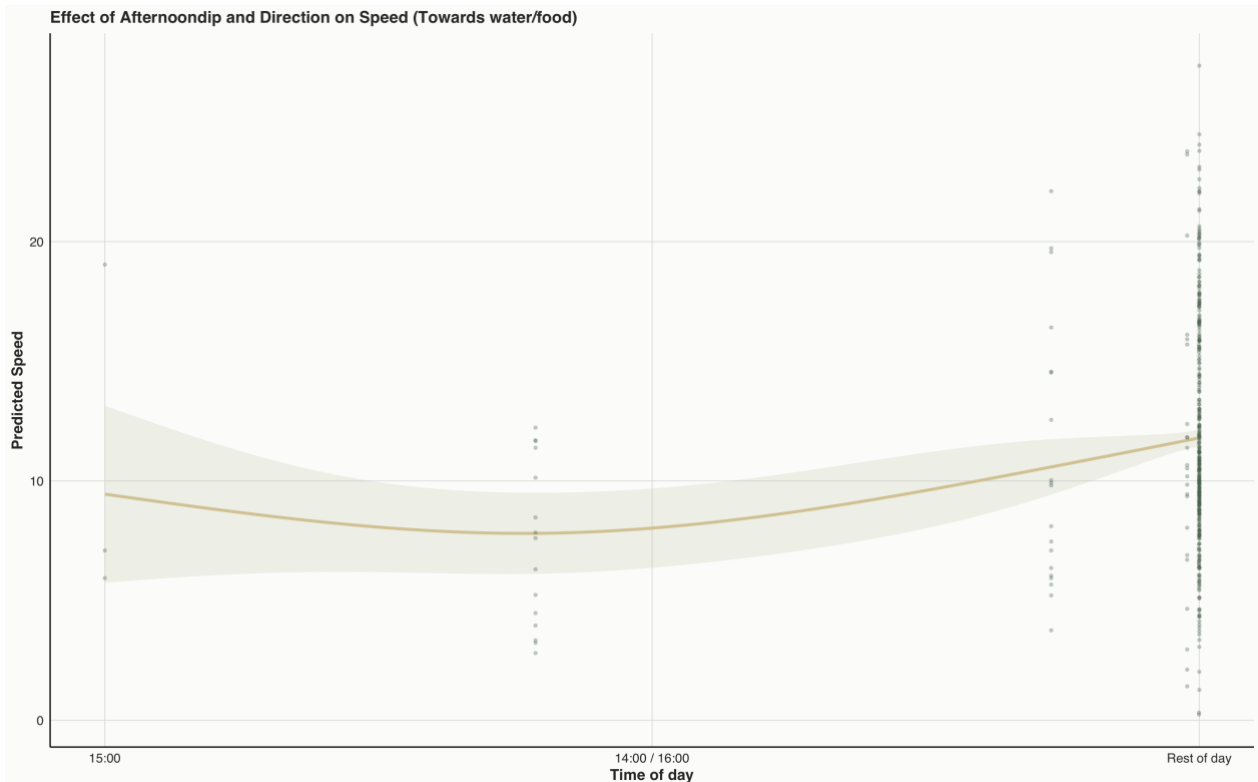


Figure 14. Effect of afternoon dip time transformation and direction on speed for walking direction towards water/food source. The plot shows the predicted relationship between the afternoon dip and speed, differentiated by direction ("Left"). The smooth line represents the fitted values from a generalized additive model (GAM), and the shaded area represents the 95% confidence interval around the predictions.

To explore directional movement patterns across the full daily cycle, including potential nighttime increases in movement speed associated with crop-foraging activity, a 24H interaction model was additionally tested.

The 24H interaction GAM also yielded a significant effect for both moving towards the food/water source (edf = 4.534, ref.df = 5.578, $p < 0.001$, $R^2 = 0.531$, AIC = 5320) as well as moving inland (edf = 7.559, ref.df = 8.505, $p < 0.001$, $R^2 = 0.531$, AIC = 5320). For movement towards the food/water source, the plot reveals a clear sinusoidal pattern, with a peak around midnight and a valley close to noon. This indicates that movement is faster during the night, reaching its highest speed right before/after midnight, and then decelerating as the day progresses, with a notable drop in speed close to noon. The plot for movement inland shows a parabolic relationship, with a peak just before 6:00 AM/PM. This suggests that movement inland is fastest during dusk and dawn, before gradually decreasing in speed as the day progresses toward noon or midnight. Full results, including those of the non-significant models, are provided in Appendix 2 (Table A2.12, A2.13). Residual plots for the figures are provided in Appendix 3 (Figure A3.5, A3.6).

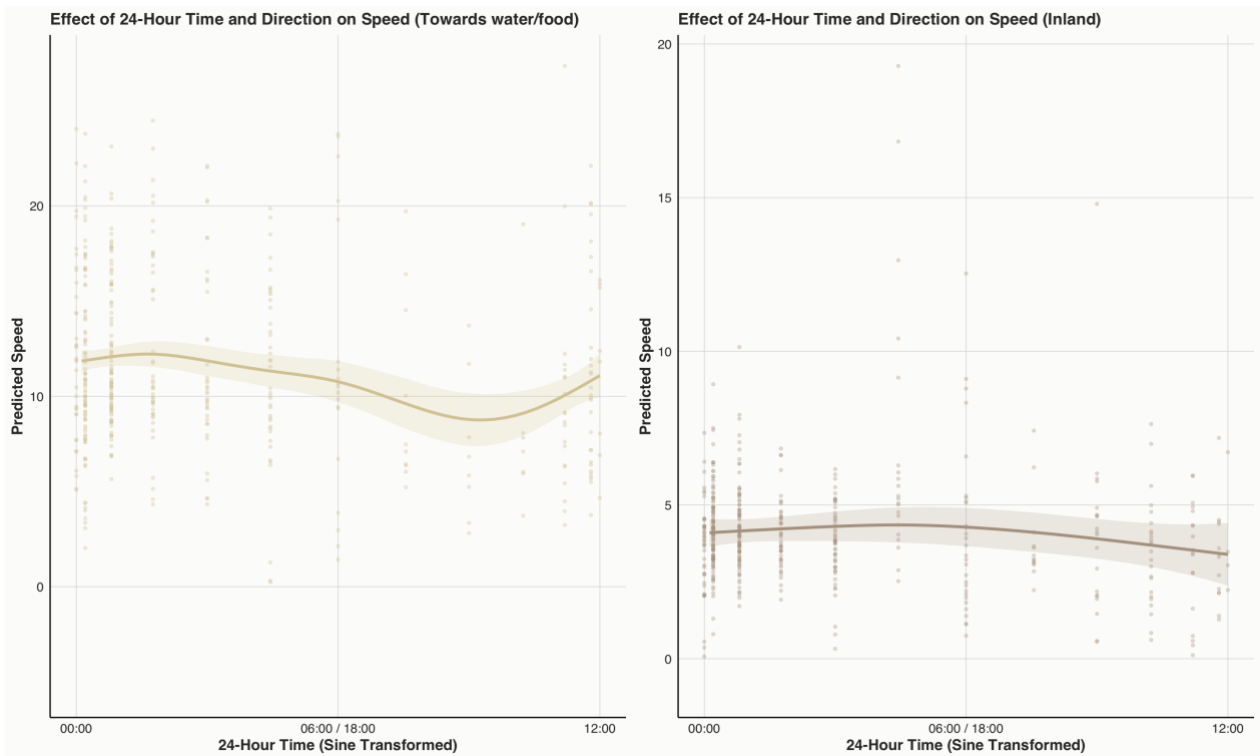


Figure 15. Predicted speed as a GAM function of 24-hour time and direction. The smooth line represents the fitted values from a generalized additive model (GAM), and the shaded area represents the 95% confidence interval.

Temperature x walking direction

A significant effect of temperature on leftward movement (towards water/food sources) was found in the GAM (edf = 1.002, ref.df = 1.003, $p < 0.01$, AIC = 5363.5), with lower temperatures resulting in faster movement towards these areas. As shown in Figure 16, speeds decreased with rising temperatures.

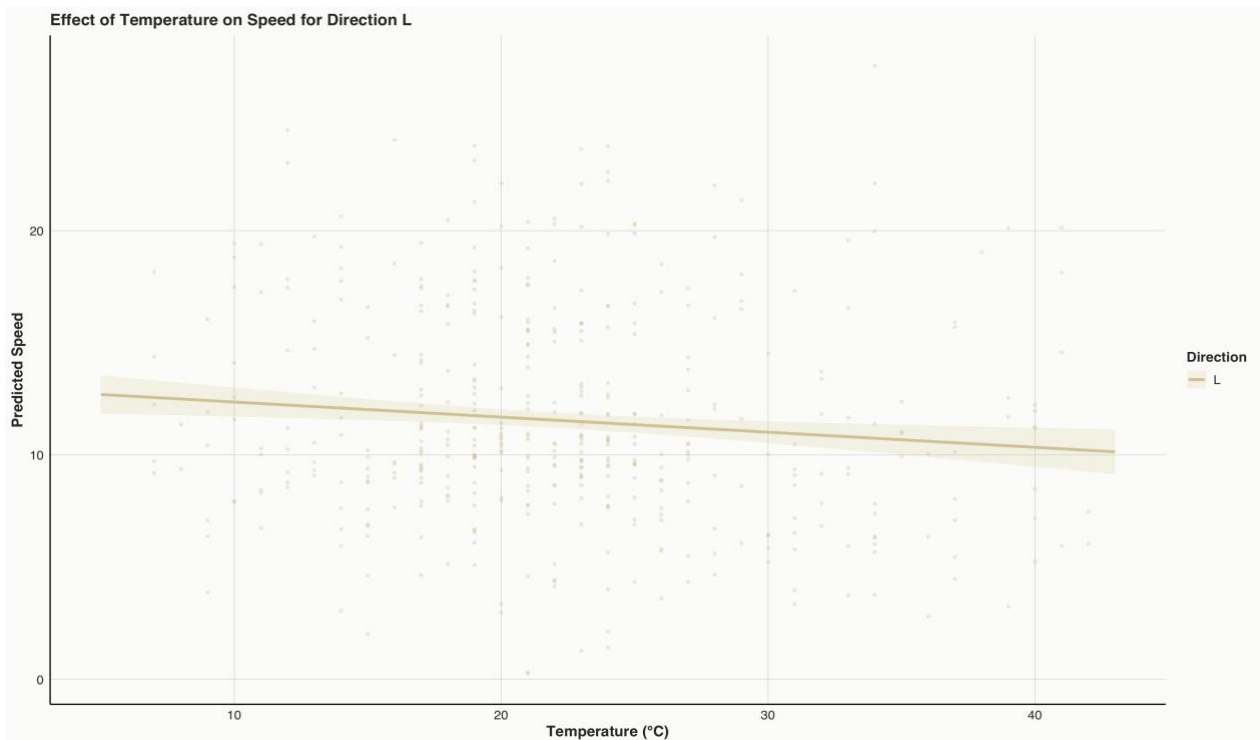


Figure 16. Predicted speed as a GAM function of temperature and direction. The smooth line represents the fitted values from a generalized additive model (GAM), and the shaded area represents the 95% confidence interval.

In contrast, no significant effect of temperature on rightward movement was observed, and neither the GAM nor the linear models showed significant results for rightward movement. Full results, including those of the non-significant models, are provided in Appendix 2 (Table A2.14, A2.15). Residual plots for the figure are provided in Appendix 3 (Figure A3.7).

Discussion

Overview key results

Walking direction had the most pronounced and consistent effect. Elephants moved significantly faster in one direction, which was towards water or food sources, compared to the opposite of moving inland, with this variable alone explaining over 50% of speed variation at the big (data-rich) site. This aligns with the directional movement hypothesis (H_D), which poses that elephants exhibit goal-oriented acceleration when moving towards known resources. Directional asymmetries in movement speed have also been reported in other large herbivores such as wildebeest and zebras during seasonal migrations (Bartlam-Brooks et al., 2013; Holdo et al., 2009). These movement patterns likely indicate that elephants aim to conserve energy by moving efficiently toward key resources, then slowing down or shifting to other behaviours, such as foraging or thermoregulation, once they reach their destination (Owen-Smith et al., 2010; Yackulic et al., 2017).

Time of day was also a significant predictor. Different models showed significance and therefore highlighted different temporal patterns in walking speed. The best-fitting GAM model captured a clear 24-hour rhythm in speed, with elephants moving faster during nighttime and slower around midday. This pattern reflects a circadian activity rhythm shaped by thermoregulatory constraints, as elephants typically reduce activity during the hottest parts of the day to avoid overheating (Kinahan et al., 2007; Shannon et al., 2009). This pattern was confirmed by a significant model for a time transformation that showed a dip in walking speed around the afternoon, which coincides with maximum daily temperatures in the region. This confirms a behavioural adaptation to avoid thermally stressful conditions. Such diurnal patterns have been documented in both wild and semi-captive elephant populations (Kinahan et al., 2007; Shannon et al., 2009), as well as in other arid-zone herbivores like oryx and antelopes (Blank & Li, 2022; Hetem et al., 2012). This concept was additionally confirmed by the interaction between time of day and temperature, as it showed that during the afternoon, when temperatures reached their daily peak, movement speed showed the most significant decrease. Additionally, at high temperatures, walking speed was higher during the night than during the day, indicating a possible relationship to heat from sun exposure (Figure 13).

Of the environmental factors shaping this temporal pattern, temperature appears to be a key proximate driver, influencing movement decisions throughout the day. The results partially support the hypothesis that higher temperatures lead to reduced walking speed (H_B). However, speed actually increased with rising temperature up to a certain point, after which it began to decline. This pattern suggests the presence of an optimal thermal window for activity, a concept consistent with thermal performance curves observed in endotherms (Angilletta et al., 2010), where behavioural output peaks within a specific temperature range before dropping under heat stress. In elephants, this likely reflects a trade-off between thermoregulation and the need to reach distant resources (Owen-Smith & Chafota, 2012).

However, beyond temperature effects, nocturnal movement may also serve as a risk mitigation strategy. In human-modified landscapes, elephants often shift their activity to nighttime to avoid encounters with people and reduce the risk of conflict, particularly when moving through or near

agricultural zones, known as crop raiding (Graham et al., 2009; Graham et al., 2010). This explanation would support our nighttime activity hypothesis (H_A). The way elephants adapt their behaviour to both natural and human-related pressures suggests that their movement patterns over time result from a mix of ecological needs and social dynamics.

Looking at both time of day and walking direction together helped reveal how elephants' movement speed changed throughout the day, depending on which way they were going. The 24-hour interaction model revealed a sinusoidal pattern in the speed of movement towards water/food sources, with movement being fastest during the night and decreasing during midday for elephants moving towards the water/food source. For elephants moving inwards, however, the plot shows a parabolic relationship, whereby walking speed is fastest during dusk and dawn and decreasing towards midnight. These findings indicate that the effects of time of day on speed are different depending on what direction the elephants walk in. This could indicate signs of crop raiding behaviour.

Temperature also significantly affected movement speed when traveling towards water or food sources, with speed decreasing as temperatures rose (Figure 16). This is expected in line with the results from temperature as a sole predictor. However, the fact that this interaction effect is only present in the walking direction towards the water/food source suggests that temperature effects are primarily direction-specific, influencing movement towards food or water sources but not inland. The absence of an effect in the inland direction could suggest less urgency or more shaded/resting behavior when elephants are not on an outbound trip toward known resources (Owen-Smith et al., 2010; Polansky et al., 2015). This interaction does not directly support a crop raiding explanation, as movement speed decreased with rising temperatures when heading towards food or water sources. Since crop raiding typically occurs at night under cooler conditions and involves fast and directed movement (Graham et al., 2010; Wall et al., 2013), the observed pattern likely reflects thermoregulatory constraints during daytime rather than nighttime foraging behaviour.

While walking direction, time of day and temperature explained meaningful variation in movement speed, several other factors contributed little to the observed patterns. Rainfall, though statistically significant in some models, had an extremely low explanatory value ($R^2 < 0.005$), suggesting limited biological relevance and not supporting the hypothesis (H_C). This aligns with previous findings where short-term precipitation often exerts minimal influence on elephant movement (Bohrer et al., 2014). Additionally, the individual trait sex had no statistical power due to a very low count of cows in this dataset. Data was therefore not sufficient to support the hypothesis (H_E). Lastly, the predictor age showed no significant effects on speed, also not supporting the hypothesis (H_F).

Conservation implications

To develop more effective conservation strategies, it is crucial to understand how elephants navigate their environment, especially in regions heavily influenced by human activity. The findings of this study underscore the role of resource availability (water and food sources) in shaping their movement patterns. Given the observed nocturnal and temperature-dependent movements towards water sources and agricultural areas, conservation strategies should prioritize reducing human-elephant conflict by taking these patterns into account when designing and implementing mitigation measures.

Several approaches have been developed to reduce human-elephant conflict, particularly in the context of crop raiding. Common methods include the use of beehive fences (King et al., 2017),

chili pepper deterrents (Osborn, 2002), electric fencing (Graham et al., 2009), and noise (Graham & Ochieng, 2008). Furthermore, creating migration corridors and buffer zones around agricultural areas can help steer elephants away from farmlands, thus reducing the risk of crop raiding. The patterns identified in this study support these strategies, highlighting that elephants tend to move more at night and in response to temperature changes, with increased movement toward water and agricultural zones during the night. This suggests that interventions, such as enhancing deterrence measures at night, could help mitigate crop raiding (Graham et al., 2009).

While relocating agricultural areas away from water sources may initially seem like a viable solution, it presents several challenges. In many regions, water sources are scarce, and farmers depend on their proximity for irrigation. Moving agriculture further from these sources could create significant economic challenges (Temoso et al., 2015). Additionally, elephants may be forced to travel longer distances, increasing the likelihood of encountering farmlands and thereby raising the risk of conflict (Madden, 2004).

These findings also matter in the context of climate change. As temperatures rise, elephants may experience more heat stress, which could push them to shift their movement habits even further. Warmer temperatures may therefore result in further reductions in daytime activity or alterations in movement towards key resources. Understanding these shifts will be essential for anticipating and managing potential changes in elephant behavior in the coming decades.

It is important to emphasise that walking speed is an indirect proxy for behaviours such as crop raiding. Elephants may increase their speed for various reasons unrelated to foraging, such as social dynamics, thermoregulation, or disturbance. Therefore, while changes in walking speed can hint at certain behavioural patterns, they should not be taken as definitive evidence of crop raiding without additional contextual data. This limits the extent to which direct conservation actions can be based solely on walking speed data.

Limitations and future research

Using both linear models (LMs) and generalized additive models (GAMs) made it possible to capture a fuller picture of how different factors influenced movement, from clear trends to more complex, non-linear patterns. While LMs provided a baseline understanding of directional trends, GAMs proved particularly valuable in capturing complex, non-linear effects, especially in temporal variables like time of day and temperature. The flexibility of GAMs enabled the detection of subtle behavioural rhythms and interaction effects that would likely be obscured in strictly linear frameworks.

However, several limitations should be taken into account when interpreting these results. First, the explanatory power varied significantly across models: while walking direction accounted for a large proportion of variance ($R^2 > 0.5$), other predictors had much lower R^2 values. This indicates that there may be additional, unmeasured factors, such as habitat structure, human presence, or more detailed social context, which could have a significant impact on movement speed. Second, the uneven distribution of individual traits (e.g., sex) reduced the statistical power of some models. Specifically, the low number of female elephants limited the ability to detect sex-based differences.

Another important limitation is the low variability in the walking direction predictor. This variable consisted of only two categories (left and right), and was derived from only two camera trap sites, of which one had a very small dataset. This low variation increases the risk of overestimating its effect. For instance, it could be argued that elephants move faster in one direction due to environmental features such as terrain slope. However, the elephant pathways at both sites are not

located on a slope (Evans, pers. comm., 2025). Still, the limited variation in walking direction and site number remains a concern for model robustness and should be interpreted with caution.

Furthermore, this study excluded all observations with a walking speed of zero, meaning that stationary behaviours, such as feeding, resting, or social interactions, were not included in the analysis. As a result, general elephant presence and behaviours were not considered, with the focus solely on the walking speed of actively moving individuals. This limitation restricts the interpretation of predictors like rainfall, which may influence broader patterns of presence or displacement, rather than movement speed alone. Future research should include non-movement states and behavioural classifications to better capture the environmental factors driving elephant activity.

Another limitation concerns the spatial and temporal scope of the dataset. The analyses were based on data from only two sites, EFA02 and EFA06, with a notably smaller sample size at EFA02. This reduces statistical power and complicates efforts to generalize the findings. Additionally, since the data collection periods did not overlap between the two sites, direct temporal comparisons are not feasible, and site-specific effects cannot be separated from broader temporal or behavioural trends. Expanding future studies to include a wider range of sites and ensuring consistent, overlapping data collection would enhance the robustness and generalizability of the results.

Additionally, this study concentrated solely on daily and circadian variation, without accounting for seasonal changes. Considering the potential influence of the seasonal availability of key resources, such as grass or fruit, which are influenced by rainfall patterns, future research should investigate how long-term environmental changes affect both the speed and direction of elephant movements. This would provide valuable insights into how elephants adapt their foraging strategies to different ecological conditions over time. Furthermore, walking speed was calculated based on timestamps recorded in whole seconds rather than milliseconds. This reduces the precision of the speed estimates, particularly for faster movements. While general patterns and trends remain detectable, working with milliseconds would improve accuracy.

While the interaction models revealed important behavioural patterns, interpretation of interaction effects, particularly in GAMs, can be sensitive to model specification and uneven sampling across factor levels. Caution is therefore warranted in generalising interaction results without replication or external validation. Moreover, since the dataset is limited to a specific spatial and temporal context, the results may not accurately reflect elephant behaviour across different seasons or broader landscapes.

Ideally, to better confirm whether the observed increase in walking speed towards the river relates to crop raiding behaviour, future studies should monitor elephant movement between the river and agricultural fields directly. This was attempted during the current study but proved difficult due to practical limitations. Camera traps placed in agricultural zones were often stolen due to their high value or face resistance from local farmers concerned about privacy. Therefore, despite not observing the direct behaviour between river and crops, this study interprets the increased walking speed towards the river during night-time hours as a cautious indirect proxy for crop raiding activity.

Despite these constraints, the modelling framework applied here offers valuable insights into elephant movement ecology and provides a strong basis for future studies. Incorporating additional covariates, such as vegetation, proximity to infrastructure, or social group composition, could further illuminate the ecological and anthropogenic drivers of movement speed.

Conclusion

This study aimed to provide valuable insights into the movement ecology of elephants. Results highlight the significant role of walking direction, time of day, and temperature in shaping walking speed patterns. Elephants exhibited faster speeds when moving towards water and food sources, particularly at night, with clear diurnal and temperature-driven rhythms. These patterns suggest a complex interplay of thermoregulatory needs and risk mitigation strategies, including avoidance of human-elephant conflict. The findings support existing crop raiding mitigation strategies, such as increased deterrence efforts at night and the creation of migration corridors. All in all, this research shows how vital it is to factor in both natural and human influences when planning conservation efforts for elephants living in human-shaped environments.

Acknowledgements

First and foremost, I want to thank my two supervisors, Dr. Kate Evans and Dr. Søren Faurby. Kate, thank you for your infectious enthusiasm, knowledge sharing, and genuine passion for both elephants and my project idea(s). Søren, your insights have pushed me to think one step further (and occasionally in completely new directions). Together, you pulled me through the tougher moments, always realistic, honest, and willing to brainstorm with me. Thankyou! Also, a sincere thank-you to Stephanie Kong at Elephants for Africa for always being on standby for any of my questions regarding the on-site materials. To my parents: thank you for your unconditional trust and support, and for always answering my endless calls. Your love has been a constant support over the past year, despite the distance. And finally, a big hug to the friends who shared the thesis struggle with me in the touchdown area. Thanks for the coffee runs, the mutual pep talks, the after-work's and most off all lots of laughter. I wouldn't have stayed sane without you.

References

- Allen, C. (2022). *Importance of older males: influence of age structure on social dynamics between males in an elephant bull area* [Dissertation, University of Exeter]. <https://ore.exeter.ac.uk/repository/handle/10871/128720>
- Allen, C. R. B., Brent, L. J. N., Motsentwa, T., & Croft, D. P. (2021). Field evidence supporting monitoring of chemical information on pathways by male African elephants. *Animal Behaviour*, *176*, 193-206. <https://doi.org/10.1016/j.anbehav.2021.04.004>
- Allen, C. R. B., Brent, L. J. N., Motsentwa, T., Weiss, M. N., & Croft, D. P. (2020). Importance of old bulls: leaders and followers in collective movements of all-male groups in African savannah elephants (*Loxodonta africana*). *Scientific reports*, *10*(1), 13996. <https://doi.org/10.1038/s41598-020-70682-y>
- Angilletta, M. J., Cooper, B. S., Schuler, M. S., & Boyles, J. G. (2010). The evolution of thermal physiology in endotherms. *Frontiers in Bioscience E*, *2*, 861-881.
- Baillie, I., & Cole, M. M. (1987). The savannas: biogeography and geobotany. *Journal of Tropical Ecology*, *3*(4). <https://doi.org/10.1017/S0266467400002352>
- Bartlam-Brooks, H. L. A., Beck, P. S. A., Bohrer, G., & Harris, S. (2013). In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, *118*(4), 1427-1437. <https://doi.org/10.1002/jgrg.20096>

- Blank, D., & Li, Y. (2022). Antelope adaptations to counteract overheating and water deficit in arid environments. *Journal of Arid Land*, 14(10), 1069-1085. <https://doi.org/10.1007/s40333-022-0076-y>
- Bohrer, G., Beck, P. S., Ngene, S. M., Skidmore, A. K., & Douglas-Hamilton, I. (2014). Elephant movement closely tracks precipitation-driven vegetation dynamics in a Kenyan forest-savanna landscape. *Movement Ecology*, 2(1). <https://doi.org/10.1186/2051-3933-2-2>
- Breheeny, P., & Burchett, W. (2017). Visualization of Regression Models Using visreg. *The R Journal*, 9(2), 56-71.
- Brooks, C. J. (2005). *The foraging behaviour of Burchell's zebra (Equus burchelli antiquorum)* [Dissertation, University of Bristol]. <https://research-information.bris.ac.uk/ws/portalfiles/portal/34500922/DX243926.pdf>
- Campos-Arceiz, A., & Blake, S. (2011). Megagardeners of the forest – the role of elephants in seed dispersal. *Acta Oecologica*, 37(6), 542-553. <https://doi.org/10.1016/j.actao.2011.01.014>
- Chamaillé-Jammes, S., Mtare, G., Makuwe, E., & Fritz, H. (2013). African Elephants Adjust Speed in Response to Surface-Water Constraint on Foraging during the Dry-Season. *PLOS ONE*, 8(3), e59164. <https://doi.org/10.1371/journal.pone.0059164>
- Chase, M. (2015). *Dry season aerial survey of elephants and wildlife in Northern Botswana July - October 2014*. <https://doi.org/10.13140/RG.2.2.35514.80325>
- Chase, M. J., Schlossberg, S., Griffin, C. R., Bouché, P. J. C., Djene, S. W., Elkan, P. W., Ferreira, S., Grossman, F., Kohi, E. M., Landen, K., Omondi, P., Peltier, A., Selier, S. A. J., & Sutcliffe, R. (2016). Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, 4, e2354. <https://doi.org/10.7717/peerj.2354>
- Douglas-Hamilton, I., Krink, T., & Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften*, 92(4), 158-163. <https://doi.org/10.1007/s00114-004-0606-9>
- Enukwa, E. H. (2017). Human-Elephant conflict mitigation methods: A review of effectiveness and sustainability. *Journal of Wildlife and Biodiversity*, 1(2), 69-78. <https://doi.org/10.22120/jwb.2017.28260>
- Evans, K. (2006). *The behavioural ecology and movements of adolescent male African elephant (Loxodonta africana) in the Okavango Delta, Botswana* [Dissertation, University of Bristol]. https://www.elephantsforafrica.org/wp-content/uploads/2013/07/PhD2006_KateEvans.pdf
- Evans, K. (2019). Elephants for Africa: male Savannah elephant *Loxodonta africana* sociality, the Makgadikgadi and resource competition. *International Zoo Yearbook*, 53(1), 200-207. <https://doi.org/10.1111/izy.12238>
- Evans, K. E., & Harris, S. (2008). Adolescence in male African elephants, *Loxodonta africana*, and the importance of sociality. *Animal Behaviour*, 76(3), 779-787. <https://doi.org/10.1016/j.anbehav.2008.03.019>
- Ferry, N., Dray, S., Fritz, H., Ipavec, A., Wigley, B. J., Charles-Dominique, T., Bourgarel, M., Sebele, L., & Valeix, M. (2021). Long-term high densities of African elephants clear the understorey and promote a new stable savanna woodland community. *Journal of Vegetation Science*, 32(6), e13101. <https://doi.org/10.1111/jvs.13101>
- Garstang, M., Davis, R. E., Leggett, K., Frauenfeld, O. W., Greco, S., Zipser, E., & Peterson, M. (2014). Response of African Elephants (*Loxodonta africana*) to Seasonal Changes in Rainfall. *PLOS ONE*, 9(10), e108736. <https://doi.org/10.1371/journal.pone.0108736>

- Gerhardt, K. V., Niekerk, A. V., Kidd, M., Samways, M., & Hanks, J. (2014). The role of elephant *Loxodonta africana* pathways as a spatial variable in crop-raiding location. *Oryx*, 48(3), 436-444. <https://doi.org/10.1017/S003060531200138X>
- Gobush, K. S., Edwards, C. T. T., Balfour, D., Wittemyer, G., Maisels, F., & Taylor, R. D. (2022). *Loxodonta africana* (amended version of 2021 assessment). *The IUCN Red List of Threatened Species 2022: e.T181008073A223031019*. <https://doi.org/https://dx.doi.org/10.2305/IUCN.UK.2022-2.RLTS.T181008073A223031019.en>
- Gontse, K., Mbaiwa, J. E., & Thakadu, O. T. (2018). Effects of wildlife crop raiding on the livelihoods of arable farmers in Khumaga, Boteti sub-district, Botswana. *Development Southern Africa*, 35(6), 791-802. <https://doi.org/10.1080/0376835X.2018.1495061>
- Goswami, V. R., Medhi, K., Nichols, J. D., & Oli, M. K. (2015). Mechanistic understanding of human–wildlife conflict through a novel application of dynamic occupancy models. *Conservation Biology*, 29(4), 1100-1110. <https://doi.org/10.1111/cobi.12475>
- 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>
- Graham, M. D., Notter, B., Adams, W. M., Lee, P. C., & Ochieng, T. N. (2010). Patterns of crop-raiding by elephants, *Loxodonta africana*, in Laikipia, Kenya, and the management of human–elephant conflict. *Systematics and Biodiversity*, 8(4), 435-445. <https://doi.org/10.1080/14772000.2010.533716>
- Graham, M. D., & Ochieng, T. (2008). Uptake and performance of farm-based measures for reducing crop raiding by elephants *Loxodonta africana* among smallholder farms in Laikipia District, Kenya. *Oryx*, 42(1), 76-82. <https://doi.org/10.1017/S0030605308000677>
- Grainger, M., Aarde, R. v., & Whyte, I. (2005). Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *African Journal of Ecology*, 43(4), 369-375. <https://doi.org/10.1111/j.1365-2028.2005.00592.x>
- Haynes, G. (2012). Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology*, 157, 99-107. <https://doi.org/10.1016/j.geomorph.2011.04.045>
- Hetem, R. S., Strauss, W. M., Fick, L. G., Maloney, S. K., Meyer, L. C. R., Shobrak, M., Fuller, A., & Mitchell, D. (2012). Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? *Zoology*, 115(6), 411-416. <https://doi.org/10.1016/j.zool.2012.04.005>
- Hoare, R. (2015). Lessons From 20 Years of Human–Elephant Conflict Mitigation in Africa. *Human Dimensions of Wildlife*, 20(4), 289-295. <https://doi.org/10.1080/10871209.2015.1005855>
- Holdo, R. M., Holt, R. D., & Fryxell, J. M. (2009). Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti. *The American Naturalist*, 173(4), 431-445. <https://doi.org/10.1086/597229>
- Hyvarinen, O., Beest, M. T., Roux, E. I., Kerley, G., Groot, E. d., Vinita, R., & Cromsigt, J. P. G. M. (2021). Megaherbivore impacts on ecosystem and Earth system functioning: the current state of the science. *Ecography*, 44(11), 1579-1594. <https://doi.org/10.1111/ecog.05703>
- Ihwagi, F. W., Thouless, C., Wang, T., Skidmore, A. K., Omondi, P., & Douglas-Hamilton, I. (2018). Night-day speed ratio of elephants as indicator of poaching levels. *Ecological Indicators*, 84, 38-44. <https://doi.org/10.1016/j.ecolind.2017.08.039>

- Kgathi, D. K., & Kalikawe, M. C. (1993). Seasonal distribution of zebra and wildebeest in Makgadikgadi Pans Game Reserve, Botswana. *African Journal of Ecology*, 31(3), 210-219. <https://doi.org/10.1111/j.1365-2028.1993.tb00534.x>
- Kinahan, A. A., Pimm, S. L., & Aarde, R. J. v. (2007). Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. *Journal of Thermal Biology*, 32(1), 47-58. <https://doi.org/10.1016/j.jtherbio.2006.09.002>
- King, L. E., Lala, F., Nzumu, H., Mwambingu, E., & Douglas-Hamilton, I. (2017). Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conservation Biology*, 31(4), 743-752. <https://doi.org/10.1111/cobi.12898>
- Lee, P. C., & Moss, C. J. (1999). The social context for learning and behavioural development among wild African elephants. *Mammalian social learning: Comparative and ecological perspectives*, 102-125.
- Lee, P. C., Poole, J. H., Njiraini, N., Sayialel, C. N., & Moss, C. J. (2011). Male social dynamics: independence and beyond. *survival*, 36(50), 54. <https://doi.org/https://doi.org/10.7208/9780226542263-019>
- Madden, F. (2004). Creating coexistence between humans and wildlife: global perspectives on local efforts to address human-wildlife conflict. *Human Dimensions of Wildlife*, 9(4), 247-257. <https://doi.org/https://doi.org/10.1080/10871200490505675>
- 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. https://doi.org/10.4103/cs.cs_16_132
- Meynell, P., & Parry, D. (2002). Environmental appraisal for the construction of a game proof fence around Makgadikgadi Pans National Park. *Gaborone, Botswana: Scott Wilson Kirkpatrick & Partners*.
- Moss, C., & Poole, J. (1983). Relationships and social structure of African elephants. *Primate social relationships: an integrated approach*, 315, 325.
- Nishihara, T. (2003). Elephant poaching and ivory trafficking in African tropical forests with special reference to the Republic of Congo. *Pachyderm*(34), 66-74. <https://doi.org/https://doi.org/10.69649/pachyderm.v34i1.1135>
- Nishihara, T. (2012). Demand for forest elephant ivory in Japan. *Pachyderm*, 52, 55-65. <https://doi.org/10.69649/pachyderm.v52i.307>
- Osborn, F. V. (2002). Capsicum oleoresin as an elephant repellent: field trials in the communal lands of Zimbabwe. *The Journal of Wildlife Management*, 674-677. <https://doi.org/https://doi.org/10.2307/3803133>
- Osborne, C. P., Charles-Dominique, T., Stevens, N., Bond, W. J., Midgley, G., & Lehmann, C. E. R. (2018). Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*, 220(1), 10-24. <https://doi.org/10.1111/nph.15236>
- Owen-Smith, N., & Chafota, J. (2012). Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *Journal of Mammalogy*, 93(3), 698-705. <https://doi.org/10.1644/11-MAMM-A-350.1>
- Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2267-2278. <https://doi.org/10.1098/rstb.2010.0095>

- Polansky, L., Kilian, J., & Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *Proceedings. Biological sciences / The Royal Society*, 282(1805), 20143042. <https://doi.org/10.1098/rspb.2014.3042>
- Pontzer, H., Rimbach, R., Paltan, J., Ivory, E. L., & Kendall, C. J. (2020). Air temperature and diet influence body composition and water turnover in zoo-living African elephants (*Loxodonta africana*). *Royal Society Open Science*, 7(11), 201155. <https://doi.org/10.1098/rsos.201155>
- Presotto, A., Fayrer-Hosken, R., Curry, C., & Madden, M. (2019). Spatial mapping shows that some African elephants use cognitive maps to navigate the core but not the periphery of their home ranges. *Animal Cognition*, 22(2), 251-263. <https://doi.org/10.1007/s10071-019-01242-9>
- R Core Team. (2025). *R: A language and environment for statistical computing*. In R Foundation for Statistical Computing. <https://www.R-project.org/>
- Redmore, L. E. (2024). Understanding human-elephant interactions across time is key to illuminate pathways toward coexistence. *Ecology and Society*, 29(3), 33, Article 33. <https://doi.org/10.5751/ES-15343-290333>
- Rozen-Rechels, D., Valls-Fox, H., Mabika, C. T., & Chamaillé-Jammes, S. (2020). Temperature as a constraint on the timing and duration of African elephant foraging trips. *Journal of Mammalogy*, 101(6), 1670-1679. <https://doi.org/10.1093/jmammal/gyaa129>
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., & Cardona, A. (2012). Fiji: an open-source platform for biological-image analysis. *Nature Methods* 2012 9:7, 9(7). <https://doi.org/10.1038/nmeth.2019>
- Shannon, G., Matthews, W. S., Page, B. R., Parker, G. E., & Smith, R. J. (2009). The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*, 15(5), 776-783. <https://doi.org/10.1111/j.1472-4642.2009.00581.x>
- Sitienei, A. J., Jiwen, G., & Ngene, S. M. (2014). Assessing the cost of living with elephants (*Loxodonta africana*) in areas adjacent to Meru National Park, Kenya. *European Journal of Wildlife Research*, 60(2), 323-330. <https://doi.org/10.1007/s10344-013-0789-5>
- SnapshotSafari. *Snapshots Elephants for Africa*. <https://www.zooniverse.org/projects/shuebner729/snapshot-elephants-for-africa>
- Songhurst, A., & Coulson, T. (2014). Exploring the effects of spatial autocorrelation when identifying key drivers of wildlife crop-raiding. *Ecology and evolution*, 4(5), 582–593. <https://doi.org/10.1002/ece3.837>
- Stiles, D. (2004). The ivory trade and elephant conservation. *Environmental Conservation*, 31(4), 309-321. <https://doi.org/10.1017/S0376892904001614>
- Tang, Y., Horikoshi, M., & Li, W. (2016). ggfortify: Unified Interface to Visualize Statistical Result of Popular R Packages. *The R Journal*, 8(2), 474-485. <https://doi.org/10.32614/RJ-2016-060>
- Temoso, O., Villano, R., & Hadley, D. (2015). Agricultural productivity, efficiency and growth in a semi-arid country: A case study of Botswana. *African Journal of Agricultural and Resource Economics*, 10(3), 192-206. <https://doi.org/10.22004/ag.econ.211667>
- Thaker, M., Gupte, P. R., Prins, H. H. T., Slotow, R., & Vanak, A. T. (2019). Fine-Scale tracking of ambient temperature and movement reveals shuttling behavior of elephants to water. *Frontiers in Ecology and Evolution*, 7, 4. <https://doi.org/10.3389/fevo.2019.00004>

- Thomas, D., & Shaw, P. A. (1991). *The Kalahari Environment*. Cambridge University Press.
- Thouless, C., Dublin, H. T., Blanc, J., Skinner, D., Daniel, T., Taylor, R., Maisels, F., Frederick, H., & Bouché, P. (2016). *African elephant status report 2016*.
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., & Douglas-Hamilton, I. (2013). Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biological Conservation*, 157, 60-68. <https://doi.org/10.1016/j.biocon.2012.07.019>
- Wato, Y. A., Prins, H. H. T., Heitkönig, I. M. A., Wahungu, G. M., Ngene, S. M., Njumbi, S., & van Langevelde, F. (2018). Movement patterns of African Elephants (*Loxodonta africana*) in a semi-arid savanna suggest that they have information on the location of dispersed water sources. *Frontiers in Ecology and Evolution*, 6, 167. <https://doi.org/10.3389/fevo.2018.00167>
- Webber, C. E., Sereivathana, T., Maltby, M. P., & Lee, P. C. (2011). Elephant crop-raiding and human–elephant conflict in Cambodia: crop selection and seasonal timings of raids. *Oryx*, 45(2), 243-251. <https://doi.org/10.1017/S0030605310000335>
- White, L. J. T. (1994). Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*, 10(3), 289-312. <https://doi.org/10.1017/S0266467400007975>
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. <https://ggplot2.tidyverse.org>
- Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A Grammar of Data Manipulation*. In <https://CRAN.R-project.org/package=dplyr>
- Wickham, H., & Henry, L. (2025). *purrr: Functional Programming Tools*. In <https://CRAN.R-project.org/package=purrr>
- Wickham, H., Vaughan, D., & Girlich, M. (2024). *tidyr: Tidy Messy Data*. In <https://CRAN.R-project.org/package=tidyr>
- Wittemyer, G., Daballen, D., & Douglas-Hamilton, I. (2013). Comparative Demography of an At-Risk African Elephant Population. *PLOS ONE*, 8(1), e53726. <https://doi.org/10.1371/journal.pone.0053726>
- Wittemyer, G., Douglas-Hamilton, I., & Getz, W. M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, 69(6), 1357-1371. <https://doi.org/10.1016/j.anbehav.2004.08.018>
- Wittemyer, G., Getz, W. M., Vollrath, F., & Douglas-Hamilton, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology*, 61(12), 1919-1931. <https://doi.org/10.1007/s00265-007-0432-0>
- Wittemyer, G., Northrup, J. M., Blanc, J., Douglas-Hamilton, I., Omondi, P., & Burnham, K. P. (2014). Illegal killing for ivory drives global decline in African elephants. *Proceedings of the National Academy of Sciences*, 111(36), 13117-13121. <https://doi.org/10.1073/pnas.1403984111>
- Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R* (2 ed.). Chapman and Hall/CRC.
- Wright, P. G., & Luck, C. P. (1984). Do elephants need to sweat? *South African Journal of Zoology*, 19(4), 270-274. <https://doi.org/10.1080/02541858.1984.11447892>

- Yackulic, C. B., Blake, S., & Bastille-Rousseau, G. (2017). Benefits of the destinations, not costs of the journeys, shape partial migration patterns. *Journal of Animal Ecology*, 86(4), 972-982. <https://doi.org/10.1111/1365-2656.12679>
- Young, K. D., Ferreira, S. M., & Aarde, R. J. V. (2009). The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. *Austral Ecology*, 34(3), 329-342. <https://doi.org/10.1111/j.1442-9993.2009.01934.x>
- Zeileis, A., & Grothendieck, G. (2005). zoo: S3 Infrastructure for Regular and Irregular Time Series. *Journal of Statistical Software*, 14(6), 1-27. <https://doi.org/10.18637/jss.v014.i06>
- Zyambo, P. (2016). Woodland conversion by elephants in Africa: The search for causal factors, processes, mechanisms and management strategies. *Open Journal of Ecology*, 6(2), 93-101. <https://doi.org/10.4236/oje.2016.62010>

Appendix 1 Popular science summary

Why Elephants Pick Up the Pace at Night

Heat, hunger, humans, and high-stakes choices in Botswana's savannah

Imagine walking through a scorching, open landscape with little shade, searching for food or water. You're being watched. Not by predators, but by farmers. And the wrong move could mean danger. And now imagine being that farmer. The crops you've worked for all year are being eyeballed by the biggest living land mammals. For elephants and farmers living in Botswana's savannah, specifically in Makgadikgadi Pans National Park, this is an everyday struggle.



The elephant in the crop field

Crop raiding is when wild animals, like elephants, enter farmland and feed on or destroy agricultural crops. In Botswana, this often leads to significant losses for farmers and intensifies human-wildlife conflict. It's mostly male elephants that raid crops, often moving fast in what researchers call 'streaking'. In my research, I studied walking speed of male African savannah elephants (*Loxodonta africana*) using camera trap. The goal: to understand how they navigate an environment shaped by heat, drought, and conflict with humans.

Faster under cover of night

The initial finding? Elephants walk faster at night. The next question is of course, why? There are two possibilities, the first one being that it helps them avoid humans, especially when approaching risky areas like crop fields. Night-time crop raiding is a known strategy in other elephant populations too. The faster pace likely reflects a smart tactic: get in, get out, and stay safe. This kind of behaviour shows how elephants are actively adapting to increasingly human-dominated landscapes.

Hot weather slows them down

However, is this finding truly due to crop raiding? The other explanation could be temperature. I discovered that temperature also plays a big role. When it got hotter, elephants moved more slowly, probably to avoid overheating. In open, dry landscapes like Makgadikgadi, this is essential for conserving water and energy. My study showed that at the same temperature, elephants still moved faster at night than during the day. So apart from heat, either crop raiding behaviour or sun exposure can be explanations for this behaviour.

Direction is everything

What mattered most, above all, was where the elephants were going. They sped up significantly when heading toward key resources, like a river or crop fields. This suggests elephants know exactly where they're going and remember these places well. When moving away from these places, speeds dropped, especially during the midday heat.

Now what?

These patterns can help reduce human-elephant conflict. Since elephants are more active at night near farms, mitigation efforts, like lights or barriers, should focus on that period. That's a lot easier said than done, though. Re-imagine being the farmer. After your workday you now have to put nighttime alarms to scare off these elephants, still possibly triggering aggression and risking your life instead of your crops. So, how do we practically help in this situation?

The next steps

For the farmers, the short-term focus should be on mitigation efforts. The more tools there are in this toolbox, the more options farmers have to find a method that works for them and their surroundings. And what about long-term research? Well, there are many ways to go. For example, looking at elephant presence/absence additional to their walking might tell us a lot more about their activity patterns. Another question might be if these results also apply to different regions.

In short, there's still much to learn, but if we want elephants and people to coexist in the landscapes, they both rely on, we need to understand how these giants move through the world.

Appendix 2 Tables

Table A2.1. Linear model results for the effect of walking direction on speed. Summary of linear model estimates (β), standard errors, t-values, p-values, R^2 and AIC for the effect of walking direction across sites.

Site	β	Std. Error	t-value	P-value	R^2	AIC
Combined	-7.44	0.236	-31.5	1.43E-148	0.52	5039
EFA02	-3.34	1.04	-3.22	2.07E-3	0.15	354
EFA06	-7.9	0.233	-33.9	2.65E-161	0.57	4608

Table A2.2. Summary of LM models for time of day across combined data and by site. Linear model results showing estimated effects (β), standard errors, significance (p-value), model fit (R^2), and AIC for different time of day transformations across sites.

Site	Model	Stat. model	β	Std. Error	P-value	R^2	AIC
Combined	24H	LM	-0.475	0.264	0.0725	0.0035	5710.9
Combined	12H	LM	-0.16	0.256	0.532	0.0004	5713.8
Combined	Noondip	LM	-1.48	1.01	0.144	0.0023	5712
Combined	AfternoonDip	LM	4.32	0.808	1.14E-07	0.0298	5686
EFA02	24H	LM	-0.96	0.74	0.199	0.0269	362
EFA02	12H	LM	-0.498	0.746	0.507	0.00725	363
EFA02	Noondip	LM	3.76	2.94	0.205	0.0261	362
EFA02	Afternoon Dip	LM	-0.318	2.01	0.875	0.00041	364
EFA06	24H	LM	-0.353	0.28	0.208	0.00183	5341
EFA06	12H	LM	-0.0822	0.269	0.76	0.00011	5342
EFA06	Noondip	LM	-1.93	1.06	0.0694	0.0038	5339
EFA06	Afternoon Dip	LM	4.71	0.865	6.99E-08	0.033	5313

Table A2.3. Summary of GAM models for time of day across combined data and by site. Generalized additive model results showing effective degrees of freedom (Edf), reference degrees of freedom (Ref.df), significance (p-value), model fit (R^2), and AIC values across sites and time-of-day models.

Site	Model	Statistic model	Edf	Ref.df	P-value	R^2	AIC
Combined	24H	GAM	6.77	7.9	4.60E-06	0.042	5347
Combined	12H	GAM	2.95	3.58	0.367	0.005	5376
Combined	Noondip	GAM	3.95	4	0.00026	0.02	5363
Combined	Afternoondip	GAM	1.3	1.53	0	0.039	5339
EFA02	24H	GAM	1	1	0.204	0.029	334
EFA02	12H	GAM	7.59	7.99	0.128	0.171	336
EFA02	Noondip	GAM	3.8	3.96	0.0908	0.115	332
EFA02	Afternoondip	GAM	3.91	3.99	0.0023	0.213	324
EFA06	24H	GAM	6.82	7.94	1.76E-06	0.047	5005
EFA06	12H	GAM	7.67	8.11	0.0196	0.022	5032
EFA06	Noondip	GAM	3.97	4	1.32E-05	0.027	5019
EFA06	Afternoondip	GAM	1	1	0	0.045	4995

Table A2.4. Summary of LM models for temperature across combined data and by site. Linear model results showing estimated effects (β), standard errors, significance (p-value), model fit (R^2), and AIC for temperature and its squared term across sites.

Site	Model	Term	β	Std. Error	P-value	R^2	AIC
Combined	LM	temp	0.478	0.095	5.02E-07	0.028	5690
Combined	LM	temp ²	-0.01	0.002	3.41E-07	0.028	5690
EFA02	LM	temp	-0.415	0.469	0.38	0.021	364
EFA02	LM	temp ²	0.0066	0.0086	0.441	0.021	364
EFA06	LM	temp	0.521	0.098	1.20E-07	0.032	5316
EFA06	LM	temp ²	-0.011	0.002	1.53E-07	0.032	5316

Table A2.5. Summary of GAM models for temperature across combined data and by site. Generalized additive model results showing estimated degrees of freedom (edf), reference degrees of freedom (Ref.df), significance (p-value), explained deviance, and AICs.

Site	Model	Term	Edf	Ref.df	P-value	Deviance Explained	AIC
Combined	GAM	s(temp)	5.26	6.37	5.26E-06	0.042	5347
EFA02	GAM	s(temp)	1	1	0.365	0.023	337
EFA06	GAM	s(temp)	6.9	7.95	1.16E-06	0.051	5003

Table A2.6. Linear model (LM) results for the effect of 30-day rolling average rainfall on walking speed. Summary of linear model estimates (β), standard errors, t-values, p-values, R^2 and AIC for the effect of 30-day rolling average rainfall on walking speed across all sites and individual sites.

Site	β	Std. Error	t-value	P-value	R^2	AIC
All	0.745	0.371	2.01	0.045	0.004	5539
EFA02	-0.092	0.158	-0.581	0.564	0.006	363
EFA06	0.384	0.153	2.5	0.013	0.007	5336

Table A2.7. Generalized additive model (GAM, Gamma family) results for the effect of rainfall. Summary of generalized additive model results showing degrees of freedom (Edf), reference degrees of freedom (Ref.df), p-value, deviance explained, and AIC for the effect of rainfall on walking speed across sites.

Site	Term	Edf	Ref.df	P-value	Deviance Explained	AIC
Combined	s(rainfall)	1.59	1.97	0.306	0.0033	5375
EFA02	s(rainfall)	1	1	0.576	0.0058	335
EFA06	s(rainfall)	1	1	0.024	0.0059	5033

Table A2.8. Linear model results for the effect of sex on speed. Summary of linear model estimates (β), standard errors, t-values, p-values, R^2 and AIC for the effect of sex on walking speed across sites.

Site	β	Std. Error	t-value	P-value	R^2	AIC
Combined	-0.98	0.69	-1.42	0.155	0.002	5712
EFA06	-0.84	0.698	-1.21	0.227	0.002	5341

Table A2.9. Linear model results for Age. Summary of linear model estimates (β), standard errors, t-values, p-values, R^2 and AIC for the effect of age on walking speed across combined data and by site.

Site	Term	β	Std. Error	t-value	P-value	R^2	AIC
Combined	Juvenile (0-9 years)	-0.945	0.644	-1.47	0.143	0.004	5515
Combined	Sub-adult (10-20 years)	0.192	0.384	0.499	0.618	0.004	5515
EFA02	Juvenile (0-9 years)	-3.01	4.31	-0.698	0.488	0.008	360
EFA02	Sub-adult (10-20 years)	-0.101	1.1	-0.092	0.927	0.008	360
EFA06	Juvenile (0-9 years)	-1.08	0.659	-1.63	0.103	0.005	5148
EFA06	Sub-adult (10-20 years)	0.162	0.405	0.4	0.689	0.005	5148

Table A2.10. Linear model (LM) results for the interaction between time of day and temperature for speed. Summary of linear model estimates (β), standard errors, t-values, p-values, R^2 and AIC for the interaction between temperature and hour of the day for walking speed across different time periods.

Model	Term	β	Std. Error	t-value	P-value	R^2	AIC
24H	Temp	-0.465	0.232	-2	0.046	0.029	6024
24H	Temp ²	0.00981	0.00442	2.22	0.027	0.029	6024
12H	Temp	0.232	0.146	1.59	0.112	0.04	6013
12H	Temp ²	-0.00716	0.00304	-2.36	0.019	0.04	6013
Noondip	Temp	1.43	2.57	0.56	0.577	0.043	6011
Noondip	Temp ²	-0.0325	0.0391	-0.83	0.406	0.043	6011
Afternoondip	Temp	-1.17	2.92	-0.4	0.688	0.047	6006
Afternoondip	Temp ²	0.015	0.0406	0.37	0.712	0.047	6006

Table A2.11. Generalized additive model (GAM, Gamma family) results for the interaction between time of day and temperature for speed. Summary of generalized additive model results showing degrees of freedom (Edf), reference degrees of freedom (Ref.df), p-value, deviance explained, R^2 and AIC for the interaction between temperature and hour of the day for walking speed.

Model	Edf	Ref.df	P-value	Deviance Explained	R^2	AIC
24H	3.5	3.83	3.35E-06	0.0605	0.054	6003
12H	5.66	7.83	0.00658	0.063	0.053	6012
Noondip	3.41	3.65	0.024	0.0657	0.055	6004
Afternoondip	9.29	10.33	0.0007	0.115	0.098	5965

Table A2.12. Linear model (LM) results for the interaction between direction and hour of the day for speed. Summary of linear model estimates (β), standard errors, t-values, p-values, R^2 and AIC for the interaction between walking direction and hour of the day for walking speed.

Model	Estimate (β)	Std. Error	t-value	P-value	R^2	AIC
24H	-7.01	0.293	-23.94	< 2e-16	0.505	5362
12H	-7.16	0.253	-28.27	< 2e-16	0.501	5370
Noondip	-7.88	1.5	-5.27	1.72E-07	0.499	5375
Afternoondip	-3.4	1.38	-2.46	0.0141	0.508	5357

Table A2.13. GAM results for the interaction between direction and hour of the day for speed. Summary of generalized additive model results showing degrees of freedom (Edf), reference degrees of freedom (Ref.df), p-values, deviance explained, R^2 , and AIC for the interaction between walking direction and hour of the day for walking speed.

Model	Direction	Edf	Ref.df	P-value	Deviance Explained	R^2	AIC
24H	L	4.53	5.58	7.66E-05	53.70%	0.531	5320
24H	R	7.56	8.51	2.91E-06	53.70%	0.531	5320
12H	L	1.36	1.63	0.306	51.20%	0.508	5359
12H	R	5.32	5.8	0.00356	51.20%	0.508	5359
Noondip	L	2.17	2.55	0.382	50.10%	0.498	5374
Noondip	R	1.01	1.02	0.309	50.10%	0.498	5374
Afternoondip	L	2.12	2.54	0.000123	51.00%	0.508	5355
Afternoondip	R	1	1	0.0817	51.00%	0.508	5355

Table A2.14. Linear model (LM) results for the interaction between direction and temperature for speed. Summary of linear model estimates (β), standard errors, t-values, p-values, R^2 and AIC for the interaction between walking direction and temperature for walking speed.

Term	Estimate (β)	Std. Error	t-value	P-value	R^2	AIC
Temp	0.264	0.143	1.85	0.0643	0.504	5364
Temp ²	-0.00426	0.00292	-1.46	0.1454	0.504	5364

Table A2.15. GAM results for the interaction between direction and temperature for speed. Summary of generalized additive model results showing degrees of freedom (Edf), reference degrees of freedom (Ref.df), p-values, deviance explained, R^2 , and AIC for the interaction between walking direction and temperature for walking speed.

Direction	Edf	Ref.df	P-value	Deviance Explained	R^2	AIC
L	1	1	0.00117	50.70%	0.504	5363
R	2.35	2.93	0.157	50.70%	0.504	5363

Appendix 3 Residuals

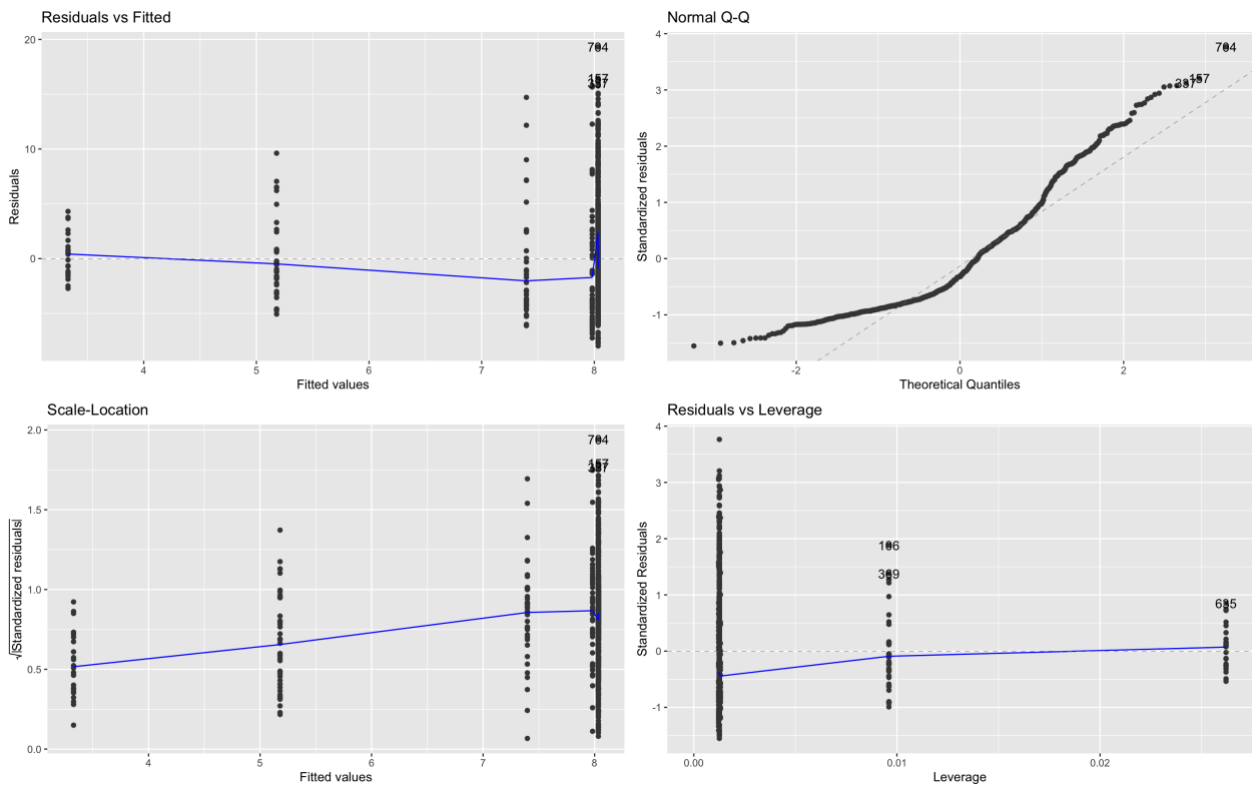


Figure A3.1. Diagnostic plots for the linear regression model predicting walking speed from afternoon dip values for site EFA06. The top-left panel shows residuals versus fitted values, indicating potential non-linearity or heteroscedasticity if a clear pattern is present. The top-right Q-Q plot assesses the normality of residuals; deviations from the line suggest non-normality. The bottom-left scale-location plot ($\sqrt{\text{standardized residuals}}$ versus fitted) evaluates homoscedasticity. The bottom-right plot displays standardized residuals versus leverage, identifying influential observations

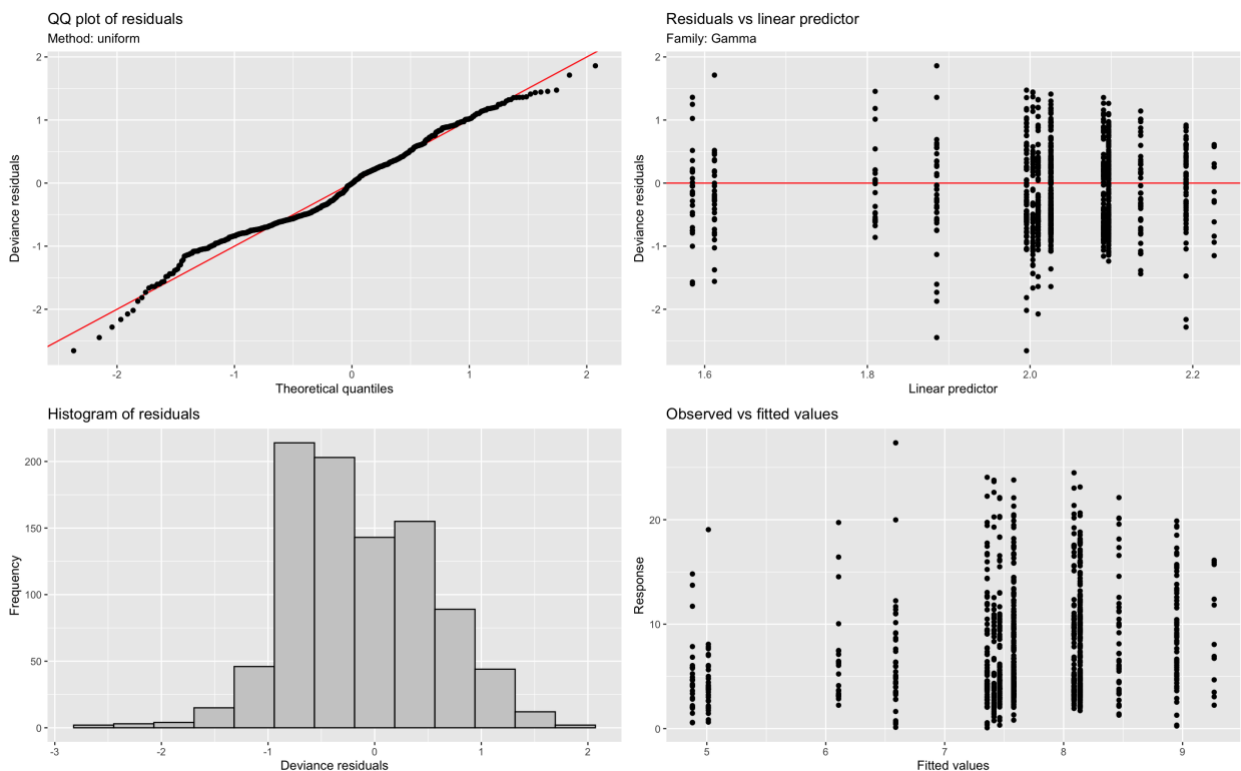


Figure A3.2. Diagnostic plots for the Generalized Additive Model (GAM) predicting walking speed from afternoon dip values for site EFA06. The top-left panel shows a Q-Q plot assessing the normality of residuals. The top-right panel displays a histogram of residuals, indicating the overall distribution. The bottom-left plot shows residuals versus fitted values, allowing assessment of potential non-linearity or patterns suggesting model misfit. The bottom-right scale-location plot helps evaluate homoscedasticity across the range of fitted values.

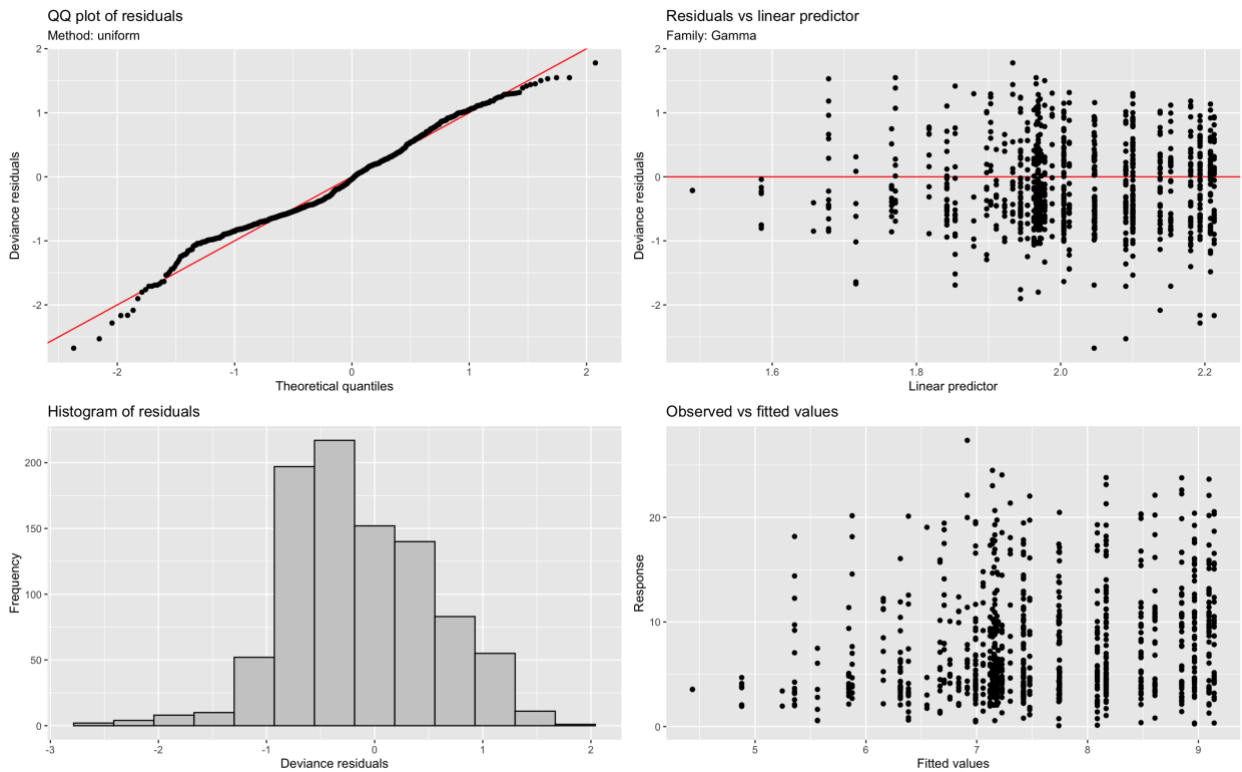


Figure A3.3. Diagnostic plots for the Generalized Additive Model (GAM) predicting walking speed from temperature for site EFA06. The top-left panel shows a Q-Q plot assessing the normality of residuals. The top-right panel displays a histogram of residuals, indicating the overall distribution. The bottom-left plot shows residuals versus fitted values, allowing assessment of potential non-linearity or patterns suggesting model misfit. The bottom-right scale-location plot helps evaluate homoscedasticity across the range of fitted values.

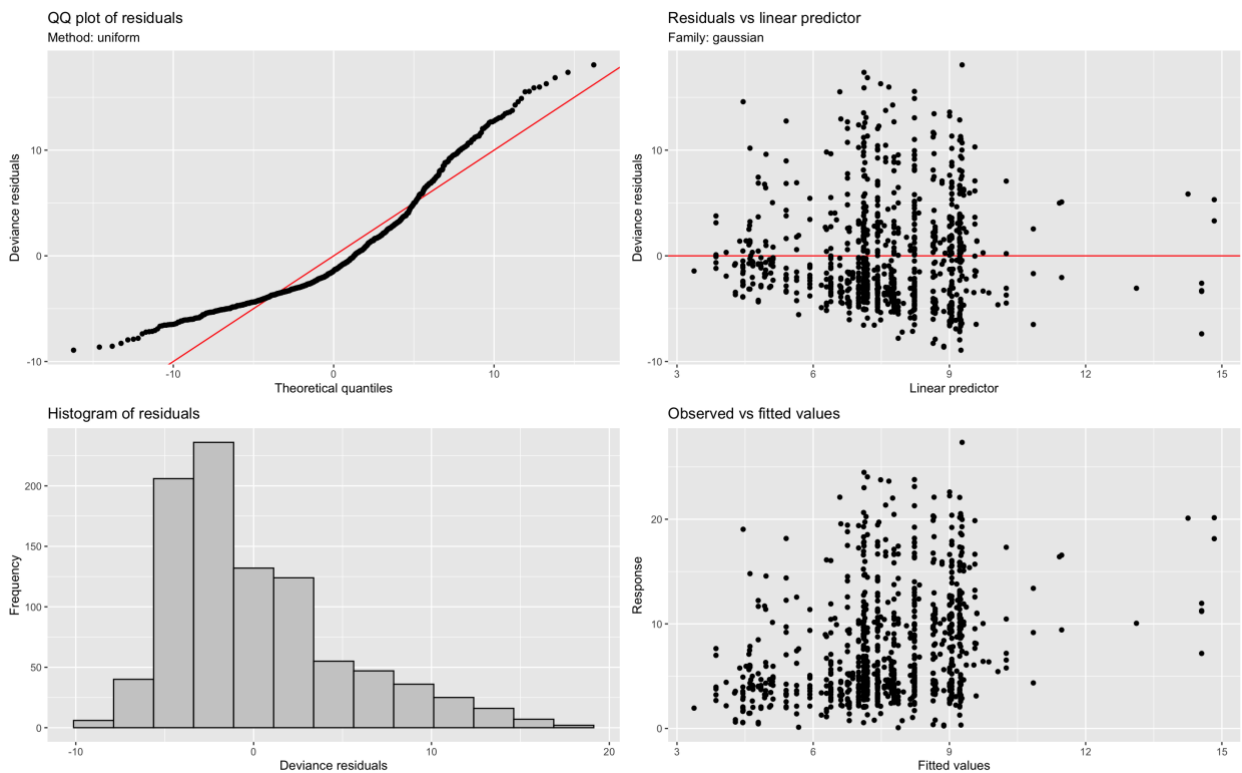


Figure A3.4. Diagnostic plots for the Generalized Additive Model (GAM) predicting walking speed from temperature, afternoon dip, and their interaction (site EFA06). The Q-Q plot (top-left) assesses the normality of residuals; deviations from the reference line indicate non-normality. The histogram (top-right) provides an overview of residual distribution. The residuals versus fitted values plot (bottom-left) reveals any systematic patterns or non-linearities, while the scale-location plot (bottom-right) evaluates homoscedasticity.

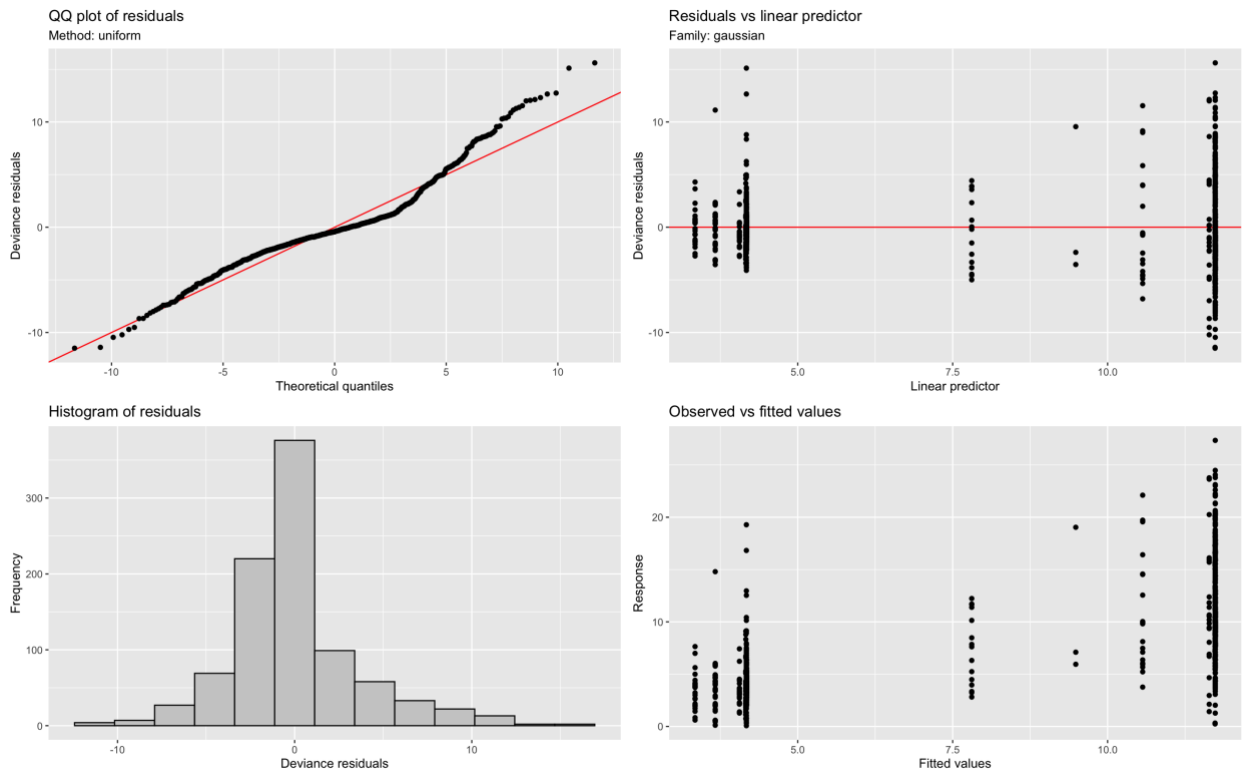


Figure A3.5. Diagnostic plots for the Generalized Additive Model (GAM) predicting walking speed from direction, afternoon dip, and their interaction (site EFA06). The Q-Q plot (top-left) assesses the normality of residuals; deviations from the reference line indicate non-normality. The histogram (top-right) provides an overview of residual distribution. The residuals versus fitted values plot (bottom-left) reveals any systematic patterns or non-linearities, while the scale-location plot (bottom-right) evaluates homoscedasticity.

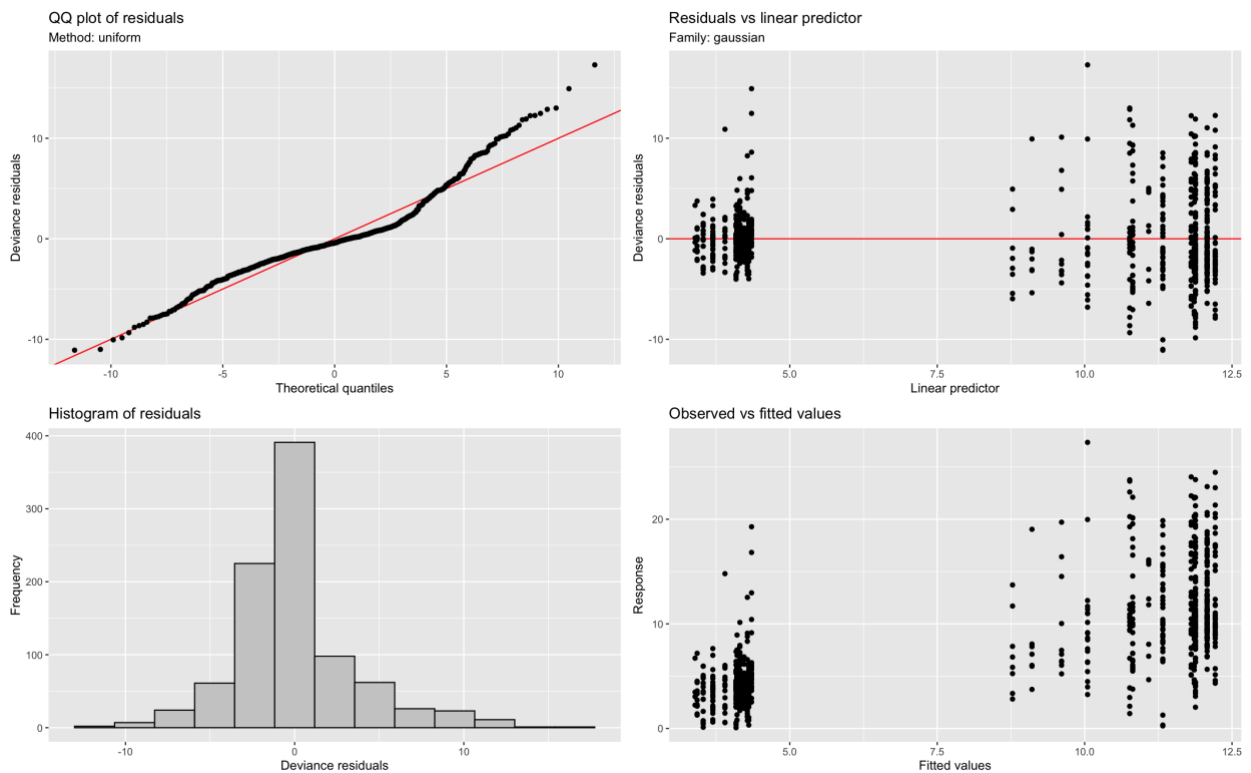


Figure A3.6. Diagnostic plots for the Generalized Additive Model (GAM) predicting walking speed from direction, 24hour time of day, and their interaction (site EFA06). The Q-Q plot (top-left) assesses the normality of residuals; deviations from the reference line indicate non-normality. The histogram (top-right) provides an overview of residual distribution. The residuals versus fitted values plot (bottom-left) reveals any systematic patterns or non-linearities, while the scale-location plot (bottom-right) evaluates homoscedasticity.

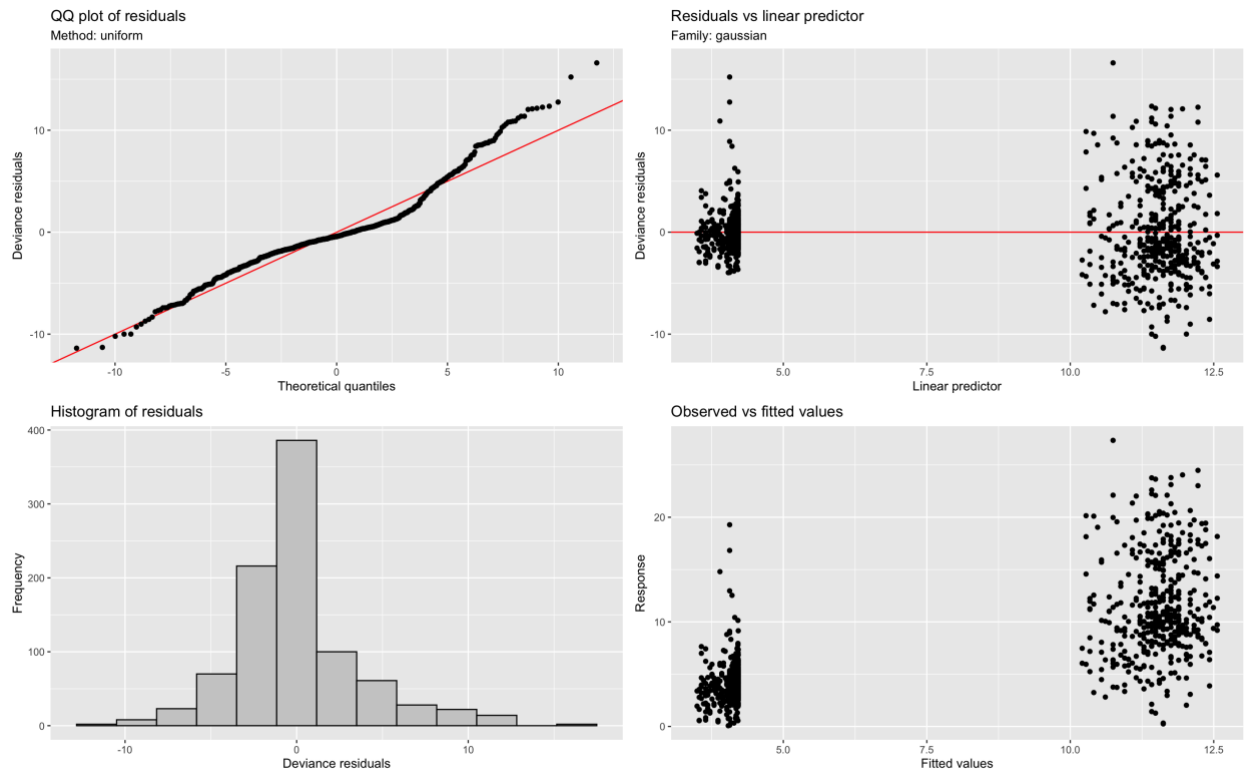


Figure A3.7. Diagnostic plots for the Generalized Additive Model (GAM) predicting walking speed from direction, temperature, and their interaction (site EFA06). The Q-Q plot (top-left) assesses the normality of residuals; deviations from the reference line indicate non-normality. The histogram (top-right) provides an overview of residual distribution. The residuals versus fitted values plot (bottom-left) reveals any systematic patterns or non-linearities, while the scale-location plot (bottom-right) evaluates homoscedasticity.