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Mémoire

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Investigating the Drivers of Elephant Break-ins into Fenced Properties within a Nature Reserve to Mitigate Human-Elephant Conflict

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Investigating the Drivers of Elephant Break-ins into Fenced Properties within a Nature Reserve to Mitigate Human-Elephant Conflict | Lisa Cimetta | Promotors: Dr. Flavien Collart and Paul Allin | Department of Biology, Ecology and Evolution, ULiège | August 2025

Abstract

Human–Elephant Conflict (HEC) represents a major socio-ecological challenge across the range of elephants, where people and wildlife increasingly share space. Despite decades of mitigation efforts, including the creation of large protected areas, conflicts continue to emerge even within reserves. Elephant break-ins into fenced properties represent a particularly striking form of conflict, as they cause material damage and pose risks to human safety, thereby exacerbating tensions between people and wildlife. While elephant crop-raiding has been widely studied, little attention has been given to property break-ins inside protected areas. In 2024, a sharp rise in such events was recorded in Olifants West Nature Reserve, a private reserve adjoining Kruger National Park in South Africa, underlining the urgency of identifying the factors that drive this behaviour.

This study addressed this gap by examining four key questions: (1) which sex and age classes of elephants were most frequently involved in break-ins; (2) when these incidents occurred across daily and seasonal cycles; (3) how environmental features influenced their spatial distribution within the reserve: and (4) which property-level characteristics shaped vulnerability. To answer these questions, security records were combined with interviews and vegetation inventories carried out for each fenced property, together with additional environmental and anthropogenic variables to assess how break-ins were shaped across multiple scales.

The results revealed that intrusions were overwhelmingly carried out by adult males, concentrated in the dry season, and occurred mainly during hours of darkness, suggesting that elephants time their behaviour to minimise encounters with humans. Water availability emerged as a central driver, with fewer break-ins near rivers and large waterholes but more frequent events near small and medium-sized ones. At the property scale, well-maintained fences consistently reduced risk, while larger properties were more frequently targeted. Vegetation indices provided little explanatory power, yet the tendency of elephants to feed on the same species found outside properties suggests that vegetation quality, rather than greenness alone, may influence their choices.

Taken together, these findings show that property-level measures are necessary but insufficient on their own. Reinforcing fences and adapting deterrents to nocturnal activity may help reduce vulnerability, but longer-term solutions will require broader-scale strategies, including improved water management and closer collaboration with property owners. Such measures will be crucial to reduce conflict intensity and support coexistence between elephants and people in protected landscapes.

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Résumé

Les conflits entre humains et éléphants constituent un défi socio-écologique majeur dans l’ensemble de leur aire de répartition, où la cohabitation s’intensifie. Malgré des décennies d’efforts de mitigation, y compris la création de vastes aires protégées, ces conflits persistent, parfois même à l’intérieur des réserves. Les intrusions d’éléphants dans des propriétés clôturées en représentent une forme particulièrement préoccupante, car elles entraînent des dégâts matériels et menacent la sécurité des personnes, renforçant ainsi les tensions. Alors que les pillages de cultures sont bien documentés, les intrusions dans les propriétés situées en zone protégée restent peu étudiées. En 2024, une forte augmentation de ces événements a été observée dans l’Olifants West Nature Reserve, une réserve privée attenante au parc national Kruger en Afrique du Sud, soulignant la nécessité d’en comprendre les déterminants.

Cette étude s’est centrée sur quatre questions : (1) quelles classes d’âge et de sexe d’éléphants sont les plus fréquemment impliquées dans les intrusions ; (2) à quels moments de la journée et de l’année elles se produisent ; (3) quels facteurs environnementaux influencent leur répartition spatiale dans la réserve ; et (4) quelles caractéristiques propres aux propriétés expliquent leur vulnérabilité. Pour y répondre, des registres de sécurité ont été croisés avec des entretiens menés auprès des propriétaires et avec un inventaire systématique des propriétés, complétés par des variables environnementales et anthropiques analysées à plusieurs échelles.

Les résultats révèlent que les intrusions sont presque exclusivement le fait de mâles adultes, concentrées durant la saison sèche et principalement de nuit, ce qui suggère une stratégie visant à limiter les contacts avec les humains. La disponibilité en eau apparaît déterminante : les intrusions sont moins fréquentes près des rivières et grands points d’eau, mais plus nombreuses à proximité de points moyens ou petits. À l’échelle des propriétés, des clôtures bien entretenues réduisent significativement le risque, tandis que les grandes parcelles sont davantage ciblées. Les indices de végétation expliquent peu les intrusions, mais le fait que les éléphants consomment les mêmes espèces que celles présentes autour des propriétés suggère que la qualité des plantes joue un rôle plus important que leur simple verdure.

Dans l’ensemble, ces résultats montrent que les mesures locales, bien qu’indispensables, ne suffisent pas. Le renforcement des clôtures et l’adaptation des dispositifs de dissuasion aux activités nocturnes pourraient réduire la vulnérabilité, mais des solutions durables exigent une approche à plus large échelle, incluant une meilleure gestion de l’eau et une coopération accrue avec les propriétaires. Ces actions seront essentielles pour atténuer l’intensité des conflits et favoriser la coexistence entre éléphants et humains dans les paysages protégés.

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1. Introduction

Year after year, biodiversity continues to decline rapidly, primarily driven by human activities (Brodie et al., 2021). For large mammals, in particular, population declines over the past century have been the outcome of threats such as habitat loss, unsustainable land use, overexploitation, and human-wildlife conflicts (Brodie et al., 2021; Ripple et al., 2017). To address this issue, it has been suggested that more land must be protected or managed for conservation purposes (Pacifici et al., 2020). This is particularly critical, as human population growth exerts considerable pressure on ecosystems through urbanization and the conversion of natural habitats for agriculture and livestock (Brodie et al., 2021; Pacifici et al., 2020). These processes lead to the fragmentation and degradation of habitats, which severely limits the range of many species. As habitats become increasingly fragmented, they can no longer sustain viable populations, and many species become confined to smaller, isolated patches (Bennett & Saunders, 2010). This results in diminished access to essential resources such as food, water, and breeding sites, forcing wildlife into human-dominated areas in search of these resources. At the same time, human settlements have increasingly expanded into wildlife-rich areas, leading to greater spatial overlap between humans and wildlife. This bidirectional process amplifies human-wildlife interactions, intensifying competition for resources and space (Abrahms, 2021; Anand & Radhakrishna, 2017).

Among the many species affected by these pressures, the African elephant (*Loxodonta africana*) stands out both for its vulnerability and its ecological importance. Classified as an endangered species by the IUCN (Gobush et al, 2022), it is the largest terrestrial mammal, with males weighing between 5,500 and 6,000 kg and females between 2,500 and 2,800 kg. As their habitats become increasingly fragmented and depleted due to expanding human activities, elephants face growing challenges in accessing essential resources such as food and water. This often compels them to move beyond protected areas and into human-occupied landscapes, where the risk of conflict with local communities is significantly heightened (Di Minin et al., 2021; Leimgruber et al., 2003; Tripathy et al., 2021). Despite these challenges, African elephants continue to play a key role in the socio-ecological dynamics of the ecosystems they occupy (Lindsay et al., 2017; Van De Water et al., 2023). Their presence is a major economic driver in many regions, particularly through ecotourism, which generates substantial revenue and supports conservation initiatives (Van De Water et al., 2023). They also hold significant cultural and social value, being perceived as central elements of heritage and collective identity in some communities (Van De Water et al., 2023). Ecologically, elephants play a keystone role in savanna landscapes. They act as ecosystem engineers by actively modifying habitat structure through processes such as tree uprooting and vegetation clearance, which in turn influence landscape dynamics and key ecological processes (Jones et al., 1994). These modifications contribute to shaping ecosystem structure and function, with cascading effects on species composition and resource availability (Jones et al., 1994). By breaking branches or knocking down trees, they make foliage accessible to smaller herbivores that cannot browse at greater heights (Rutina et al., 2005). Elephants also play a vital role in seed dispersal across long distances, transporting seeds in their digestive tract and depositing them through defecation. In some cases, the acidic conditions in their gut can even enhance the germination potential of certain plant species (Bunney et al., 2017).

Due to their substantial body mass, the African elephant can tolerate lower-quality diets, allowing them to exploit a broad range of ecosystems, from productive, verdant habitats to nutrient-poor arid zones (Owen-Smith & Chafota, 2012). However, despite this adaptability, they exhibit pronounced foraging selectivity, consuming on average 300 to 400 kg of fresh food for male and 250 Kg for female (Pretorius et al., 2012). Elephants adjust their diet according to seasonal variations in plant resources (Codron et al., 2011; Owen-Smith & Chafota, 2012). During the wet season, it preferentially consumes grasses, which are at their peak in terms of availability and nutritional quality, particularly nitrogen content. In the dry season, as grasses become scarcer and less nutritious, elephants shift their diets toward woody plants, feeding on leaves, twigs, bark, and roots (Codron et al., 2011; Kos et al., 2012). This transition to a more browse-dominated diet is, however, less pronounced in habitats with low trees diversity. In these environments, elephants continue to feed on grasses despite their lower nutritional quality (Codron et al., 2011). Furthermore, elephants consume large amounts of water, typically ranging from 150 to 300 liters daily, although they can survive for up to four days without access to water (Skinner & Chimimba, 2005). Water resources are not always readily available, especially during dry seasons when rainfall is low (Naidoo et al., 2020). During times of water scarcity, elephants rely on spatial memory to navigate short- and long-distances between permanent water sources (Polansky et al., 2015). However, spatial memory alone does not fully explain how they detect water in ephemeral sources or track rainfall events (Wood et al., 2022). Olfaction also plays a crucial role in their foraging strategies and resource acquisition (Plotnik et al., 2014) as well as in locating available water sources in their environment (Wood et al., 2022).

Elephants are generally non-territorial. Home range sizes vary seasonally and spatially depending on habitat type, resource availability, and climatic conditions, ranging from 15–50 km² in resource-rich areas to over 500–3,000 km² in arid or fragmented landscapes, with some exceptions exceeding these values (Thouless, 1996). Elephant movements and foraging behaviors are therefore non-random and closely shaped by the spatial and temporal availability of resources across multiple scales. (Jones et al., 1994). At the landscape scale, elephant movements appear to be primarily determined by the spatial and temporal distribution of essential resources, such as water and vegetation (Boettiger et al., 2011; Shannon et al., 2009; Wall et al., 2013). In semi-arid environments, where resource availability can be highly heterogenous, elephants tend to aggregate in areas offering higher resource availability. At larger spatial scales, elephant movements track the seasonal and spatial dynamics of vegetation growth and distribution, allowing them to exploit areas with optimal forage conditions (Wall et al., 2013). After selecting a general location at a broader scale, they rely on their ability to differentiate plant odour profiles to target preferred plant species, thereby reducing foraging time (Plotnik et al., 2014; Schmitt et al., 2018). This ability enables them to efficiently select specific plants both between and within different patches (Plotnik et al., 2014; Schmitt et al., 2018). Furthermore, the distribution of permanent or seasonal water points promotes elephant aggregation, especially during the dry season, when natural water sources become limited (Naidoo et al., 2020; Shannon et al., 2009). When these water points are located near human infrastructure, they often cause human-elephant encounters. Studies have shown that elephants generally tend to avoid human-occupied areas and human disturbance, especially during daylight hours when humans are more active (Boettiger et al., 2011; Jackson et al., 2008). However, during periods of water scarcity, their proximity to human settlements increases, suggesting a growing dependence on water sources near anthropogenic zones (Valls-Fox et al., 2018).

Over time, these shifting movement patterns driven by resource distribution, can bring elephants increasingly close to human-dominated spaces. As ecological constraints intensify, particularly during dry seasons or prolonged droughts, elephants are more likely to extend their range into human-modified landscapes in search of alternative food and water sources (Valls-Fox et al., 2018). The expansion of human settlements and agricultural activities further exacerbates this trend, increasing the spatial overlap between elephants and human populations (Chase et al., 2016). This overlap is a primary driver of human-elephant conflict (HEC), as elephants venture into agricultural fields, plantations, and domestic gardens in search of sustenance (Köpke et al., 2024; Munyao et al., 2020). These conflicts include the real and perceived impacts of elephants on human populations, such as injuries, damage to crops and infrastructure, causing food insecurity and a decline in psychological well-being (Sampson et al., 2021; Van De Water et al., 2023). Such tensions foster negative attitudes toward elephants and may lead to retaliatory actions, such as poaching, uninformed culling, or the implementation of lethal deterrence measures (Goswami et al., 2014).

To mitigate human-elephant conflicts and support elephant conservation, many elephant populations have been confined to protected areas, reducing anthropogenic pressures, while dispersal corridors have been established to facilitate safe movement (Pretorius et al., 2019). However, despite these efforts, conflicts continue to emerge within protected areas. Human interventions such as translocation, the presence of enclosing fences, limited habitat size, and other anthropogenic disturbances can significantly influence elephant behaviour and disrupt their social organisation (Shannon et al., 2013; Slotow et al., 2000).

In naturally open ecosystems, elephants live within a highly structured, multi-tiered social system dominated by females (Wittemyer et al., 2005). At the base of this hierarchy lies the mother–calf bond, which constitutes the core of a family unit. These units generally include the matriarch, her female relatives, and their dependent offspring. On average, such groups consist of about ten individuals, and females typically remain within their natal units throughout their lives, maintaining close kin-based associations. Multiple family units that share genetic ties may occasionally come together to form bond groups. When several of these bond groups associate, they create larger, loosely connected social formations called clans, which interact intermittently. This layered social organisation fosters knowledge transmission, coordinated movement, and collective protection (Wittemyer et al., 2005). Male elephants follow a different social trajectory. As they reach adolescence, typically around 12 to 15 years of age, young bulls begin to detach from their maternal groups and may even be actively excluded by older females. During this transitional period, they often form bachelor groups composed exclusively of males. With maturity, many bulls adopt a more solitary lifestyle but continue to engage in social interactions with other males to assert or negotiate dominance. Young bulls tend to associate with mature individuals, whose experience and behaviour play a critical role in their social learning (Chiyo et al., 2011; Evans & Harris, 2008). These associations help younger males understand social hierarchies, navigate periods of musth, and develop reproductive strategies (Slotow et al., 2000). However, interventions such as translocation and habitat fragmentation have disrupted these important processes. Early translocation efforts often involved moving young elephants alone or in small groups, severing them from their social networks. In the absence of appropriate social partners or other elephants altogether, these individuals were more likely to exhibit behavioural anomalies. For instance, bulls translocated without older companions sometimes entered musth prematurely and demonstrated heightened aggression, including attempts to escape, destruction of vegetation, or attacks on vehicles, humans, or other animals (Slotow et al., 2000). The social and behavioural consequences of these practices were long underestimated. Only after decades of implementation have the full effects of juvenile-only translocations been recognised (Pretorius et al., 2019). As a result, current protocols favour moving intact family groups and mature bulls, guided by a well-defined set of best practices aimed at preserving social cohesion and reducing stress-related outcomes (Water et al., 2024).

While the African elephants (*Loxodonta africana*) have experienced a marked population decline across the continent (Chase et al., 2016; Wittemyer et al., 2014), South African population has tripled since 1992 (Pretorius et al., 2019). In fact, the country comprises 87 reserves, parks, or protected areas that hold elephants, encompassing 78 distinct populations (Pretorius et al., 2019). This expansion is partly due to the rise in smaller, fenced reserves since the mid-1980s, many of which were stocked through the translocation of juvenile elephants spared during the culling operations in Kruger National Park prior to 1996 (Garaï et al., 2004). Kruger National Park is the largest protected area in South Africa (Figure 1). It forms the core of the Greater Kruger system, an extensive conservation landscape that encompasses a network of adjacent private and community-managed reserves. Since the early 1990s, many of the fences separating Kruger from these neighbouring reserves have been removed, allowing for unrestricted wildlife movement across the landscape. As a result, the Greater Kruger system now spans over 20,000 km^2, functioning as a unified ecological area that supports natural dispersal and migration processes. By 2015, the elephant population in Kruger accounted for 78% of South Africa's total elephant population (Pretorius et al., 2019). Between 2013 and 2020, the elephant population in Greater Kruger grew exponentially at a rate of approximately 5.3% annually, reaching 31,324 individuals in 2020. It is highly probable that this upward trend has continued beyond this period (Ferreira et al., 2024).

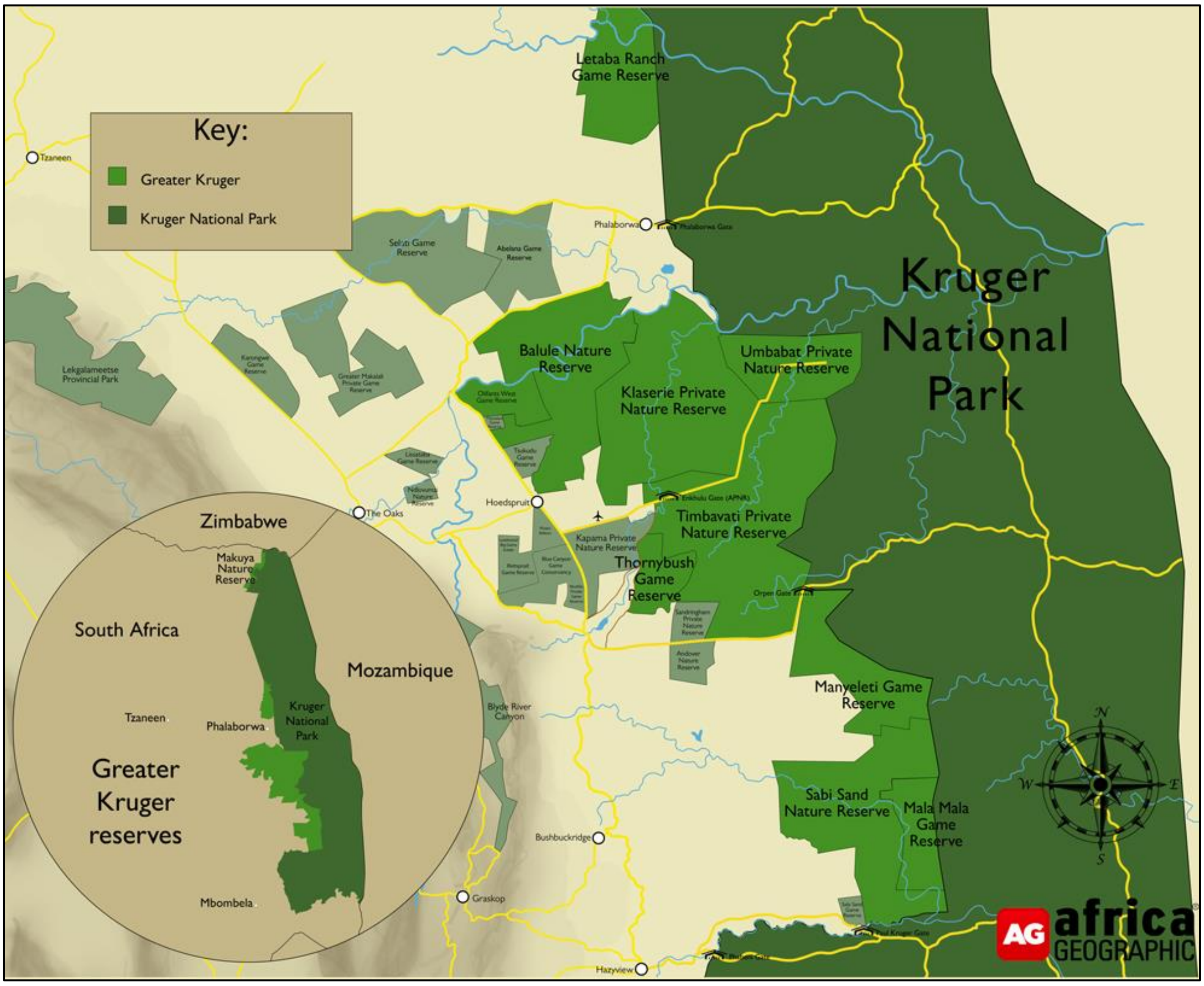


Figure 1. Map of Kruger National Park and the Greater Kruger. *Representation of Kruger National Park (dark green) and the adjoining private reserves constituting the Greater Kruger (light green). Source: Africa Geographic.*

Olifants West Nature Reserve (OWNR), which is located on the western edge of the Greater Kruger system and forms part of Balule Nature Reserve, appears to be directly affected by the increasing elephant numbers. In this reserve, numerous houses and lodges are each surrounded by elephant-exclusion fences. However, these barriers are not always effective, as elephants occasionally breach them, resulting in material damage and posing significant risks to both residents and visitors. Although break-ins have historically been rare within the reserve, a notable surge in incidents was recorded in 2024. This raises important questions about why elephants continue to enter these properties despite having access to extensive areas. While numerous studies have investigated the factors influencing crop-raiding behaviour in elephants, particularly in agricultural landscapes, there appears to be a lack of research focusing specifically on elephant break-ins into fenced properties within protected areas (Jackson et al., 2008; Osborn, 2004; Tripathy et al., 2021). This gap is noteworthy, as the dynamics of such intrusions may differ significantly from crop-raiding events in farmlands, given the differences in resource distribution, landscape configuration, and human activity patterns. Addressing this knowledge gap requires examining the environmental, temporal, and anthropogenic factors that may influence the occurrence and distribution of such break-ins across multiple scales.

For instance, areas characterised by high vegetation productivity are likely to attract elephants, making nearby properties more susceptible to break-ins. The same applies to those located near water points, as elephants are known to frequent such areas during periods of drought. However, the influence of water points is likely to differ depending on their type and size. Small sources, often artificial and shallow, are likely to provide only short-term drinking opportunities, whereas medium to large sources, typically more natural, are more likely to attract elephants for extended periods, supporting activities such as mud bathing and social interactions (Smith et al., 2024). Rivers, in particular, offer additional ecological benefits through continuous water availability and the presence of riparian vegetation (I. P. J. Smit & Ferreira, 2010). Such differences may influence whether elephants linger in the vicinity or merely pass through, potentially affecting the likelihood of them approaching nearby human properties. Similarly, drainage lines, or dry riverbeds, can play an important role in elephant movements. These linear features retain moisture for longer periods, promoting the growth of denser, more diverse, and often more nutritious vegetation (Pittiglio et al., 2014). They can also function as natural movement corridors, providing both vegetative cover and occasional access to residual water (Giliba et al., 2023). Properties located near a drainage line are likely to present a higher probability of break-ins, as they are situated close to a corridor regularly used by elephants. In contrast, steep slopes tend to be avoided due to the high energetic costs associated with traversing these areas (Wall et al., 2006). Properties located in rugged or less accessible terrain could therefore have a lower likelihood of intrusion. However, elephants might favour rugged landscapes, as these areas often provide higher nutrient concentrations and greater forage density compared to flatter regions (Nellemann et al., 2002). They also tend to avoid roads with high traffic levels but may either show no preference or actively select low-traffic roads, as these can facilitate easier movement (Blake et al., 2008; Dickson et al., 2005). Therefore, road density can be a significant factor influencing elephant movement patterns, with elephants potentially avoiding busy roads while selecting less-trafficked routes that provide easier navigation. Property density could also influence elephant spatial patterns, as they generally tend to avoid human-occupied areas and human disturbance (Boettiger et al., 2011; Jackson et al., 2008).

The decision of elephants to break into human settlements may also be influenced by localized factors at smaller scales. At this finer scale, elephants must decide whether to forage within properties or in the surrounding environment, based on the relative availability and accessibility of preferred resources within and outside properties. These decisions may be based on Volatile Organic Compounds (VOCs) emitted by plants. These compounds can act as olfactory signals that elephants use to identify nutrient-rich plants or to avoid those containing potentially toxic Plant Secondary Metabolites (PSMs) (Schmitt, Shuttleworth, et al., 2020; Shrader et al., 2012). The presence of either preferred or repellent plant species within properties relative to outside properties may significantly influence the elephants' decision to enter. Moreover, elephants might target the same types of vegetation both inside and outside properties. This might be the case when vegetation within properties maintains their nutritional quality due to factors such as regular irrigation during the dry season, which reduces water stress and enhances its nutritional value (Bista et al., 2018). In contrast, vegetation outside these areas may experience a decline in nutritional quality, partly due to water stress and greater herbivory pressure, which can stimulate the production of defensive compounds like tannins, terpenes, or alkaloids through secondary metabolic processes (Metlen et al., 2009). These compounds can decrease plant palatability by exhibiting antinutritional properties that reduce food nutritive value or by acting as toxins that disrupt cellular, tissue, and organ function in herbivores. (Estell, 2010). Consequently, they may influence elephants' foraging decisions by reducing the attractiveness of plants outside properties, thereby increasing the relative preference for those within. While it has been suggested that areas characterised by high vegetation productivity may attract elephants and increase the risk of break-ins (see previous paragraph), the opposite dynamic may also be considered. In landscapes where the surrounding environment remains ecologically rich and supports high-quality forage, elephants may find sufficient resources outside and therefore show less motivation to enter properties. This highlights the importance of evaluating not only the absolute resource availability within properties, but also its relative attractiveness compared to adjacent areas. Furthermore, the availability of fresh water sources within these properties could further increase the likelihood of elephant break-ins, as elephants exhibit a clear preference for fresh water over stagnant or muddy water typically found outside (Ndlovu et al., 2018). In cases where no accessible water sources are present in the surrounding environment, the presence of water within properties may become an even stronger driver of elephant entry. Nonetheless, the design of properties themselves may also play a role in discouraging elephant intrusions. One of the most common deterrent strategies involves the use of various types of electric fencing, specifically designed to prevent elephants from entering. In addition to these primary barriers, secondary deterrents are also commonly used to surround properties, for example, placing natural rocks or artificial concrete pyramids around the base of trees or along fences. These structures aim to deter elephants by creating an uneven and uncomfortable surface, making it painful or difficult for them to step close enough to cause damage (Baker, 2013). However, not all fences may be equally effective. Their ability to prevent break-ins can depend on several factors, including the type of barrier used, its structural design, and the level of maintenance it receives.

Multiple factors are likely to influence elephant break-ins into properties, yet these relationships remain insufficiently understood and require rigorous investigation. Given the notable surge in elephant break-ins in 2024, which could recur in the coming years and increase tensions between humans and elephants, this study aims to investigate the spatiotemporal drivers of elephant break-ins to develop practical and tailored recommendations for property owners by addressing four key questions:

Q1) Which types of elephants (sex and age) are most frequently involved in property break-ins?
I hypothesize that males, especially subadult males, are more likely to enter properties. Subadult males tend to be more risk-prone and are still learning appropriate behaviors, while females may be more cautious due to their role in caring for offspring.

Q2) What are the intra-daily and seasonal patterns of elephant break-ins into properties?
I hypothesize that the number of elephant break-ins will occur primarily during times of reduced human activity (nighttime or early morning hours) and be negatively correlated with rainfall,

with a higher frequency during drier periods. Indeed, elephants may avoid human presence and are more likely to enter properties when they perceive a lower risk of disturbance. During dry periods, the scarcity of natural resources such as water and forage likely increases the appeal of irrigated vegetation and artificial water sources found within properties, potentially encouraging elephants to break in despite fences.

Q3) Which areas within the reserve are most affected by elephant break-ins, and how do environmental and anthropogenic factors influence the spatial distribution of these break-ins?
I hypothesize that proximity to water, human presence, reduced accessibility, or abundant natural vegetation in the surrounding environment will play a crucial role in explaining elephant break-ins.

Q4) What factors influence the attractiveness of individual properties to elephants, and how effective are deterrent measures such as fence type and condition?
I hypothesize that water availability, lush or irrigated vegetation, and plant species commonly consumed by elephants, will increase the chance of break-ins. Conversely, fence type and condition may affect deterrence effectiveness and lower the risk of intrusions.

2. Methodology

2.1. Study site

This study was conducted in Olifants West Nature Reserve (OWNR, 24°214′ S, 30°858′ E), a private conservation area within the Greater Kruger system, in the Maruleng municipal area of Limpopo Province, South Africa. The reserve spans approximately 8800 hectares and is bordered by the R40 road to the west, the Olifants River to the north, and Balule Nature Reserve to the east and south (Figure 2). Its eastern and southern boundaries are unfenced, allowing for unrestricted wildlife movement into the broader Greater Kruger landscape, while the western boundary is fenced, marking the limit of animal dispersal in that direction. Consequently, the reserve does not exert direct control over its elephant population.

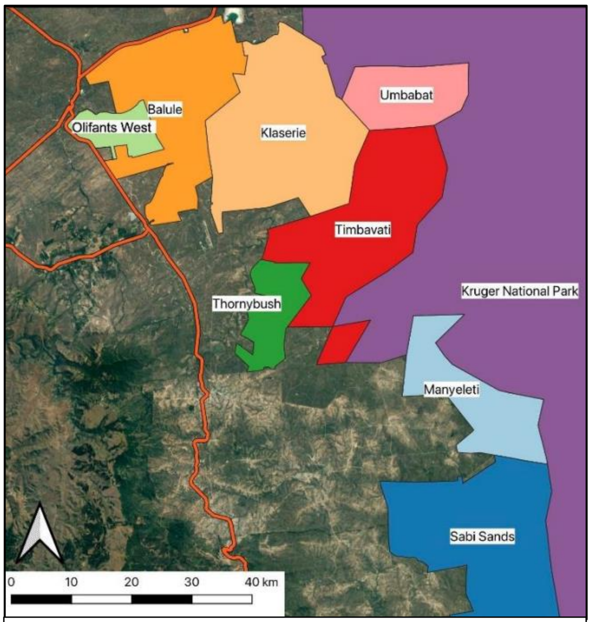


Figure 2. Location of the Olifants West Nature Reserve (OWNR) within the Greater Kruger landscape *(Spencer & Allin, 2023).*

OWNR is located within the Savannah Biome featuring well-developed woodland interspersed with extensive grass layers. The reserve is characterized by a distinct summer-rainfall climate. Precipitation is concentrated in the warm, wet season from November to April, whereas the cool, dry season extends from May to October. During the dry season, nocturnal temperatures can decrease to 0°C in higher-altitude regions (Mucina & Rutherford, 2006). The altitude of the study area ranges from 338 to 360 meters. The predominant soil types found are granitic- and gabbro-derived (Kos et al., 2012).

This study was conducted under the supervision of Transfrontier Africa (TA), a non-governmental organization that has been active in the Olifants West Nature Reserve (OWNR) since 2006. TA has been mandated by the reserve's management committee to carry out several key responsibilities, including security operations (such as anti-poaching), ecological management, and support for scientific research. The reserve is composed exclusively of private landholdings (62 in total). Although each parcel is owned by one or more landholders, all have agreed to remove internal fences in accordance with a shared conservation vision, promoting unrestricted movement of wildlife. Among these 62 land parcels, 49 contain fenced properties. A total of 57 fenced properties were identified, of which 49 were surveyed for this study.

2.2. Data collection

This study focuses on elephant break-ins that occurred in OWNR during the year 2024. Data on these incidents were compiled from several pre-existing sources, including the reserve's security reports and information provided by property owners through a Google form initially developed by TA's research assistant. These records included key details such as the date and time of the incident, as well as the number of elephants involved. However, many entries were incomplete or missing, as break-ins were not systematically reported. Reporting largely depends on the initiative of the property owners: some request assistance from TA, others choose to chase the elephants away themselves and therefore do not always report the incident, and only a minority take the time to complete the designated form. As a result, a significant number of incidents went undocumented, leading to substantial gaps in the initial dataset. To address this issue, interviews were conducted with each on the 49 property owners, and an inventory was carried out for every fenced property. The interview form used during fieldwork is provided in Appendix 1. Finally, environmental and anthropogenic variables potentially influencing the spatial distribution of break-ins were collected and analysed using QGIS version 3.38.3. All parameters used to address the research questions are summarised in Table 1.

Table 1. Summary of data collection steps, types of data obtained, and their role in addressing the research questions. Data were collected in the 49 fenced properties of OWNR through four complementary approaches, providing the basis for the analyses presented in this study.

Data collection step	Type of data obtained	Role in the study
1) Compilation and harmonisation of pre-existing records from reserve security reports and Google form entries	– **Temporal information** (incident date & time) – **Elephant profile** (number of elephants, sex, age class: juvenile, subadult, adult) – **Damaged features** (damaged vegetation, water sources, fence, gate)	Core dataset of break-in events, forming the basis for **Q1** (elephant profile), **Q2** (temporal patterns), and **Q4** (attractiveness of properties and targeted features)
2) Interviews conducted with property owners	– **Property context** (primary use: lodge, primary residence, secondary residence, staff compound; typical occupancy status) – **Break-in characteristics** (number and description of incidents in 2024; common entry points: fence type, gate, weak spots; mechanisms used to breach barriers; fencing modifications; operational status: electrification, maintenance) – **Attractive features** (vegetation consumed and changes since previous year; confirmation of water sources and their use by elephants; irrigation frequency; fertilisation practices) – **Deterrent measures** (methods used: dogs, noise devices, others)	Improved completeness of the incident dataset (**Q2**); and provided detailed property-level information on potential drivers of break-ins and effectiveness of deterrents (**Q4**)

3) Systematic field inventory of all fenced properties	– **Fence type and condition** – **Water availability** (open/closed sources) **- Vegetation survey** (species recorded at random points inside properties and 50-m buffers; calculation of vegetation metrics: species richness and completeness, community composition and β-diversity [Bray–Curtis, turnover, nestedness], and proportion of species attractive to elephants)	Explanatory variables for **Q3** (contrast between properties and their immediate environment) and **Q4** (property-level factors such as fence effectiveness, water availability, and vegetation attractiveness/composition)
4) Extraction and processing of environmental variables in QGIS and R	– **Water sources** (waterhole dataset updated with satellite imagery; classified by size; distances calculated to 10 combinations of source types) – **Neighbouring properties** (minimum distance to the nearest property, as a proxy for spatial isolation and human activity) – **Drainage lines** (minimum distance to nearest drainage line, considered as ecological corridors in savanna systems) – **Vegetation indices** (NDVI, NDRE, NDWI from Sentinel-2 imagery; extracted within properties and 100 m buffers)	Explanatory variables for **Q3** (reserve-scale environmental and anthropogenic factors: distances to water, drainage, neighbouring properties, vegetation productivity in buffers) and **Q4** (property-scale vegetation indices reflecting attractiveness and moisture conditions)

2.2.1. Semi-structured interviews

To enhance the reliability and completeness of the dataset, semi-structured interviews were conducted with each property owner or staff member. This approach ensured the systematic collection of contextual information related to the break-ins and facilitated the resolution of inconsistencies within the existing records.

First, information was collected regarding the primary use of each property, namely whether it functioned as a lodge, a primary residence, a secondary residence, or a staff compound. This categorization aimed to assess whether certain property types are more susceptible to elephant break-ins. For instance, lodges, which are typically more populated due to the regular presence of guests and staff, might be less exposed to intrusions than secondary residences, which may be less frequently occupied. Given that elephants generally avoid areas with high levels of human activity, this factor could potentially influence their behaviour (Boettiger et al., 2011; Jackson et al., 2008). To explore this hypothesis further, property owners were also asked about the typical occupancy status of their properties, in order to evaluate whether patterns of human presence could be associated with varying levels of vulnerability to elephant intrusions.

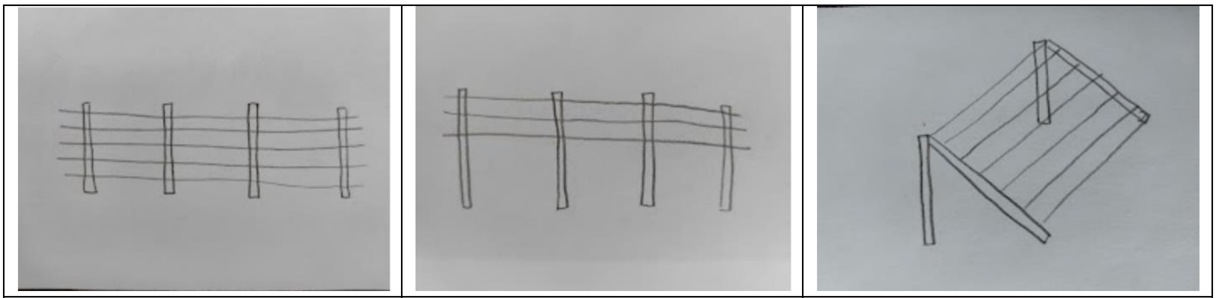
Subsequently, questions focused on the occurrence and characteristics of break-ins. The number of break-ins experienced during 2024 was collected from each property to compare with the incidents recorded in the existing database, thereby enabling an assessment of the completeness of the initial reports. For each break-in, a general description was obtained to identify the most common entry points used by elephants. Property owners were asked whether the animals typically entered by breaching the fence (specifying the type, as multiple fence types could be present) and/or through the gate, and whether they exploited specific weak points, such as pedestrian access gates or poorly maintained sections. Additional information was gathered on the mechanisms used to breach the barriers (e.g., pushing or stepping over fences, knocking down fence poles, or pushing trees onto the barriers to create openings). These details were intended to assess the relative effectiveness of different fence types and the vulnerability of gates or other structural elements. Data were also collected on any modifications to the fencing system since the previous year, as well as on the operational status of the fence during break-ins, including whether it was electrified.

Finally, the interviews included questions on potential attractants that might influence elephant behaviour. Data on vegetation consumed by elephants within each property were recorded, with species identification requested when possible. Property owners were asked to report any changes in vegetation since the previous year to ensure the accuracy of the field-based vegetation inventory. They were also invited to confirm the presence of water sources identified during the field inventory, both inside and outside the property, and to indicate whether off-property waterholes were supplied year-round. Any use of or damage to water infrastructure by elephants was documented, specifying whether the affected sources were open or closed systems. Additional information was gathered on the use of potential attractants, such as irrigation and fertilisation; for irrigation, owners were asked to indicate its frequency (e.g., daily, weekly, seasonal). Finally, owners were asked whether any deterrent methods were used to prevent elephant intrusions, such as guard dogs, noise devices, or other mitigation tools.

2.2.2. Fiel-based property assessment

Fence type and condition

First, an inventory of the fences was conducted to identify potential patterns in their effectiveness. Various types of fences are employed to prevent elephants from entering properties. Primary fences include standard, exclusion, and Kenya-style designs, which are generally electrified (Figure 3). These may consist of a single type along the entire perimeter or a combination of two or more types and can be further reinforced with secondary barriers such as cattle grids, rock lines, or whip antennas installed directly on the electric fence. In some cases, multiple fence types are used continuously around the entire property, whereas in others, different types are installed at specific locations. This variability was accounted for during data encoding by creating a “mixed” category: a value of 1 was assigned when multiple fence types were present along the entire perimeter, and a value of 0 when different fence types alternated across specific sections. Fence condition was assessed using a three-point scale, with 1 denoting good condition with no visible damage, 2 indicating moderate condition with weak points such as sagging wires or partial damage, and 3 representing poor condition characterised by marked deterioration or structural failure.



STANDARD | EXCLUSION | KENYA

Figure 3. Schematic representation of the three primary fence types used to prevent elephant intrusions. *Standard fences consist of vertical posts with multiple horizontal wires spanning from top to bottom; exclusion fences typically comprise only two or three horizontal wires; and Kenya-style fences feature diagonal bracing combined with horizontal wires spanning from top to bottom.*

Water availability

Water sources within the properties were inventoried, noting the presence or absence of open and closed sources. Open sources included waterholes, ornamental water features, ponds, and swimming pools, and were further subdivided into small (<1 m²) and medium. Closed sources, in turn, comprised JoJo tanks, sealed reservoirs, and water pipes. Although not directly accessible, these were considered relevant because elephants can detect water up to 1.5 m underground and dig with their tusks to reach it during dry periods (Ramey et al., 2013), potentially damaging or destroying such structures in the process.

Vegetation survey and metrics

To assess plant diversity within each property and its immediate surroundings, a random vegetation inventory was conducted. Using QGIS, a polygon layer representing the boundaries of each property was created. From this, a 50-meter buffer was generated around each property to define its surrounding area. This distance was chosen based on evidence suggesting that elephants have limited visual acuity beyond 50 meters, which may influence their foraging decisions (Shyan-Norwalt et al., 2010).

Within both the property boundaries and their respective buffers, random sampling points were generated in QGIS. The number of points was proportional to the property's surface area and kept equal between the inside and the buffer to ensure consistent sampling effort. A minimum of 10 points was assigned for properties ≤ 0.5 ha. The number of points was then increased by 2 for every additional 0.1 ha up to 1 ha (i.e., 20 points), and by 1 for every 0.1 ha beyond 1 ha, up to a maximum of 25 points. This upper limit was set to keep the fieldwork feasible, given that property sizes ranged from 0.04 ha to 4.786 ha.

At each sampling point, a 2-meter stick held horizontally above the ground was used to delineate the sampling radius. All plants (trees, shrubs, succulents, etc.) taller than 0.5 meters and either located within this radius or with canopies intersecting it were recorded with their genus and species. This approach enabled the compilation of estimated species lists and abundance data for both the interior of each property and its immediate surroundings.

To assess the adequacy of the sampling effort and to estimate species richness (Thompson & Thompson, 2007), species accumulation curves were constructed for each property and each sampling zone (inside and outside). For each group, an incidence matrix (inventory points × species) was generated, with inventory points lacking observed species included as empty sites. The observed and estimated species richness were calculated using the Chao1 estimator, which corrects for unseen species based on the occurrence of rare species within the dataset (Chao et al., 2014). Sampling completeness was expressed as the ratio (%) of observed to estimated richness. All analyses were conducted in R, using the vegan package (v2.6-4) (Oksanen et al., 2025).

Differences in vegetation composition between the interior of properties and their immediate surroundings were assessed with Bray–Curtis dissimilarity indices, computed for each property based on species abundance data. For each site, a community matrix was constructed with species as columns and abundance values for the "in" (property) and "out" (50-m buffer) zones. This index was calculated using the vegdist function from the vegan package. To further explore the structure of β-diversity, species abundance data were converted to presence/absence, and Sørensen-based turnover (β_{sim}) and nestedness (β_{sne}) components were computed for each property using the betapart package (v1.5.6), following Baselga, 2010.

Finally, the proportion of individuals belonging to species attractive to elephants was calculated for each property based on the vegetation inventories. This proportion was defined as the ratio between the number of individuals identified as belonging to species known to be consumed by elephants and the total number of individuals recorded. The list of attractive species was compiled from three complementary sources: feedback gathered during interviews with property owners, the intrusion incident database reporting plant species that were effectively browsed or damaged during events, and scientific literature related to the feeding ecology of African elephants in the Lowveld region (Viljoen et al., 2013). The complete list of species considered attractive can be found in Appendix 2.

2.2.3. Extraction of environmental and anthropogenic variables

Spatial data were processed in QGIS and R (version 4.4.2). QGIS was used to create and visualise spatial layers, and to check their geometry integrity and projection consistency. All layers were projected to WGS 84 / UTM zone 36S (EPSG:32736) to ensure accurate and comparable spatial computations. Subsequent analyses, including distance calculations, were conducted in R using the sf package (Pebesma, 2018).

Water source classification and distance calculation

A water-source layer representing the waterholes located within the reserve during the study period was created using a pre-existing dataset provided by Transfrontier Africa (TA). This layer was updated with interview data indicating whether each waterhole was actively supplied with water, and its accuracy was verified using Google Earth satellite imagery (11 July 2024, the most recent available) to confirm the presence or absence of water during the study period. Water points were subsequently classified into three categories based on size, with a fourth category defined specifically for the river (Table 2).

To account for the potential differential effects of various combinations of water source types, ten distance metrics were calculated for each property: (1) distance to small waterholes, (2) distance to medium waterholes, (3) distance to large waterholes, (4) distance to the river, (5) distance to small or medium waterholes, (6) distance to medium or large waterholes, (7) distance to large waterholes or the river, (8) distance to medium or large waterholes or the river, (9) distance to all waterholes, and (10) distance to all water sources (regardless of size).

Table 2. Size-based classification of water points within the Olifants West Nature Reserve. Descriptive statistics for water points classified into three size categories: small (< 25 m²), medium (25–< 100 m²), and large (≥ 100 m²). Values indicate the number of water points in each category (count), as well as the mean, median, minimum, maximum, and standard deviation of their surface area (in m²).

Size class	Count	Mean ± SD	Median	Minimum	Maximum
Small (< 25 m²)	26	13.6 ± 8.9	13.9	0.9	25.0
Medium (25–<100 m²)	12	55.7 ± 23.6	54.1	26.1	90.7
Large (≥ 100 m2)	15	377.4± 245.9	270.7	138.1	869.1

Proximity to neighbouring properties

The minimum distance between each property and its nearest neighbouring property was calculated to assess the degree of spatial isolation. The underlying hypothesis is that properties located closer to others may be less exposed to intrusions, as elephants would have multiple alternative options. Additionally, a higher density of surrounding properties may reflect increased human activity, which elephants are generally known to avoid.

Proximity to drainage lines

The minimum distance between each property and the nearest drainage line was calculated using the property layer and a linear drainage layer provided by Transfrontier Africa (TA). Unlike roads, which are evenly distributed throughout the reserve and do not allow for the distinction between major and minor routes (as they are all similar dirt tracks), drainage lines were included in the analysis due to their ecological importance in savanna ecosystems.

Extraction of Mean NDVI in the Vicinity of Properties

To quantify vegetation productivity in the vicinity of each property, a mean NDVI raster (10 m resolution) was generated for the entire reserve over the study period (01 May to 31 October 2024) (Huang et al., 2021). This layer was created using Google Earth Engine from Sentinel-2 surface reflectance data (COPERNICUS/S2_SR_HARMONIZED) and using a modified version of a code provided by Prof F. Jonard. NDVI was calculated using the red (Band 4) and near-infrared (Band 8) bands (Table 3). A maximum cloud probability threshold of 25% was applied using the COPERNICUS/S2_CLOUD_ PROBABILITY collection to exclude cloud-contaminated pixels (Liepa et al., 2024).

In R, the NDVI raster was extracted for 100 m buffers generated around each property using the **terra** package (Hijmans et al., 2025). Extraction was conducted using area-weighted values to account for the proportion of each pixel intersecting a given buffer. NDVI values lower than 0, generally associated with water bodies, were masked (set as NA) to avoid potential bias near the river (Fan et al., 2020).

Extraction of NDRE, NDVI, and NDWI within properties

Following the same processing workflow described above, average NDRE, NDVI, and NDWI rasters were generated for the entire study period (Table 3). The NDRE (20 m resolution) was specifically selected to assess vegetation vigor within properties, as it offers greater sensitivity to chlorophyll content under high biomass conditions compared to the traditional NDVI (Li et al., 2014). While the NDVI is known to saturate in densely vegetated areas due to strong absorption in the red band, the NDRE, based on the red-edge band (Band 5), remains responsive to subtle variations in chlorophyll concentration (Huang et al., 2021; Rehman et al., 2022) However, given the coarser resolution of the NDRE raster, the NDVI (10 m) was also extracted to enable comparisons, especially for smaller properties.

To complement this assessment, the NDWI (20 m), calculated using the near-infrared (Band 8) and shortwave infrared (Band 11) bands, was extracted for each property. This index serves as a proxy for leaf water content (Gao, 1996) and provides additional insight into vegetation moisture levels, which may reflect irrigation practices or plant water stress (Serrano et al., 2019).

Raster values for the three indices were extracted within each property polygon in RStudio using the **terra** package. Area-weighted extraction was applied to account for the proportion of each pixel overlapping the property. Invalid values (NDRE < 0; NDVI < 0) were excluded from the analysis (set to NA) to reduce bias from non-vegetated or artificial surfaces such as rooftops, paved areas, or water features.

Table 3. Spectral indices used in this study. Summary of the spectral indices applied, including their equations, spectral bands, and sensitivity characteristics.

Index	Equation	Spectral Bands Used	Sensitivity
NDVI *(Normalized Difference Vegetation Index)*	$\frac{NIR - Red}{NIR + Red}$	NIR (~840 nm) Red (~660 nm)	Saturates quickly in dense vegetation
NDRE *(Normalized Difference Red Edge Index)*	$\frac{NIR - RedEdge}{NIR + RedEdge}$	NIR (~840 nm) Red Edge (~710–730 nm)	Less saturation, better performance in dense vegetation
NDWI *(Normalized Difference Water Index – Gao, 1996)*	$\frac{NIR - \mathrm{SWIR}}{NIR + \mathrm{SWIR}}$	NIR (~860 nm) SWIR (~1240–1610 nm)	Sensitive to internal leaf moisture levels

2.3. Data analysis

Data from the reserve's security reports and additional information provided by property owners via a Google Form were compiled and cross-checked to create a single, consolidated database, avoiding duplicate entries. This allowed for the identification of reported break-ins and comparison with the actual number of events estimated through field interviews. The resulting database was also used to examine how many elephants were typically involved in each break-in, as well as their sex and maturity status when such information was available (Q1).

2.3.1. Temporal patterns (Q2)

This database, which included the dates and times of each intrusion, was used to analyze the temporal dynamics of the phenomenon. A graph showing the number of intrusions per month was produced alongside monthly rainfall totals to explore a potential relationship between intrusion frequency and rainfall variability. Rainfall data were obtained from a weather station located at the scientific base of Transfrontier Africa. An additional graph depicting annual total rainfall over the past ten years was also generated to assess the possible influence of long-term climatic trends on elephant behavior.

Finally, to detect potential daily patterns in break-ins, each event was categorized into one of four time intervals based on the reported time: *Night* (22:00 – 05:00), *Early morning* (05:00 – 09:00), *Daytime* (09:00 – 17:00), and *Evening* (17:00 – 22:00).

2.3.2. Identification of drivers of break-ins using a cumulative ordinal logistic regression model (Q3 & Q4).

The estimated number of elephant break-ins reported for each property in 2024, as obtained from interviews, was classified into three ordinal categories: low (0–3), moderate (4–11), and high (≥11). This classification was guided by two main considerations. First, beyond a certain threshold, respondents often struggled to recall the exact number of incidents and tended to provide approximate values; grouping into classes helped account for this uncertainty. Second, the classes were defined to ensure a relatively balanced distribution of observations, thereby improving the statistical robustness of subsequent analyses.

The resulting response variable reflects a natural progression of intrusion severity, from low to high, without assuming equal or linear distances between categories. To account for this ordinal structure while modelling the relationship between break-in severity and property or environmental characteristics, a cumulative ordinal logistic regression model was employed. This model estimates the probability of a property falling into a higher break-in category as a function of selected predictors. It relies on the proportional odds assumption, which states that the relationship between each predictor and the log-odds of being in a higher category is constant across all thresholds (Yee, 2010).

Variable selection and modelling

To investigate potential drivers of break-in severity, a comprehensive set of environmental and property-level variables was incorporated into the modelling process, with their expected effects summarised in Table 4. Gate type was not considered, as elephants rarely used gates to enter properties. In most cases where entry occurred via a gate, it was simply because the gate had been left open. Water sources located within properties were also excluded as explanatory variables, as they were present on the vast majority of properties and were not considered a major driver of elephant break-ins based on preliminary observations. However, a complementary analysis was performed to assess whether the distance to the nearest external water source differed between properties that experienced water-related damage or use (e.g., destruction of JoJo tanks, use of open water sources) and those that did not. For this comparison, a Wilcoxon rank-sum test was used to evaluate potential differences in distance between the two groups.

Prior to modelling, exploratory analyses were conducted on all explanatory variables. Continuous variables were examined to assess their distributions and detect potential skewness or extreme values. In particular, the twelve distance-related variables and property area were strongly right-skewed, prompting a log(x+1) transformation to improve symmetry and reduce the disproportionate influence of extreme values. Other continuous variables were retained in their original scale (Table 4). Categorical variables were checked to ensure sufficient representation across break-in categories and were reclassified or simplified where necessary to avoid unbalanced factor levels. Histograms and boxplots stratified by break-in level were used to visually assess these distributions and guide modelling decisions (Appendix 3). Additionally, pairwise Pearson correlation coefficients were computed among continuous predictors, and variables with correlations above |0.6| were flagged for potential collinearity prior to model fitting (Dormann et al., 2013).

Table 4. Explanatory variables included in the analysis of elephant break-in severity, grouped by category, with their model notation and expected direction of effect. Signs in the "Expected effect" column indicate whether an increase in the predictor was hypothesised to raise ("+") or lower ("–") the probability of belonging to a higher break-in category (low: 0–3; moderate: 4–11; high: 11+). Variables with the prefix log_ were log(x+1) transformed to reduce skewness and limit the influence of extreme values, with "+1" allowing zero distances to be retained. Expected effects are based on ecological hypotheses rather than model results.

Category	Variable	Model notation	Expected effect on break-in frequency	
Spatial proximity to resources and landscape features	Distance to small waterholes	**log**_dist_small	Closer proximity to water may raise break-in probability	+
	Distance to medium waterholes	**log**_dist_medium	Same as above	+
	Distance to large waterholes	**log**_dist_large	Closer proximity may strongly increase break-ins, since large waterholes support drinking, bathing, and social activities	+
	Distance to the river	**log**_dist_to_river	Closer distance may increase break-ins, though abundant riparian vegetation could reduce risk by providing sufficient forage	- / +
	Distance to small or medium waterholes	**log**_dist_small_medium	Closer proximity to water may raise break-in probability	+

	Distance to medium or large waterholes	**log_dist_medium_large**	Same as above	+
	Distance to large waterholes or the river	**log**_dist_to_no_small_medium	Same as above	+
	Distance to medium or large waterholes or the river	**log**_dist_to_no_small	Same as above	+
	Distance to all waterholes	**log**_dist_waterholes	Same as above	+
	Distance to all water sources	**log**_dist_to_any_water	Same as above	+
	Distance to the nearest neighbouring property	**log**_dist_to_nearest_property	Greater distance to neighbouring properties expected to raise break-in probability, as isolated sites may appear less associated with human presence	-
	Distance to the nearest drainage line	**log**_dist_to_drainage	Closer proximity may increase break-ins, as drainage lines act as corridors with denser vegetation and occasional water	+
	Mean NDVI in the surrounding buffer zone	buffer_ndvi	Higher buffer NDVI could either attract elephants to the area or reduce break-ins if abundant vegetation outside lowers the need to enter properties	- / +
Vegetation composition contrast	Bray–Curtis dissimilarity index	BrayCurtis	Higher dissimilarity may increase break-ins, as strong contrasts in vegetation composition could attract elephants	+
	Turnover	Turnover	High turnover may increase break-ins, as additional species inside could provide complementary forage	+
	Nestedness	Nestedness	High nestedness may reduce break-ins, as inside vegetation mainly overlaps with outside species	-
Property characteristics	Mean NDVI	mean_ndvi	Higher mean NDVI indicates greater vegetation productivity and biomass, which may increase break-in probability	+
	Mean NDRE	mean_ndre	Same as above	+
	Mean NDWI	mean_ndwi	Water index estimating vegetation water content and moisture conditions	+
	Proportion of attractive species	prop_attractive	Ratio of plants belonging to species known to be consumed by elephants	+
	Primary use of the property	Primary.use	Main functional purpose, which may affect elephant break-ins via human presence	/
	Property area	**log**_area	Larger areas may present more forage, potentially increasing risk	+
	Type of fence	Fence	Fence type and structural design may influence break-in frequency	/
	Fence maintain	Maintain	Well-maintained fences expected to lower break-in probability	-
	Fence structure and maintenance	Fence_Maintain	Same as above	-
	Irrigation level	Irrigation_level	Higher irrigation frequency may increase risk by keeping vegetation green	+

A systematic variable selection procedure was thus conducted in two steps following the approach proposed by (Adde et al., 2023): 1) univariate analyses to identify the most relevant predictors and remove highly correlated ones; 2) selection of the best variable combination in a multivariate model.

For variable selection prior to multivariate modelling (Step 1), univariate ordinal logistic regression models were fitted using the polr() function from the **MASS** package (Venables & Ripley, 2002), without evaluating the proportional odds assumption at this stage, as the aim was solely to screen explanatory variables. The response variable Breakin_level was treated as ordinal. For continuous predictors, three alternative functional forms were considered: a linear term (X), a quadratic term (X^2), or both ($X + X^2$). The initial full model ($X + X^2$) was fitted with polr(), and the stepAIC() function from **MASS** was used to select the form with the lowest Akaike Information Criterion (AIC). The selected model was then compared to a null model using a likelihood ratio test (ANOVA), and the associated p-value was extracted. The same approach was applied to categorical predictors, but without testing alternative polynomial forms. Subsequently, in each pair of highly correlated predictors, the one with the highest p-value in the univariate analysis was removed.

A multivariate model was then fitted (Step 2), including all the selected variables from Step 1. As AIC-based selection focuses on overall model fit rather than statistical significance, some retained variables were not significant at conventional thresholds in likelihood ratio tests. This approach was intended to avoid being overly restrictive in the selection process, as some variables that are non-significant in univariate analyses may become significant when evaluated jointly in a multivariate model. The proportional odds assumption was then assessed using the Brant test (Brant, 1990), with both the omnibus and variable-specific tests returning p-values > 0.05, indicating no evidence of violation. The standard proportional odds model was therefore maintained. Finally, to identify the final model, a model selection procedure was conducted using the dredge() function from the **MuMIn** package (Bartoń, 2025). Although a dredge selection require higher computation time than a regular step AIC, this method tests and ranks all possible subsets of the global multivariate model based on their AICc values, avoiding sub-optimal model selection which could result in a regular step AIC method. The model with the lowest AICc was selected, favouring the simplest model when the ΔAICc was less than 2 (Burnham & Anderson, 2004).

The model's explanatory power was then evaluated using McFadden's pseudo-R^2, which quantifies the improvement in fit relative to the null model (McFadden, 1977). it was computed in R with the **pscl** package (Zeileis et al., 2008). As the response variable comprised only three ordinal categories, the standard McFadden's formulation was deemed suitable, and the adjustments proposed for models with a higher number of categories (Ugba & Gertheiss, 2023) were not applied. An ANOVA (likelihood ratio test) was also performed to confirm that the final model provided a significantly better fit than the null model.

3. Results

3.1. Break-in incidence and property typology

Among the 49 surveyed properties, 13 operated as commercial lodges, 22 served as primary residences, 11 as secondary residences, and 3 were designated as staff compounds. Most properties were continuously occupied, primarily due to the permanent presence of staff, with only three secondary residences and one primary residence being predominantly unoccupied.

A total of 142 break-ins were officially reported across the reserve in 2024. In contrast, interview-based estimates suggested a total of 418 break-ins, likely providing a more accurate reflection of the actual situation. This figure does not account for potential break-ins in the eight properties for which no interview was conducted. Based on these interview-derived estimates, 14 properties were classified as having a low number of break-ins (0–3), 20 as moderate (4–11), and 15 as high (≥12) (Figure 4a).

The distribution of break-in levels differed across property types (Figure 4b). Lodges, primary residences, and secondary residences each included properties in all three break-in categories, with proportions relatively evenly distributed. In contrast, all staff compounds fell exclusively within the low break-in category, with no occurrences in the moderate or high categories.

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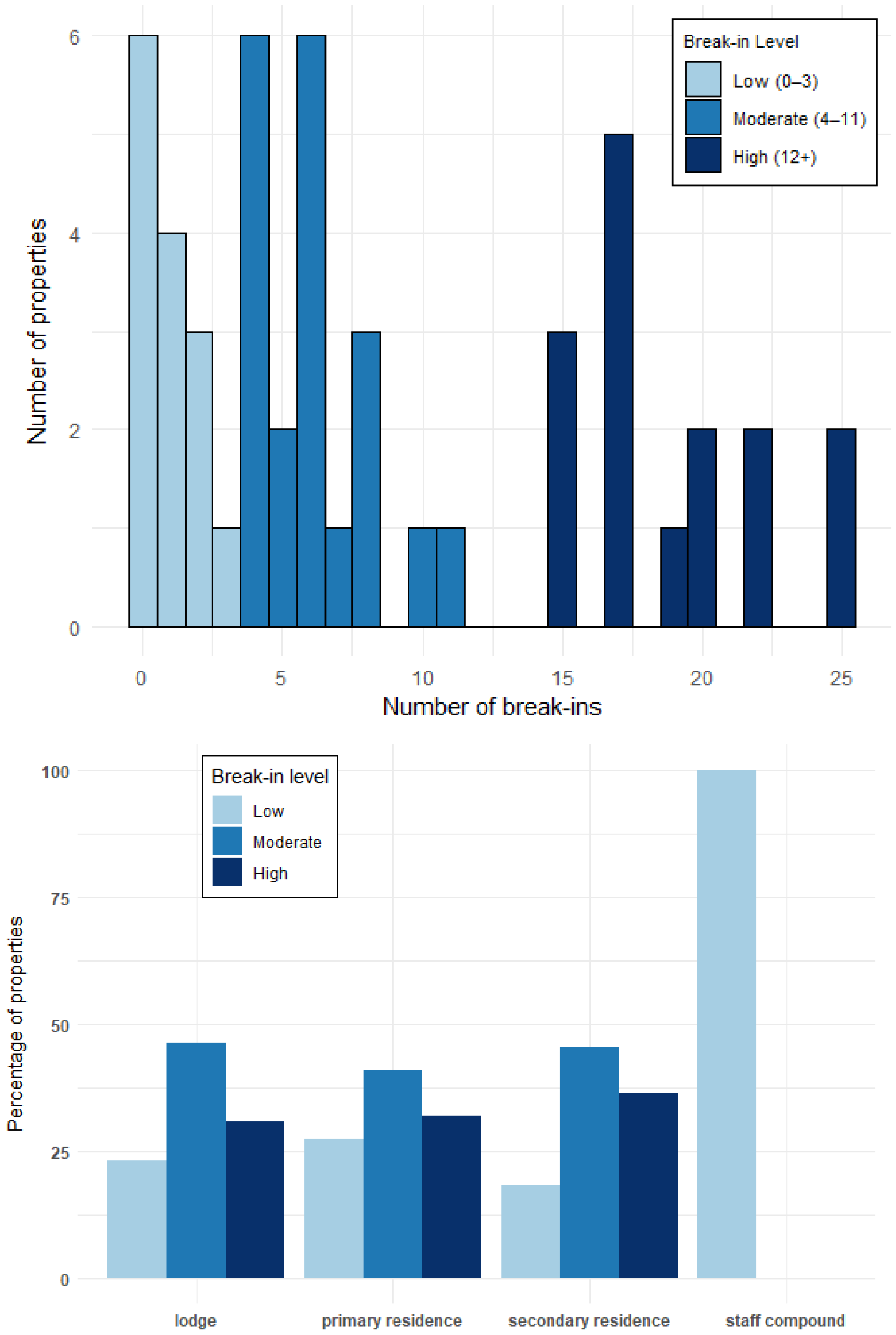


Figure 4. a) Distribution of estimated elephant break-ins per property in 2024. *Histogram showing the number of properties according to their estimated number of elephant break-ins, based on interviews with property owners. Properties are grouped into three break-in level categories: Low (0–3; n = 14), Moderate (4–11; n = 20), and High (≥12; n = 15).* ***b) Break-in levels by property type.*** *Bar plot showing the percentage of properties within each property type (lodge, n = 13; primary residence, n = 22; secondary residence, n = 11; staff compound, n = 3) classified as Low (0–3 break-ins), Moderate (4–11 break-ins), or High (≥12 break-ins). Percentages are calculated within each property type.*

3.2. Overview of elephants involved in break-ins (Q1)

Out of the 142 recorded break-ins, the number of elephants involved could not be determined for five events. For the remaining 137 break-ins, group size was estimated from observer reports. Most incidents involved one or two elephants, with occasional groups of three or more. Multiplying each reported group size by its frequency yielded an estimated total of 264 individual elephants involved (Table 5).

Among these 264 estimated individuals, 149 were identified as males, while the remaining 115 could not be individually identified. No females were identified. However, their participation cannot be excluded given the proportion of unidentified individuals. Of the identified males, 136 were classified as adults and 13 as subadults.

Table 5. Number of individuals involved per break-in event in 2024. Summary of the frequency of break-ins according to the reported number of elephants present during each event.

Numbers of Individuas	Count	Percentage (%)
1	61	44.5 %
2	43	31.4 %
3	20	14.6 %
4	10	7.3 %
5	1	0.7 %
6	2	1.5 %
NA	5	-
Total	142	100.0%

3.3. Temporal patterns (Q2)

3.3.1. Annual and seasonal trends associated with precipitation

In 2024, total annual rainfall was 279.8 mm, making it the driest year since 2017 and well below the 10-year mean of 377.9 mm. Notably, 54.4% of the year's total rainfall occurred in November (102.6 mm) and December (49.8 mm) (Figure 5a).

The monthly distribution of reported elephant break-ins and total rainfall in the Olifants West Nature Reserve (OWNR) shows that break-ins were first reported in May, coinciding with a marked decline in rainfall. The highest numbers occurred in September and October, with both months recording more than 40 events, shortly after the driest period of the year. In November, break-in frequency dropped sharply, coinciding with a substantial increase in rainfall that marked the onset of the wet season (Figure 5b).

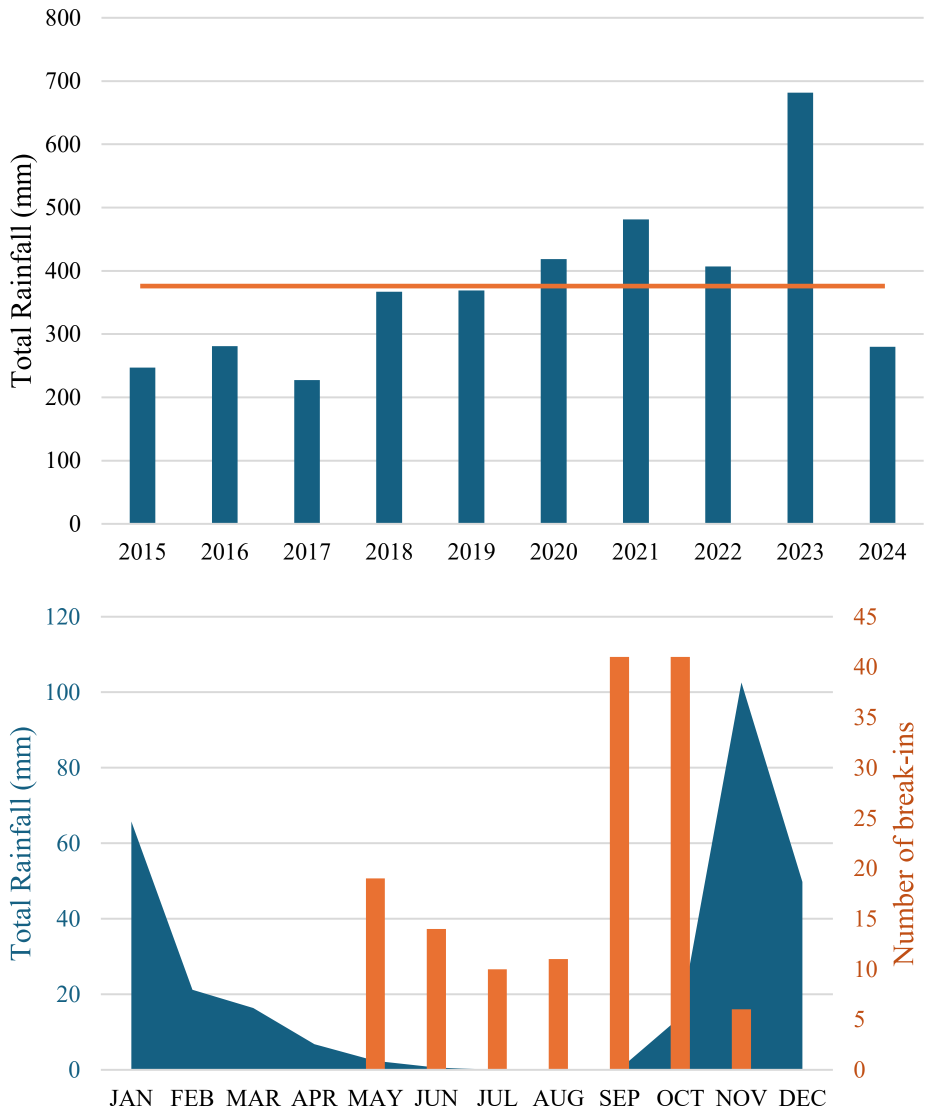


Figure 5. a) Total annual rainfall recorded in the Olifants West Nature Reserve (OWNR) between 2015 and 2024. *Bar plot showing yearly total rainfall (mm) within the reserve. The orange horizontal line represents the mean annual rainfall over the 10-year period (377.9 mm).* ***b) Monthly reported elephant break-ins and total rainfall in the Olifants West Nature Reserve (OWNR) during 2024.*** *Monthly rainfall (mm) is shown as a filled blue area, and the number of recorded elephant break-ins is shown as orange bars.*

3.3.2. Intra-daily variation

The temporal distribution of reported break-ins varied across time categories. The highest proportion occurred during the evening (37.7%), followed by the night period (24.6%). Daytime and early morning accounted for 19.6% and 18.1% of events, respectively. Although break-ins were recorded throughout the day, they were more frequent during evening and night hours.

Table 6. Time of day of reported elephant break-ins in the Olifants West Nature Reserve (OWNR) during 2024. Summary of the frequency and percentage of break-ins according to time category.

Time category	Time range	Numbers of break-ins	Percentage (%)
Night	22:00 – 05:00	34	24.6%
Early Morning	05:00 – 09:00	25	18.1%
Daytime	09:00 – 17:00	27	19.6%
Evening	17:00 – 22:00	52	37.7%
Total	-	138	100.0%

3.4. Spatial relationships between break-ins and water availability (Q3-4)

The majority of surveyed properties are concentrated in the central area of the Olifants West Nature Reserve, with a smaller cluster located along the northern boundary and a few scattered towards the periphery. Waterholes are unevenly distributed, with a high density of small and medium waterholes in close proximity to the central cluster of properties, while large waterholes are more widely dispersed. Across all size classes, relatively few waterholes are located near the river that forms the northern boundary of the reserve (Figure 6). No clear visual clustering of break-in categories around specific water sources can be identified from the map, although properties with varying break-in levels often occur in close proximity to one another.

Among the 49 properties surveyed, only one lacked any water source, whether open or closed. Thirty-eight properties contained at least one open water source exceeding 1 m^2 in surface area, such as a swimming pool or artificial pond, while two of the remaining 11 properties had at least one open source smaller than 1 m^2. Among the 40 properties with open water sources, only three reported observing elephants drinking from them. In contrast, 45 properties were equipped with at least one closed water source (e.g., JoJo tanks, boreholes, or water pipes), and 16 of these reported at least one incident of elephant-related damage, such as the destruction of JoJo tanks or breakage of water pipes.

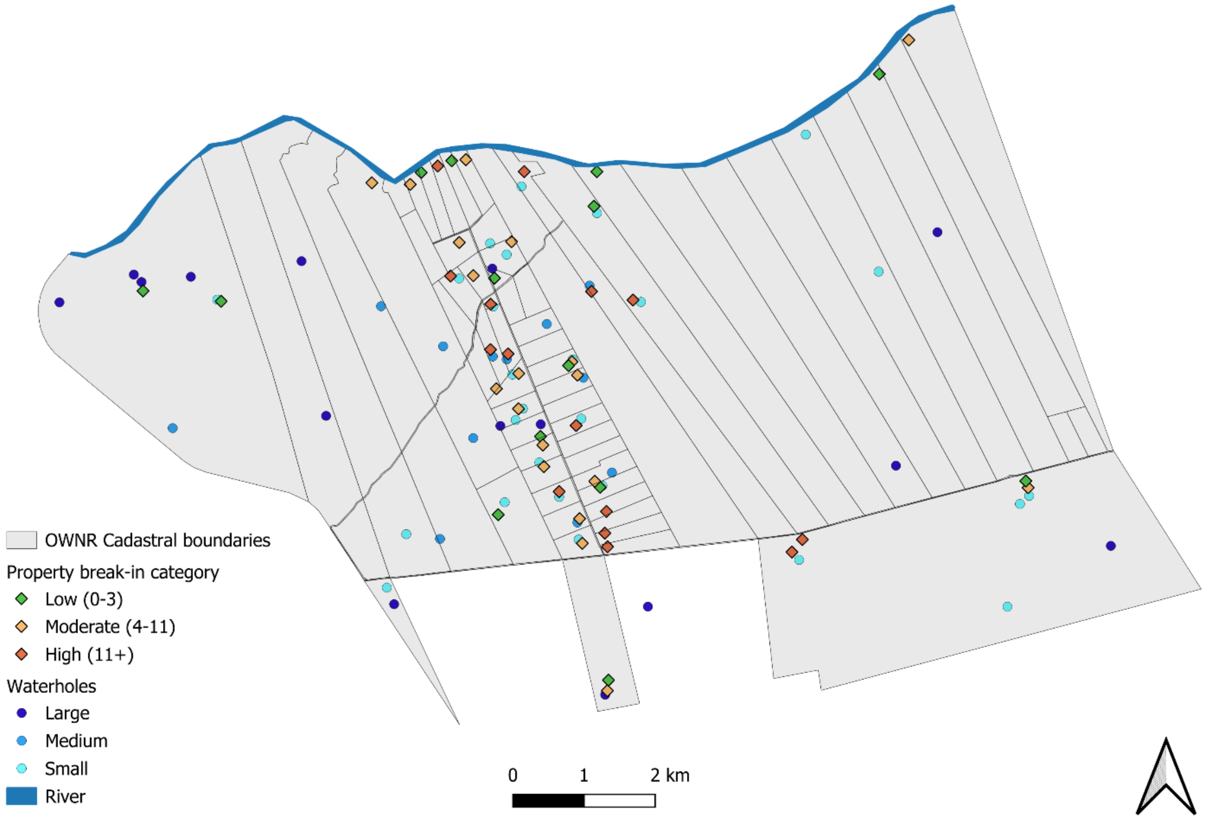


Figure 6. Spatial distribution of properties by break-in category and location of water sources in the Olifants West Nature Reserve (OWNR). *Map showing the cadastral boundaries of properties (grey) classified into Low (0–3), Moderate (4–11), and High (≥12) break-in categories based on 2024 interview estimates. The locations of waterholes (small, medium, large) and the main river are also indicated.*

Descriptive statistics indicate that the median distance to the nearest external water source was nearly twice as high for properties that experienced water-related damage (93.7 m) compared to undamaged ones (54.9 m), with the mean distance also substantially higher (169.1 m vs. 82.2 m). Greater variability was observed among damaged properties (SD = 221 m vs. 89.6 m). However, this difference was not statistically significant (Wilcoxon rank-sum test, W = 194, p = 0.14).

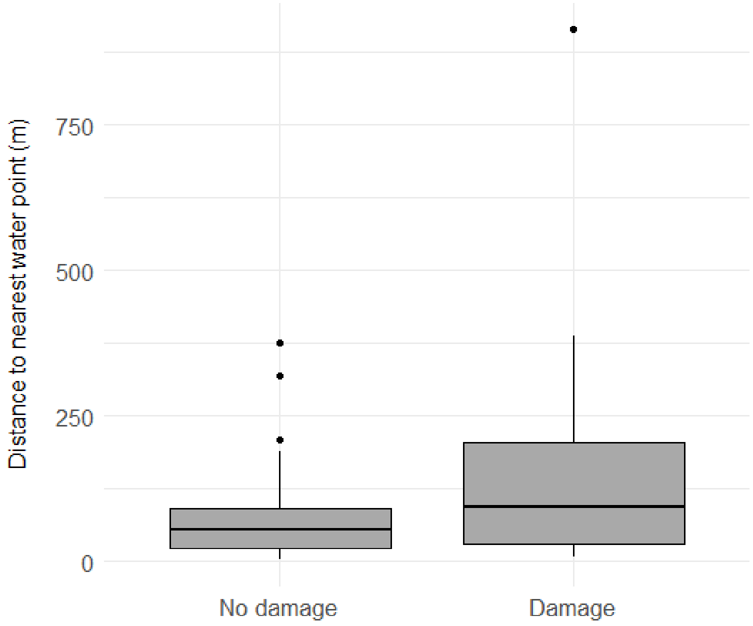


Figure 7. Distance to the nearest external water source by water-related damage status. *Boxplot illustrating the distribution of distances (m) from each property to the nearest external water source (river or waterhole of any size) located outside property boundaries. In the boxplots, the central bar represents the median, the box limits correspond to the 25th and 75th percentiles (interquartile range), and the whiskers extend to the most extreme data points within 1.5 × IQR. Values beyond this range are plotted individually as outliers. Properties were grouped according to whether they reported at least one incident of water-related damage or use (Damage, n = 17; median = 93.7 m, IQR: 30.1–205.3 m) or no such incident (No damage, n = 31; median = 54.9 m, IQR: 23.6–92.6 m). However, the difference between groups was not statistically significant (Wilcoxon rank-sum test, W = 194, p = 0.14).*

3.5. Inventory completeness by property size and sampling location

Inventory completeness, expressed as the percentage of observed versus estimated species richness, varied according to property size class and sampling location (inside versus outside). Across all classes, both “in” and “out” sampling locations exhibited a wide range of completeness, with median values generally between approximately 50% and 85%. For outside locations, completeness values appeared relatively consistent across size classes, with slightly lower values in smaller properties. In contrast, inside locations tended to show slightly lower completeness in larger properties. The “All sizes” category summarises completeness values across all property size classes (Figure 8). A detailed table reporting estimated species richness and sampling completeness for each property and sampling zone is provided in the appendix 4.

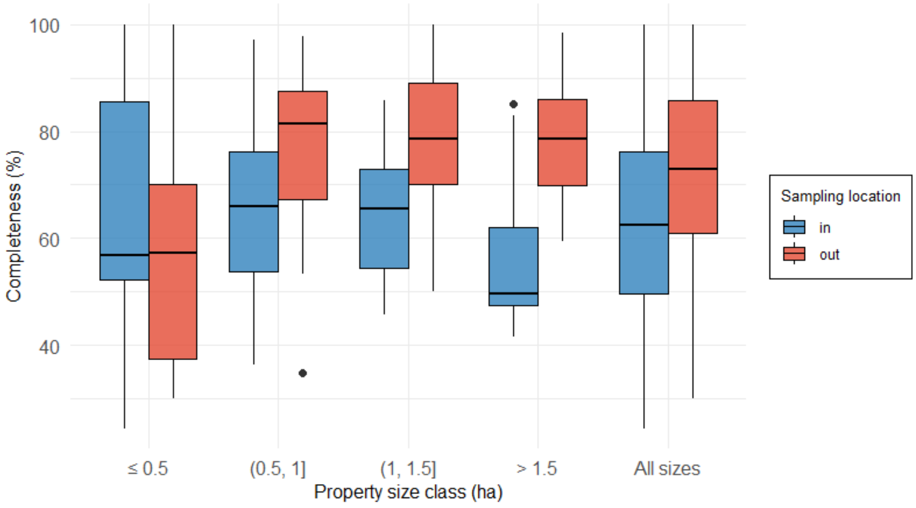


Figure 8. Completeness of vegetation inventories by property size class and sampling location. *Boxplots show completeness (%) for sampling points located inside (in, blue) and outside (out, red) properties, across four property size classes and for all sizes combined. Completeness values represent the proportion of species detected relative to the estimated species pool.*

3.6. Ordinal logistic regression results (Q3-4)

Exploratory analysis of categorical variables (histograms) and continuous variables (boxplots) stratified by break-in level suggested potential trends in some predictors, which were further evaluated in the univariate and multivariate ordinal logistic regression models (Appendix 3).

The univariate ordinal logistic regression analyses identified 13 predictors that improved model fit relative to the null model, as indicated by a reduction in AIC. Seven of these (mean_ndwi, BrayCurtis, log_dist_to_no_small_medium, log_area, log_dist_medium, Primary.use, and log_dist_small_medium) also significantly improved model fit according to likelihood ratio tests ($p < 0.05$), while the remaining six (mean_ndre, mean_ndvi, Maintain, log_dist_large, prop_attractive, and log_dist_to_river) were not statistically significant but were retained at this stage for further consideration (Table 7).

Table 7. Results of the univariate selection procedure and functional form testing for each predictor. The “Best model” column indicates the functional form (linear and/or quadratic) with the lowest AIC in the univariate analysis. A value of 1 that the variable was not retained after univariate screening. The “Coefficient” column shows the direction of the relationship between the predictor and the probability of belonging to a higher break-in category: a positive value (+) means that an increase in the predictor is associated with a higher likelihood of being in a higher break-in class, while a negative value (–) indicates the opposite. The p-value refers to the likelihood ratio test comparing this best model to the null model. Variables in green were retained for the multivariate model, while variables in red were excluded due to strong collinearity with another selected variable (the one with the lower p-value was kept).

Variable	Best_model	Coefficient	p_value
mean_ndwi	mean_ndwi	-	0

BrayCurtis	BrayCurtis	-	0.003
log_dist_to_no_small_medium	log_dist_to_no_small_medium	+	0.005
log_area	log_area	+	0.013
log_dist_medium	log_dist_medium	-	0.037
Primary.use	Primary.use	- ; + ; -	0.041
log_dist_small_medium	I(log_dist_small_medium^2)	-	0.047
mean_ndre	mean_ndre + I(mean_ndre^2)	+	0.061
mean_ndvi	mean_ndvi + I(mean_ndvi^2)	+	0.063
Maintain	Maintain	+	0.096
log_dist_large	log_dist_large	+	0.112
prop_attractive	I(prop_attractive^2)	+	0.142
log_dist_to_river	log_dist_to_river	+	0.144
log_dist_to_any_water	1	/	1
log_dist_to_no_small	1	/	1
log_dist_small	1	/	1
log_dist_medium_large	1	/	1
log_dist_waterholes	1	/	1
log_dist_to_nearest_property	1	/	1
log_dist_to_drainage	1	/	1
buffer_ndvi	1	/	1
Turnover	1	/	1
Nestedness	1	/	1
Fence	1	/	1
Fence_Maintain	1	/	1
Irrigation_level	1	/	1

Among the 13 variables retained after univariate screening, three were removed due to collinearity, leaving 10 predictors for inclusion in the multivariate model. Mean_ndre was excluded due to a high correlation (r = 0.99) with mean_ndvi. Log_dist_small_medium was moderately correlated (r = –0.69) with log_dist_no_small_medium, and log_dist_to_river was moderately correlated (r = 0.67) with the same variable; in both cases, log_dist_no_small_medium was retained as it had the lower p-value. All pairwise correlations above 0.6 are presented in appendix 5.

The retained variables were included in the multivariate analysis, and model selection using the dredge() function identified a final model with an AIC of 80.9 (AICc = 82.9):

$$\text{Breakin\_level} \sim mean\_NDWI + \text{log\_dist\_to\_no\_small\_medium} + \text{log\_area} + \text{Maintain}$$

The proportional odds model achieved a McFadden's pseudo-R^2 showed a strong model fit with a value of 0.35. The likelihood ratio test comparing the null and final models confirmed a highly significant improvement ($\chi^2 = 37.55$, df = 4, $p < 0.001$), with the degrees of freedom reflecting the number of additional parameters estimated in the final model.

In the final proportional odds model, "mean_NDWI" (mean Normalized Difference Water Index within the property) was negatively associated with break-in level, indicating that properties with lower NDWI values – i.e., less vegetation moisture or surface water – were more likely to fall into higher break-in categories. "Log_dist_to_no_small_medium" (log-transformed distance to the nearest large waterhole or the river) showed a positive association, meaning that properties farther from these permanent water sources were more likely to experience higher break-in levels. “Log_area” (log-transformed property area) was also positively associated, with larger properties more likely to fall into higher break-in categories. Finally, “Maintain” (fence maintenance status) indicated that properties without maintained fences were more likely to experience higher break-in levels, as shown by the higher proportion of “No maintain” in the High break-in category. All predictors in the final model were statistically significant, with p-values below the 0.05 threshold (Figure 9).

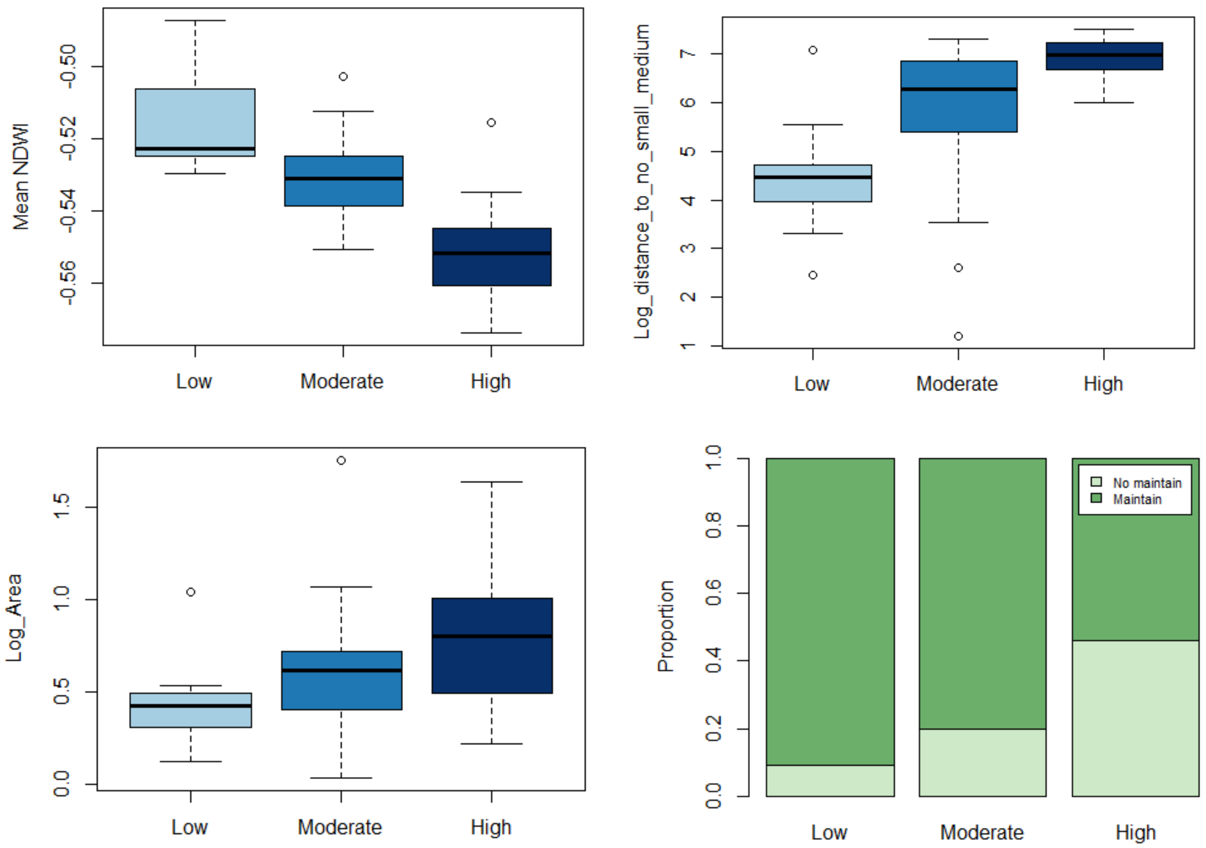


Figure 9. ***Predicted values of break-in level from the final proportional odds model for each retained predictor:*** *(a) mean_NDWI (p = 0.023), (b) log_dist_to_no_small_medium (p = 0.002), (c) log_area (p = 0.002), and (d) Maintain (p = 0.025). P-values are from likelihood ratio tests (LRT). Boxplots show the distribution of predicted values across break-in categories for continuous variables, and bar plots show proportions for the categorical variable.*

Three additional predictors, “BrayCurtis”, “log_dist_medium”, and “Primary.use”, had p-values below 0.05 in the univariate analyses but were not retained in the final model (Table 7). “BrayCurtis” showed a negative association, with properties whose vegetation communities were more similar to their surroundings experiencing fewer break-ins. “Log_dist_medium” also showed a negative association, indicating that properties located closer to medium-sized waterholes tended to experience more break-ins. For “Primary.use” (with *Lodge* as the reference category), primary residences had a lower likelihood of being in higher break-in categories, secondary residences had a higher likelihood, and staff residences had a lower likelihood compared to lodges.

4. Discussion

Understanding the factors that drive elephant break-ins into properties is essential for developing effective strategies to reduce human-elephant conflict and promote coexistence within protected areas. The marked increase in break-ins recorded in 2024 in OWNR highlights the urgency of identifying the temporal, environmental and anthropogenic variables that influence this behaviour, as well as the contexts in which mitigation measures may be most effective. This discussion interprets the findings of this study in relation to the four research questions, comparing them with existing literature to assess whether they support, refine, or challenge current knowledge on elephant movements and conflict dynamics.

The first objective of this study (**Q1**) was to determine which types of elephants are most frequently involved in property break-ins. Consistent with the hypothesis, all identified individuals were males, with adult bulls being particularly predominant, while subadult males were less frequent than expected. Although the sex of 43% of individuals could not be determined, suggesting that a small number of females may have been involved, the evidence nonetheless points to a strong male bias. This aligns with studies on crop-raiding behaviour in African elephants, where females are generally not known to engage in (Chiyo et al., 2012; Jackson et al., 2008), suggesting that such high-risk foraging strategies may be largely restricted to males. The absence of identified females highlights the possibility that female groups actively avoid properties, potentially due to their greater wariness and the need to protect calves (Lee, 1987). In addition, research has shown that male elephants engaging in crop-raiding tend to exhibit higher levels of stress hormones compared to non-raiding males, suggesting that such behaviour may be linked to elevated physiological stress (Ahlering et al., 2011). This implies that break-ins may not solely be driven by resource availability but could also reflect individual physiological conditions, potentially making certain bulls more prone to risk-taking. This finding is in line with other research indicating that male elephants, especially in musth, are more likely to take risks and approach human-modified areas (Poole & Moss, 1981).

Older males have been found to engage in raiding more frequently than younger males, indicating that this behaviour is not confined to subadult individuals. Moreover, younger bulls appear more likely to adopt raiding behaviour when associating with older raiders, particularly those within their closest social networks (Chiyo et al., 2012). This suggests that beyond individual risk-taking tendencies, male association patterns can facilitate the spread of such behaviours within populations. In the context of this study, the predominance of adult bulls in property break-ins may therefore reflect both life-history traits and opportunities for social learning, potentially sustaining or even amplifying the occurrence of this behaviour over time (Laland, 2004). Understanding these mechanisms is crucial for designing targeted mitigation measures, as interventions focusing on key individuals or social groups could reduce the propagation of high-risk behaviours within elephant populations (Ahlering et al., 2011; Jackson et al., 2008). For instance, by focusing deterrent measures on periods and locations where bulls are most active.

Building on this, the next step of this study was to consider when break-ins take place (**Q2**), since temporal patterns can reveal how ecological constraints and risk-avoidance strategies influence elephant behaviour. In 2024, the 142 officially reported break-ins occurred exclusively between May and November, delineating the observed seasonal window of incidents. This period corresponds to the dry season in South Africa, generally extending from May to October, characterised by cool, dry conditions with daytime maxima of 20–25 °C and frequent nighttime minima below 10 °C. By contrast, the wet season lasts from November to April, bringing intense thunderstorms, widespread vegetation growth, and daytime temperatures often exceeding 30 °C (van Wilgen et al., 2016). The seasonal clustering of break-ins therefore appears to be closely linked to ecological constraints associated with the dry season. In OWNR, the 2024 rainfall pattern showed a sharp decline from February onwards, reaching zero in July and August before recovering in November. This trend was mirrored in the timing of break-ins, although incidents peaked slightly later than the initial reduction in rainfall, suggesting a lagged ecological response. Interviews with property owners suggested that the true number of break-ins in 2024 was substantially higher than official reports (≈418 vs. 142), pointing to some degree of underreporting. While this may have affected absolute monthly frequencies, the seasonal pattern remains robust and consistent with rainfall and vegetation dynamics. The observed delay likely reflects temporal variation in forage availability, as residual soil moisture and groundwater reserves following the rainy season allow vegetation to remain green and nutritious for several weeks after rainfall has ceased (Clegg & O'Connor, 2017). As the dry season advances, grasses that respond quickly to short-term fluctuations in soil moisture, gradually senesce. Their protein content declines while fibre concentration increases, reducing digestibility and energetic returns (Zambatis et al., 2003). Elephants therefore adjust their diet, shifting from predominantly grazing in the wet season to greater reliance on browse in the dry months (Kos et al., 2012). This shift, however, provides only limited relief, as woody plants and forbs that follow longer seasonal cycles also decline in quality over time (Clegg & O'Connor, 2017). They become tougher and accumulate higher levels of secondary compounds such as tannins, further decreasing their palatability (Schmitt, 2017; Schmitt, Shrader, et al., 2020). With both grasses and browse providing progressively poorer forage, elephants are eventually compelled to seek alternative resources. For bolder individuals, this may involve venturing into properties, where dense and irrigated vegetation offer reliable and high-quality forage. It is consistent with other studies showing that, as natural vegetation declines, elephants increasingly turn to anthropogenic areas such as croplands and human settlements, where forage remains more reliable and energy-rich than in surrounding habitats. (Branco et al., 2019; Munyao et al., 2020).

Although water availability also decreases during the dry season, the abundance of permanent water sources in the reserve suggests that forage scarcity, rather than water limitation, is the primary driver of this behaviour. In line with this, the use of water sources inside properties occurred only in a minority of break-ins and almost always alongside feeding activity. Moreover, no significant relationship was detected between the occurrence of water-related damage and the distance to the nearest external water source. Even when water was freely accessible outside, elephants were still observed using water within properties, typically in combination with feeding activity. This may indicate that drinking inside properties reflects opportunistic use rather than a primary motivation for break-ins.

The results point to a clear link between climatic variability, forage scarcity and the occurrence of elephant break-ins. Both interviews with property owners and reports from Transfrontier Africa indicate that 2024, the driest year since 2017, was also the year most strongly affected by break-ins, whereas few incidents had been reported before. This reinforces the suggested interaction between climatic conditions and elephant behaviour. Given projections that winters in southern Africa are becoming increasingly dry, with rainfall concentrated in shorter, more intense summer events (MacFadyen et al., 2018; van Wilgen et al., 2016) the frequency of such incidents may rise in the future, underlining the importance of monitoring this dynamic at long-term scales.

Beyond seasonal and annual patterns, daily variation in break-ins provides further insight into elephant foraging strategies. Elephant break-ins were not evenly distributed across the day but occurred predominantly during periods of darkness. The majority of reported incidents took place in the evening and night, coinciding with hours between sunset (17h15–18h00) and sunrise (05h30–06h30). By contrast, only about one-fifth of break-ins occurred in daylight, when human activity is greatest. This temporal pattern indicates that elephants strategically time their intrusions to reduce the risk of encountering people, using low-light conditions as cover, as was predicted in the study's initial hypotheses. Similar behavioural adjustments have been documented elsewhere, where elephants in human-dominated landscapes shifted a large proportion of their activity into nocturnal hours compared to less disturbed areas, thereby minimising the risk of direct encounters near settlements and croplands (Adams et al., 2022; Gaynor et al., 2018). Crucially, this does not imply that elephants avoid these areas spatially. On the contrary, they continue to make use of them, but adjust the timing of their activity to avoid moments of highest human presence (R. S. Davis et al., 2023).

These findings highlight the importance of considering the temporal dimension of human–elephant conflict, since elephants tend to avoid direct encounters with people rather than human-modified areas themselves. One property owner reported having installed lamps around their property to mimic human presence, which appeared to coincide with a reduction in break-ins, suggesting that light-based deterrents warrant further consideration. Scientific evidence also supports this approach, with solar-powered strobe light barriers shown to significantly reduce elephant incursions into crop fields over a two-year period (Adams et al., 2021). However, the authors noted that in areas with high elephant density, habituation remains possible, highlighting the need for regular evaluation and complementary methods to sustain effectiveness. In this context, deterrents based on perceived human presence, such as broadcasting human voices, have also shown strong potential since elephants associate these cues with risk and tend to avoid them (Mortimer et al., 2021). A study testing this method is expected to take place soon in OWNR. Combining auditory and visual deterrents could therefore represent a promising avenue for further testing in protected areas.

While temporal avoidance clearly emerged as a key strategy, the question remains whether spatial configuration plays a comparable role in shaping elephant break-in patterns within the reserve (**Q3**). In contrast to expectations, the spatial configuration of properties did not influence break-in patterns within OWNR. The initial hypothesis was that more isolated properties would experience higher intrusion rates, yet no such effect was detected. While many studies have shown that elephants avoid human features such as villages, fields, or roads in densely settled landscapes (Adams et al., 2022; Gaynor et al., 2018; Wall et al., 2024), the situation in OWNR differs. Here, properties are sparsely distributed within core elephant habitat, human presence remains limited, and elephants are frequently observed in close proximity to houses, even during daylight. This difference in scale and context suggests that proximity to properties does not elicit the same avoidance behaviour observed in more heavily modified environments.

Since the spatial configuration of properties did not explain variation in break-in patterns, attention shifts to environmental features of the landscape. In other savanna systems, dry riverbeds and ephemeral streams have been shown to function as important movement corridors for elephants, concentrating travel routes and facilitating access to water and greener vegetation during the dry season (Giliba et al., 2023; Pittiglio et al., 2012, 2014). Properties located near such features were therefore expected to be more exposed to break-ins. In OWNR, however, distance to drainage lines did not emerge as a significant predictor. This likely reflects the specific context of the reserve, where drainage lines are relatively small, numerous, and embedded in a landscape already well supplied with both artificial and natural water sources (Bucciarelli et al., 2024). Under these conditions, elephants may not rely on them as primary pathways or resources, which could explain their limited influence on the spatial distribution of break-ins.

Given this result, water availability itself appeared to be a more relevant factor, and indeed it emerged as the most consistent driver of break-in patterns. Multiple combinations of distance-to-water metrics were tested, but not all yielded significant results. The model retained the combined variable accounting for distance to the river and to large waterholes, which together provided stronger explanatory power than either variable considered separately. This result indicated that properties located closer to these major water sources experienced fewer break-ins, whereas those further away were more frequently targeted. Conversely, a strong negative correlation was observed with distance to small and medium-sized waterholes, suggesting that proximity to these minor water sources was associated with a higher frequency of intrusions. However, these relationships were not tested jointly due to the high collinearity between variables. In contrast, distance to the nearest water source, regardless of size, was not significant, indicating that the type and scale of water bodies play a key role in shaping elephant break-in patterns (Smith et al., 2024).

The lower frequency of break-ins near rivers can be reasonably explained by the greater vegetation density in riparian areas, which provides abundant natural forage and reduces the incentive for elephants to enter properties (I. P. J. Smit et al., 2007). This interpretation is supported by the strong negative correlation between the buffer NDVI around properties and their distance to the river ($r = 0.79$). In contrast, no such relationship was found between buffer NDVI and distance to large waterholes or river ($r = -0.47$), suggesting that while vegetation might also play a role in reducing break-ins near these features, this hypothesis is not supported by the NDVI data. The underlying mechanism therefore remains uncertain and may involve factors not captured by the vegetation indices used here. An alternative explanation could be related to elephant behaviour at different types of water sources. At the study site, males were observed using large waterholes mainly during the hottest hours of the day for bathing or lying in the water to cool down, whereas medium-sized waterholes were preferred across all daily periods (Smith et al., 2024). These medium waterholes, often artificial and continuously supplied with pumped groundwater, provide cooler and fresher water, which elephants are known to favour (Ndlovu et al., 2018; Stommel et al., 2016). Since most break-ins in OWNR occurred during nocturnal hours, when large waterholes are seldom used, properties located nearby may be less exposed to intrusions, while the constant attractiveness of medium-sized waterholes may align more closely with the timing of elephant activity around properties.

The higher frequency of break-ins observed near small and medium-sized waterholes may also be linked to their spatial concentration in the central part of the reserve, where most properties are located. Although direct vegetation data were not available for this study, both property owners and Transfrontier Africa staff consistently reported a marked decline in woody cover in this area over recent years, with many large trees disappearing under sustained elephant pressure. As elephants tend to be found in higher densities closer to water (Guldemond et al., 2017), their persistent presence around small and medium-sized waterholes likely amplifies browsing pressure on local vegetation. This pattern is consistent with the well-documented piosphere effect, whereby elephant browsing intensity is highest in the vicinity of water sources and declines with increasing distance (Lange, 1969; Thrash & Derry, 1999). A recent study in Zambezi National Park showed that high densities of waterholes led to extensive vegetation degradation within 2–3 km, including drastic reductions in tree basal area and canopy volume and widespread conversion of woodland to shrubland (Wilson et al., 2021). In OWNR, the continued availability of water around these features makes them particularly important during the dry season, encouraging elephants to remain in these areas rather than moving elsewhere. However, as vegetation becomes progressively depleted under sustained browsing, properties may represent an increasingly attractive alternative food source. In this context, irrigated gardens and dense vegetation within properties may function as reliable "forage refuges" compared to the impoverished surroundings.

Interestingly, the buffer NDVI variable itself was not retained as significant in the models, despite its strong correlation with distance to rivers. One possible explanation could be methodological. Given the 10 × 10 m resolution of the NDVI raster, some pixels overlapping the buffer zone may have partly included vegetation located inside the properties themselves. Although the mean NDVI per buffer was calculated using area-weighted values to account for pixel proportion, the strong correlation between buffer NDVI and internal NDVI ($r = 0.74$) suggests that this interaction may have diluted the distinct contribution of the surrounding vegetation. It therefore remains possible that, without this overlap, buffer NDVI would have emerged as more significant. This highlights the need for methodological refinements in vegetation quantification to better disentangle property versus surrounding vegetation effects in future studies, notably by using drone imageries.

While remote-sensing metrics such as NDVI did not provide a clear signal, the vegetation inventories offered complementary insights. Overall, although Bray–Curtis was not retained in the final multivariate model, most likely because its explanatory power overlapped with other predictors, the univariate analysis nevertheless provides an important insight It suggests that elephants may favour properties that mirror their familiar foraging environment, contradicting the initial hypothesis that greater dissimilarity would attract them by providing novel resources. By contrast, neither turnover nor nestedness provided explanatory power relative to the null model. Since these indices rely solely on presence–absence data and do not account for species abundances, their lack of significance suggests that the mere occurrence of additional or unique species inside properties was insufficient to explain break-in frequency. In comparison, the signal detected through Bray–Curtis indicates that elephants responded primarily to abundance-weighted similarity in common taxa.

This perspective naturally connects with the broader question of what makes individual properties attractive to elephants (**Q4**), beyond landscape-level drivers. In line with these results, the proportion of plant species classified as attractive to elephants did not emerge as significant, which is somewhat surprising given that one might expect a higher proportion of attractive species to increase the likelihood of intrusion. Taken together with the Bray–Curtis result, these findings suggest that elephants may not be primarily driven by the absolute presence of attractive species within properties, but rather by whether the overall vegetation structure is consistent with their familiar foraging environment. It is also important to note that vegetation inventories were not exhaustive. Inventory completeness ranged from approximately 50 to 85 percent across property size classes and sampling zones, meaning that unrecorded species could have influenced the observed patterns. Nevertheless, this interpretation is consistent with the observation that the species most frequently targeted during break-ins are also commonly found in the surrounding environment. Yet this raises the question of why elephants take the risk of breaking into properties to feed on plants that are also available outside. One plausible explanation lies in differences in plant chemistry between property vegetation and surrounding wild vegetation. Plants growing outside are continuously exposed to browsing pressure and recurrent drought, both of which increase physiological stress. Stress conditions are well known to stimulate the synthesis of defensive secondary metabolites, including tannins, monoterpenes, and alkaloids (Barbehenn & Peter Constabel, 2011; Owen Smith, 1993). These compounds function as chemical defenses by precipitating proteins, reducing digestibility, or exerting toxic effects, and high concentrations are often associated with reduced palatability (Schmitt, 2017). For example, elephants are known to avoid *Combretum* species when their levels of polyphenols, especially tannins, increase, as this substantially lowers protein availability (Schmitt, Shrader, et al., 2020). In contrast, plants within properties are often irrigated, occasionally fertilized, and subject to much lower herbivory pressure, which may reduce their production of such compounds. As a result, the same species could be chemically less defended and more digestible inside properties, making them particularly attractive to elephants. This interpretation also aligns with evidence that elephants can detect volatile monoterpenes as pre-ingestive olfactory cues and actively avoid species emitting high levels of these compounds (Schmitt et al., 2018; Schmitt, Shuttleworth, et al., 2020). Examining differences in plant stress responses and secondary compound production between property and wild vegetation could help clarify whether vegetation quality contributes to elephant foraging decisions, and thus merits further investigation.

NDWI did prove significant, with properties showing lower NDWI values experiencing more break-ins. This outcome is counterintuitive because higher vegetation water content would normally be expected to increase attractiveness. The minor variation detected could be influenced by broader environmental conditions, with properties situated closer to rivers or large waterholes being embedded in more humid surroundings, which may explain why higher NDWI values were associated with fewer break-ins. However, NDWI values were uniformly low across properties, suggesting generally dry vegetation with only limited contrasts, making it difficult to draw strong ecological conclusions (Gao, 1996; Serrano et al., 2019). In addition, irrigation frequency did not show any significant effect, reinforcing the idea that elephants primarily enter properties in search of food, while a potential influence of watering on vegetation condition could not be confirmed here.

Turning to structural characteristics, property size emerged as a significant predictor, with elephants being more attracted to larger properties than to smaller ones. This pattern can be interpreted as a matter of foraging efficiency (G. H. Davis et al., 2022). Breaking into a property involves an energetic cost and a potential risk of disturbance, so the payoff must outweigh the effort. Larger properties are more likely to contain greater quantities and diversity of vegetation, increasing the probability of finding sufficient food resources once inside. In contrast to property size, primary use might also have been expected to influence break-ins by reflecting differences in human presence. It was not retained in the final multivariate model, and its apparent effect in the univariate analysis was largely driven by the three staff compounds, all of which fell within the low break-in category. Their influence also aligns with the result on property size, since two of the staff compounds were among the smallest properties in the dataset. Overall, primary use does not appear to make a strong difference, as most properties are rarely vacant and nearly always host staff. Future studies could investigate whether the actual number of people present at the time of break-ins influences elephant behaviour, but such data were not available here.

Fence type could not be identified as a significant predictor of break-ins, though this does not mean that some designs are not more effective than others. Because of the limited sample size, properties with multiple barriers were grouped into a mixed category, which simplified the analysis but reduced resolution. Within this category, certain combinations may in fact provide greater protection, but this could not be tested statistically here. Two properties adopted an additional measure by reinforcing their fences with a layer of sharp rocks on the ground. This approach, based on elephants' reluctance to walk on uncomfortable surfaces (Baker, 2013), coincided with both properties falling within the "low break-in" category. Future research would therefore benefit from evaluating the effectiveness of each barrier type separately to determine whether some designs provide stronger protection. What could be demonstrated, however, is that well-maintained fence were associated with a lower risk of break-ins. This highlights that, regardless of type, regular upkeep is a key factor in reducing elephant intrusions (Kamdar et al., 2022).

Testimonies from property owners also provided valuable insights into the strategies elephants use to overcome fences. The most frequent method involved pushing down fence posts, often combined with climbing over the fence. Gates were rarely used except when left open, and several owners noted that elephants tended to take advantage of open gates during the day but were more likely to enter through the fence at night in more secluded areas.

Elephants were also reported to exploit weak points repeatedly once identified, sometimes returning with other individuals to use the same breach. This indicates not only individual learning but also social transmission of behaviour, consistent with previous observations showing that raiding can spread through association with experienced conspecifics (Chiyo et al., 2012; Duffy et al., 2009). More deliberate tactics were also mentioned, such as pulling electric cables with their tusks, apparently after realising that they no longer carried current (Mutinda et al., 2014), or using trees to knock down fences, either by dragging them from the inside or by pushing them from the outside to disable the power supply. Taken together, these accounts illustrate the ingenuity and adaptability of elephants when faced with barriers, which complicates reliance on physical deterrents alone. Elephants are indeed well known for their intelligence and problem-solving skills, with studies documenting tool use, flexible thinking, and innovative strategies when faced with novel challenges (Jacobson & Plotnik, 2020; Plotnik & Jacobson, 2022).

These observations nevertheless open potential avenues for solutions. Since pushing down fence posts is one of the most common methods used by elephants, strengthening the posts or adding deterrent devices such as spikes or whiskers could reduce their vulnerability. Another approach involves using extendable electric wires, which do not snap under pressure and thus make fences more difficult for elephants to breach. However, previous work has also shown that fence effectiveness is not consistently linked to design, construction, or voltage, as even high-specification fences can fail while simpler ones endure (Thouless & Sakwa, 1995). This underlines the need to explore complementary deterrent methods, including more nature-based or behavioural approaches such as beehive fences, acoustic deterrents mimicking human voices, or solar-powered strobe light barriers, which are currently being tested and developed in different contexts (Adams et al., 2021; King et al., 2017; Mortimer et al., 2021; Wright et al., 2023). Despite this, the ability of elephants to innovate and share their discoveries suggests that the effectiveness of these measures is likely to be limited over time. What works in the short term may be circumvented once a new strategy is developed. This indicates that the problem is unlikely to be solved solely at the scale of individual properties. This view is reinforced by the fact that no vegetation-related variables were found to be significant in this study, nor were other factors such as the presence of water or irrigation frequency, which could theoretically be modified at this scale. Broader-scale approaches will therefore likely be required if residents genuinely wish to prevent elephants from entering their properties.

In this regard, distance to waterholes emerged as one of the most influential factors in this study. The high density of artificial water points in the reserve appears to maintain elephants in the area during the dry season, thereby increasing browsing pressure on woody vegetation and ultimately contributing to a higher risk of break-ins (Wilson et al., 2021). Similar ecological patterns have been observed at a larger scale in Kruger National Park, where decades of widespread artificial water provision resulted in overgrazing, altered herbivore distributions, and intensified elephant impacts on vegetation. Since the late 1990s, however, Kruger has progressively closed the majority of its boreholes and breached dams to restore a more natural mosaic of water availability. This policy shift did not negatively affect elephant population numbers, which continued to increase, but it did change their spatial distribution. Elephants became more strongly associated with perennial rivers while pressure decreased in formerly artificial water-dependent areas (I. Smit, 2013; I. P. J. Smit et al., 2007).

These findings suggest that a comparable strategy could be considered in Olifants West Nature Reserve. Discussions with property owners should be realized to encourage them to collectively stop maintaining artificial waterholes during the dry season while relying on naturally occurring water sources, to disperse elephants more widely across the landscape. This could shorten the duration of their presence within the reserve and consequently reduce the frequency of break-ins. This study also highlighted a limited level of communication between properties and Transfrontier Africa, with only a third of break-ins being reported. Strengthening this dialogue would not only provide a more accurate understanding of the scale of the problem but also foster more effective, coordinated strategies to mitigate elephant break-ins in the future.

5. Conclusion

Human–Elephant Conflict (HEC) remains one of the most pressing conservation challenges in southern Africa. Despite decades of mitigation efforts, conflicts persist even within protected reserves, underscoring the difficulty of reconciling human presence with elephant conservation. This study investigated the drivers of elephant break-ins into properties, a phenomenon that not only causes material damage but also fuels tensions between local stakeholders and wildlife.

The results provide new insights into the behavioural and environmental conditions under which break-ins occur, revealing that they were overwhelmingly carried out by adult males, concentrated in the dry season, and mainly during hours of darkness. Water availability emerged as a central factor, with fewer break-ins near rivers and large waterholes but more frequent events near small and medium-sized ones. At the property scale, vegetation indices provided little explanatory power, suggesting that vegetation quality, in terms of chemistry or stress responses, may play a more decisive role. Vegetation inventories, although representative, did not fully capture the complexity of plant communities, and this aspect deserves further attention in future studies. In addition, examining more directly how nutritional properties and physiological stress of plants influence elephant foraging would provide valuable insights. Tackling these points will help refine both scientific understanding and practical responses to elephant break-ins.

From a management perspective, the findings highlight that reducing elephant break-ins cannot rely solely on property-level interventions. Fence type could not be identified as a significant predictor, but well-maintained barriers consistently reduced intrusion risk, suggesting that reinforcement through stronger structures or natural barriers could help limit vulnerability. Building on the temporal patterns identified in this study, future deterrents could also benefit from targeting periods of darkness, when elephants most often attempt to enter properties while avoiding human presence. However, testimonies showed that elephants frequently exploited weak points, often returned to the same breaches, and sometimes used deliberate tactics to disable fences. Such behaviours underline both their ingenuity and their ability to share knowledge socially, making long-term dependence on physical deterrents uncertain.

This points to the importance of broader-scale strategies to complement local efforts. Water management emerged as one of the most influential drivers, with the density of artificial waterholes maintaining elephants in the area during the dry season and increasing browsing pressure. Limiting the artificial provision of water and relying more on natural sources could help disperse elephant presence, shorten their residence time, and, in parallel with improved fence maintenance, alleviate conflict intensity.

Finally, this study revealed a limited level of communication between property owners and Transfrontier Africa, with only a fraction of break-ins being reported. Strengthening this dialogue would not only improve the accuracy of monitoring but also foster more effective, coordinated mitigation strategies in the future.

6. Appendices

Appendix 1. Interview form used during fieldwork. This document contains the list of questions employed to guide interviews with property owners and to support the systematic inventory of fenced properties.

Date:

Property name:

SURVEY
Questions to ask property owners

1) What is the property's primary use?
   - ○ Primary residence
   - ○ Secondary residence
   - ○ Lodge
   - ○ Other

Add comments (Duration of property vacancy, etc):

2) Does the recorded number of break-ins seem accurate, or have there been more break-ins than recorded? Has there been a change in the frequency of break-ins over the years?

3) Would it be possible to provide a general description of the break-ins, such as how the elephants typically entered the property, what behaviour was observed (e.g., breaking fences, gates, or damaging specific)

4) Did the elephants use or damage water sources on the property?
   - ○ Used/damaged OPEN water sources on the property (water sources that are not covered or enclosed. E.g., waterholes, water features, ponds, swimming pools, etc.)
   - ○ Used/damaged CLOSED water sources on the property (water sources that are covered or enclosed. E.g., Jojo tanks, sealed reservoirs, water pipes that are not buried, etc.)
   - ○ Did not use/damage any water sources on the property
   - ○ There were no water sources on the property

Add comments:

5) Did the elephants use or damage water sources outside but within 200m the property?
   - ○ Used/damaged OPEN water sources outside but within 200m of the property
   - ○ Used/damaged CLOSED water sources outside but within 200m of the property
   - ○ Did not use/damage any water sources outside but within 200m of the property
   - ○ There were no water sources outside but within 200m of the property

Add comments:

6) Which plant group did the elephants target on the property?
   - ○ Trees
   - ○ Shrubs
   - ○ Forbs
   - ○ Grasses
   - ○ Succulents
   - ○ Other :

Add comments (What plant species? Ask the landowners to show you what plants the elephants targeted,etc)

7) Is the vegetation on the property regularly irrigated? (e.g., using a hosepipe, sprayers, watering pot, etc.)?

8) Is the vegetation on the property fertilized? (e.g., using fertilizers or compost)
   - ○ YES
   - ○ NO

9) Is the fence electrified? If yes, what is the voltage (in kV)?
   - ○ YES
   - ○ NO

Add comments (Situation at the time of the break-in?):

10) Considering that some of this information might differ between break-ins (e.g., fences might have been broken and later repaired, fence voltage increased, waterholes closed, or plant composition changed), do these changes seem to have influenced the frequency or nature of the break-ins?

11) What methods were used to chase the elephants away (horns, grenades, clapping, etc.)? Which method seemed to be the most effective?

INVENTORY

Fence type surrounding the property (Take pictures)

Property details: Water availability

1) Availability of water sources on the property:
   - ○ OPEN water sources (water sources that are not covered or enclosed. E.g., waterholes, water features, ponds, swimming pools, etc.)
   - ○ CLOSED water sources (water sources that are covered or enclosed. E.g., Jojo tanks, sealed reservoirs, water pipes that are not buried, etc.)
   - ○ NO, there are no water sources on the property.

Add comments (type, approximate size, whether the water sources are accessible (many properties have elevated jojo tanks), etc):

2) Water availability in sources within 200m of the property:
   - ○ OPEN water sources
   - ○ CLOSED water sources
   - ○ NO, there are no water sources outside but within 200m of the property.

Add comments (approximate distance, type, approximate size, whether the water sources are accessible, etc):

Property details: Gardens, lawns, and vegetation

1) Which of the following describes the vegetation on the property?

- ○ Garden (characterized by beds where plants have been artificially planted and maintained)
- ○ Lawn (characterized by an expanse of short grass)
- ○ Unaltered vegetation (no plants were artificially planted and natural vegetation kept)
- ○ Other

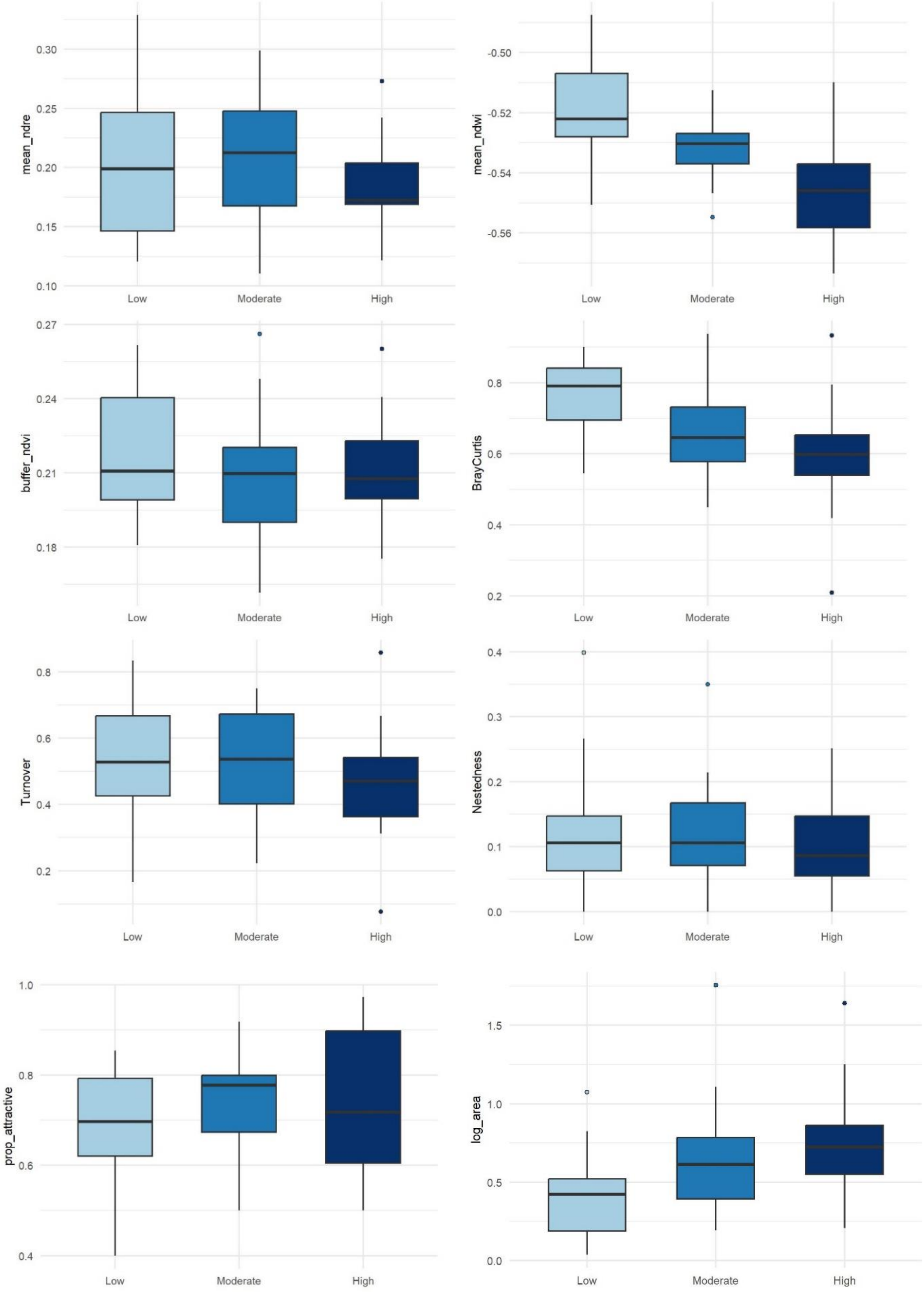
Add comments:

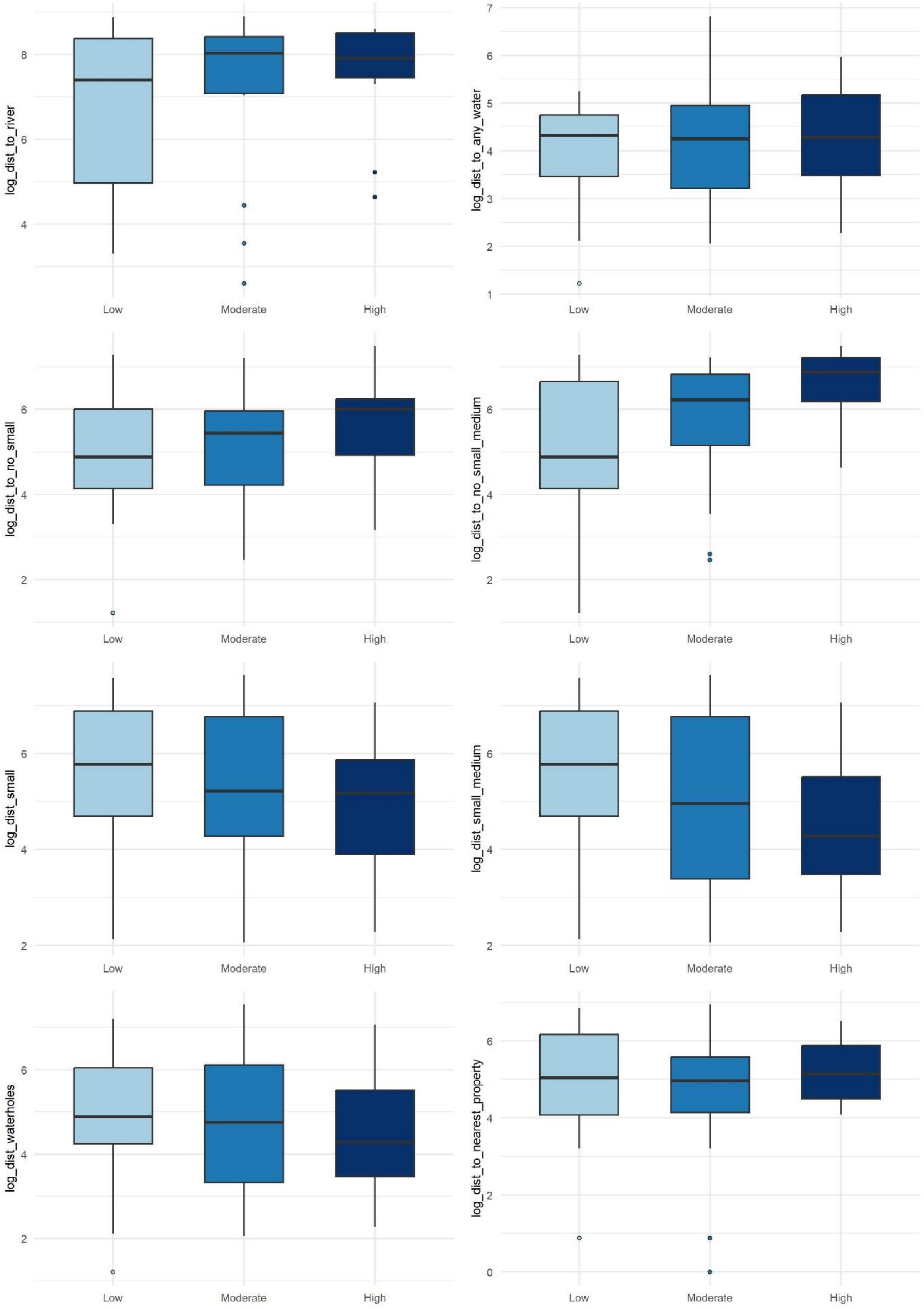
Appendix 2. List of plant species considered attractive to African elephants (*Loxodonta africana*). This list provides both scientific names and local common names specific to the Lowveld region. The classification was based on owner interviews, break-in incident records, and published literature on elephant feeding ecology in the Lowveld.

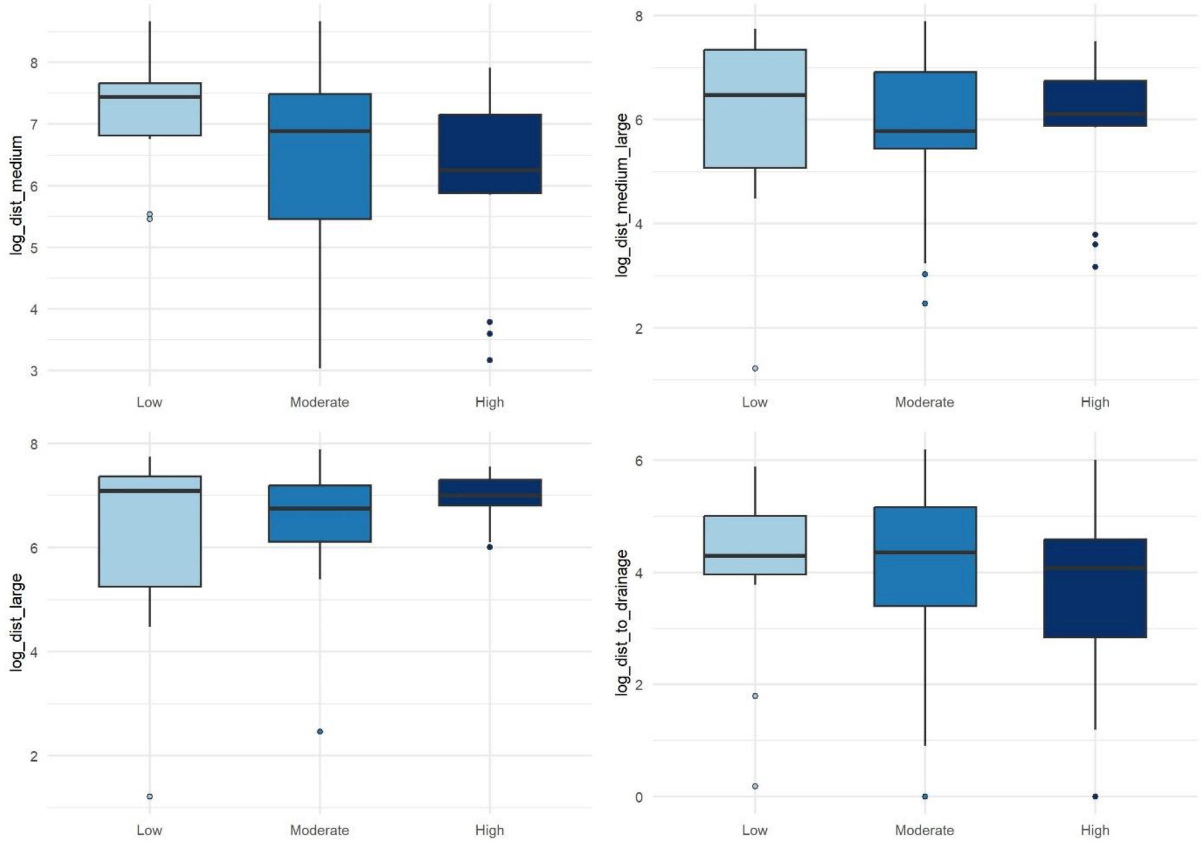
Scientific name	Common name
Adansonia digitata	baobab
Balanites maughamii	greenthorn
Bolusanthus speciosus	wisteria tree
Bougainvillea spp.	bougen vilia
Cassia abbreviata	sjambok pod
Colophospermum mopane	mopani
Combretum apiculatum	red bushwillow
Combretum imberbe	leadwood
Commiphora mollis	velvet corkwood
Cordyla africana	wild mango
Cussonia spp.	cabbage tree
Dichrostachys cinerea	sickel bush
Diospyros mespiliformis	jackalberry
Dombeya rotundifolia	wild pear
Ehretia rigida	puzzle bushes
Erythrina spp.	coral trees
Euclea crispa	blue guarri
Euphorbia tirucalli	firestick
Ficus spp.	fig trees
Flueggea virosa	white berry bush
Garcinia livingstonei	african mangosteen
Gardenia volkensii	bushveld Gardenia
Grewia bicolor	raisin bush
Grewia flava	raisin bush
Grewia flavescens	raisin bush
Grewia hexamita	raisin bush
Grewia monticola	raisin bush
Grewia villosa	raisin bush
Kigelia africana	sausage tree
Lannea schweinfurthii	false marula

Manilkara mochisia	lowveld milkberry
Mystroxylon aethiopicum	voelsitboom
Pappea capensis	jacket plum
Philenoptera violacea	appleleaves
Portulacaria afra	spekboom
Schotia brachypetala	weeping boer bean
Sclerocarya birrea	marula
Senegalia burkei	black monkey thorn
Senegalia erubescens	bluethorn
Senegalia galpinii	monkey thorn
Senegalia nigrescens	knobthorn
Solanum rautanenii	african potato bush
Sterculia rogersii	bushman’s star-chestnut
Strelitzia nicolai	giant white bird of paradise
Strelitzia reginae	bird of paradise
Syzygium spp.	waterberry
Terminalia prunioides	purple-pod clusterleaf
Terminalia sericea	silver cluster-leaf
Trichilia emetica	natal mahogani
Vachellia constricta	whitethorn acacia
Vachellia farnesiana	sweet acacia
Vachellia karroo	sweet thorn
Vachellia mellifera	blackthorn
Vachellia nilotica	scented thorn
Vachellia robusta	robust thorn
Vachellia spp.	thorn trees
Vachellia tortilis	umbrella thorn
Vachellia tortilis	umbrella thorn
Vachellia xanthophloea	fever tree
Xanthocercis zambesiaca	nyala tree
Ziziphus mucronata	buffalo thorn

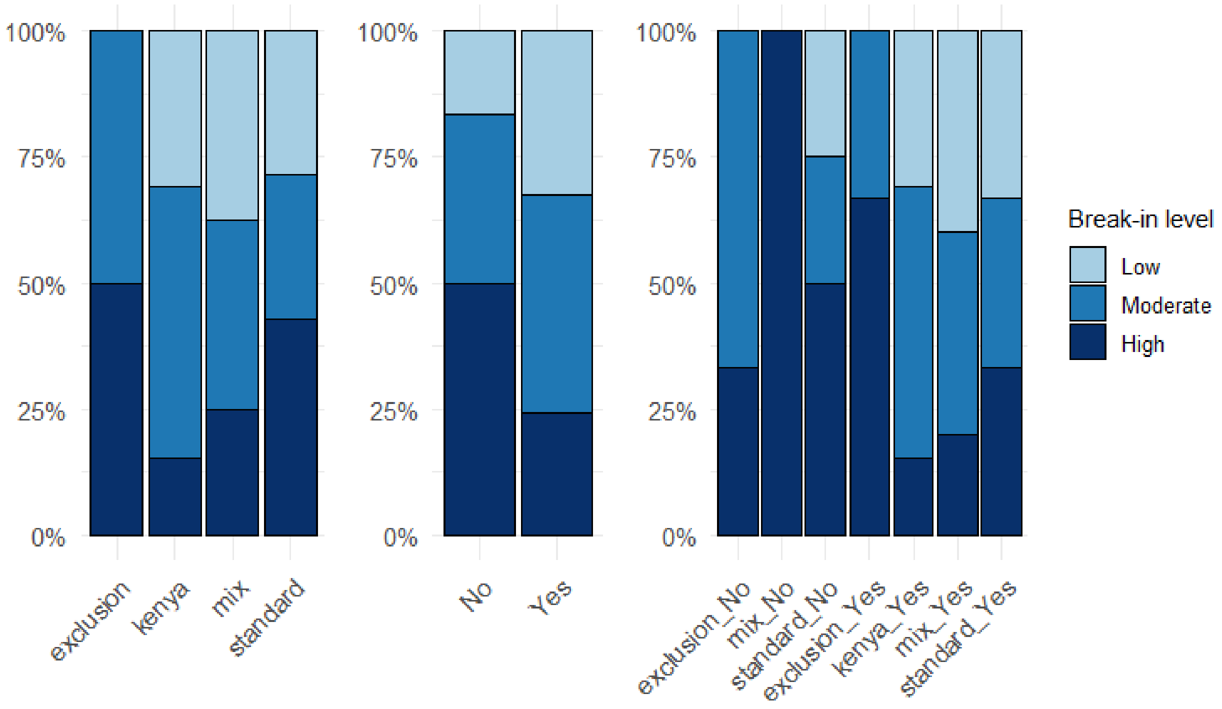
Appendix 3. Histograms and boxplots of explanatory variables stratified by break-in categories (low: 0–3, moderate: 4–11, high: 11+). Continuous variables are represented by boxplots, whereas categorical variables are represented by histograms. In the case of categorical variables, the histograms illustrate the distribution of fence types (Exclusion, Kenya, Mix, Standard) and their maintenance status (Yes/No).




log_dist_to_river
4
6
8
Low
Moderate
High
log_dist_to_any_water
1
2
3
4
5
6
7
Low
Moderate
High
log_dist_to_no_small
2
4
6
Low
Moderate
High
log_dist_to_no_small_medium
2
4
6
Low
Moderate
High
log_dist_small
2
4
6
Low
Moderate
High
log_dist_small_medium
2
4
6
Low
Moderate
High
log_dist_waterholes
2
4
6
Low
Moderate
High
log_dist_to_nearest_property
0
2
4
6
Low
Moderate
High



log_dist_medium
8
7
6
5
4
3
Low
Moderate
High
log_dist_medium_large
8
6
4
2
Low
Moderate
High
log_dist_large
8
6
4
2
Low
Moderate
High
log_dist_to_drainage
6
4
2
0
Low
Moderate
High



100%
75%
50%
25%
0%
exclusion
kenya
mix
standard
100%
75%
50%
25%
0%
No
Yes
100%
75%
50%
25%
0%
exclusion_No
mix_No
standard_No
exclusion_Yes
kenya_Yes
mix_Yes
standard_Yes
Break-in level
Low
Moderate
High

Appendix 4. Inventory completeness by property and sampling side. For each property, observed species richness (*Richesse_obs*) and estimated richness (Chao1; *Richesse_chao*) are presented together with sampling completeness (*Pourcentage* = 100 × *Richesse_obs* / *Richesse_chao*). The variable *Side* indicates the sampling location, with *inside* referring to surveys conducted within property boundaries and *outside* to those conducted in the 50-m surrounding buffer.

Name	Side	Richesse_obs	Richesse_chao	Pourcentage
Brits House	in	23	27	85.2
Brits House	out	18	21.5	83.7
Bundox	in	17	26	65.4
Bundox	out	7	8	87.5
Cam 10	in	24	31.5	76.2
Cam 10	out	13	16	81.2
Cam 13	in	12	33	36.4
Cam 13	out	11	16	68.8
Cam 27	in	15	15.42	97.2
Cam 27	out	10	15	66.7
Cam 29	in	26	48.75	53.3
Cam 29	out	16	20.2	79.2
Cam 31	in	26	39.12	66.5
Cam 31	out	9	11	81.8
Cam 35	in	19	32.75	58
Cam 35	out	14	15.2	92.1
Camp 1	in	24	43.5	55.2
Camp 1	out	15	18	83.3
Camp 2	in	18	36	50
Camp 2	out	22	31	71
Campfire Adele house	in	7	12	58.3
Campfire Adele house	out	4	4	100
CamWild	in	26	37.14	70
CamWild	out	20	36.5	54.8
Ezulwini Billy's Lodge	in	30	43.125	69.6
Ezulwini Billy's Lodge	out	17	26	65.4
Hardekool	in	21	28	75
Hardekool	out	17	21.2	80.2
Hunting Camp	in	11	16	68.8
Hunting Camp	out	8	23	34.8
Imagine Africa house	in	9	9	100
Imagine Africa house	out	9	30	30
Imagine africa lodge	in	21	48.5	43.3
Imagine africa lodge	out	13	13.2	98.5
Imagine africa staff	in	19	28	67.9
Imagine africa staff	out	12	12	100
Impala Lilly	in	12	19	63.2
Impala Lilly	out	7	7.25	96.6
Impalabos East house	in	11	13.5	81.5

Impalabos East house	out	8	8.6	93
Impalabos East staff	in	7	7	100
Impalabos East staff	out	7	12	58.3
Indulamitsi	in	26	41.17	63.2
Indulamitsi	out	20	29.43	68
Kampi ya Thude	in	22	90	24.4
Kampi ya Thude	out	12	14.5	82.8
Kamuzu	in	11	20.33	54.1
Kamuzu	out	16	29.75	53.8
Kusungula	in	33	88.2	37.4
Kusungula	out	15	16.2	92.6
Leopards View	in	15	29	51.7
Leopards View	out	9	30	30
Mangwa	in	14	26	53.8
Mangwa	out	16	18.5	86.5
Marafika	in	27	61	44.3
Marafika	out	12	22.5	53.3
Masodini	in	25	40.6	61.6
Masodini	out	16	23	69.6
Mondzewini house	in	22	52	42.3
Mondzewini house	out	10	15	66.7
Mondzewini staff	in	7	13	53.8
Mondzewini staff	out	10	15	66.7
Mvubu	in	22	27.5	80
Mvubu	out	13	20	65
Naledi house	in	17	19.625	86.6
Naledi house	out	13	35.5	36.6
Naledi lodge	in	31	62.67	49.5
Naledi lodge	out	11	11.25	97.8
Nambu Camp	in	32	70.25	45.6
Nambu Camp	out	19	25	76
Ngala ya Rila	in	14	25.25	55.4
Ngala ya Rila	out	12	21.33	56.2
Nonwane	in	12	15.75	76.2
Nonwane	out	7	8	87.5
Oxford house	in	21	43	48.8
Oxford house	out	16	17.2	93
Pagamisa	in	9	10.2	88.2
Pagamisa	out	19	26	73.1
Pondoro	in	24	29	82.8
Pondoro	out	15	20.6	72.8
Rome 6	in	17	20.5	82.9
Rome 6	out	15	37.5	40
Royal Ingwe	in	17	20.5	82.9
Royal Ingwe	out	18	27	66.7
Royal Olifants	in	36	86.6	41.6

Royal Olifants	out	22	37	59.5
Sausage tree	in	20	27	74.1
Sausage tree	out	14	28	50
Shirombirombi	in	16	29.75	53.8
Shirombirombi	out	9	11	81.8
Takalani	in	17	26	65.4
Takalani	out	13	18.25	71.2
Toroyaka	in	29	59	49.2
Toroyaka	out	15	20.25	74.1
Tundla	in	12	14	85.7
Tundla	out	15	16	93.8
Wisani	in	13	49	26.5
Wisani	out	12	34.5	34.8
Zingela	in	26	56	46.4
Zingela	out	15	19.2	78.1

Appendix 5. Pairwise Pearson correlation coefficients among continuous predictor variables. Coefficients with |r| > 0.6 are highlighted as an indicator of potential collinearity.

Var1	Var2	Value
mean_ndre	mean_ndvi	0.995
log_dist_small_medium	log_dist_small	0.905
buffer_ndvi	log_dist_to_river	-0.792
log_dist_waterholes	log_dist_small_medium	0.754
buffer_ndvi	mean_ndre	0.753
buffer_ndvi	mean_ndvi	0.743
log_dist_to_no_small_medium	log_dist_to_no_small	0.692
Nestedness	Turnover	-0.688
log_dist_small_medium	log_dist_to_no_small_medium	-0.688
Turnover	BrayCurtis	0.686
log_dist_waterholes	log_dist_small	0.674
log_dist_to_no_small_medium	log_dist_to_river	0.674
log_dist_medium_large	log_dist_large	0.672
log_dist_medium_large	log_dist_waterholes	0.668
BrayCurtis	log_area	-0.636
log_dist_waterholes	log_dist_to_any_water	0.634
log_dist_medium_large	log_dist_medium	0.633
log_dist_small	log_dist_to_no_small_medium	-0.607
mean_ndre	log_dist_to_river	-0.607

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