USING HIGH-RESOLUTION REMOTE-SENSING TO QUANTIFY NEST SITE CHARACTERISTICS OF WHITE-BACKED VULTURE (*GYPS AFRICANUS*) IN KARINGANI GAME RESERVE, MOZAMBIQUE

By

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Thesis submitted in fulfilment of the requirements for the degree **Master of Conservation Science: Nature Conservation** in the Faculty of Applied Sciences at the Cape Peninsula University of Technology

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Cape Town

October 2024

DECLARATION

I, **Tom Lautenbach**, declare that the contents of this dissertation/thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

Signed Lautenbach.

Date 30/10/2024

ABSTRACT

The decline of White-backed Vultures (WbVs), a critically endangered species, in southern Africa calls for urgent intervention and an increased understanding of their nesting requirements to improve conservation of suitable nesting trees. There is currently little research on the nesting preferences of WbVs, and few measurements on how variation in individual tree architectures or the surrounding area influences WbV nest site selection. Moreover, current methods of tree measurement are time-consuming, susceptible to inaccuracy due to human error, and potentially dangerous. This study aimed to fill these critical knowledge gaps by combining remotely sensed Light Detection and Ranging (LiDAR) data and Red-Green-Blue (RGB) imagery with helicopter surveys of nest locations (n=30) to explore nest site selection of WbVs in Karingani Game Reserve (KGR), Mozambique. The LiDAR and RGB orthomosaics allowed for precise and accurate measurement of various tree-level characteristics: canopy height, canopy area, canopy roughness, nest orientation and peripheral position, and distance to water. Surrounding vegetation cover was also measured, along with surrounding canopy height, and vegetation roughness within 100 m of nesting trees. A Resource Selection Function (RSF) analysis was used to determine which variables WbVs favoured when selecting a nesting tree. This study found that WbVs in KGR prefer nesting in trees with an average height of 14 m (10.58 m - 16.34 m), with large variation and roughness within their canopy (4.04**s**), and large canopy area, averaging 161.58m². White-backed Vultures in KGR were found to position their nests on the northern side of the tree, but with no preference for nest position in relation to canopy edge. The approach of using LiDAR and RGB imagery was found to be effective for measuring tree-level variables in a time-effective and accurate manner, while revealing more information on the nesting ecology of WbVs in KGR. This approach allowed us to gain a better understanding of the specific requirements of WbVs when selecting a tree to nest in, and thus aid protected area management by providing valuable information regarding the need to conserve specific habitats within protected areas to ensure the survival of this species. This novel approach could become the new standard for measuring trees for large raptor studies, allowing researchers to collect data from much larger areas and increased sample sizes with ease.

ACKNOWLEDGEMENTS

I wish to thank:

- My supervisor, Professor Frans Radloff – Thank your patience throughout this process. I could not have got through this without your unwavering dedication and continuous insightful guidance that has equipped me to think like a real ecologist.
- My co-supervisor, Professor Andrew Davies – Thank you for the time and resources you gave me to pursue my Master's degree. I feel very proud to be a part of the Davies Lab and honoured to be able to call you my mentor and friend.
- Karingani Game Reserve – Thank you for the funding that allowed this data to be collected, and all the shared resources that allowed me to conduct this research.
- Ellery Worth – Thank you for your dedication, swift responses, openness to helping me with this study, and making resources available to me.
- Pete Goodman – Thank you for your insightful knowledge and data sharing which allowed me to complete this study.
- Dylan Fletcher – Thank you for saving my skin and sending emails and documents whenever I had to travel for work and forgot.
- Grace Henaghan – Thank you for your assistance and guidance with the writing of my thesis. You were invaluable and I could not have got to the end of this without you.
- To my parents, Roly and Felicity Lautenbach – Thank you for the dedication and unconditional love and patience while I completed this study. I owe all of my work ethic and conduct to your exceptional parenting, and I am nothing less than 100% certain and proud that whatever I achieve going forward is because of you.

DEDICATION

To my late brother Mark Lautenbach.

I would not be the naturalist I am today without you.
Your impact and teachings are what have taught me to love and respect nature. I love you.

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GLOSSARY

Azimuth	The direction measured from a true North reference in a clockwise direction.
CHM	Canopy Height Model: A digital representation of the height of vegetation or tree canopies above the ground surface derived from LiDAR data.
DTM	Digital Terrain Model: A 3D representation of the Earth's surface excluding vegetation and man-made features, derived from LiDAR data.
DSM	Digital Surface Model: A 3D representation of the Earth's surface including all natural and man-made features, derived from LiDAR data.
HALO	A multi-sensor system attached to a UAV known as the Harvard Animal Landscape Observatory.
LiDAR	Light Detection and Ranging: A technique used to measure objects with the use of infrared light, onboard gyroscopes and GPS.
Orthomosaic	A high-resolution, geometrically corrected set of images, e.g., RGB or thermal images, that are stitched together to create an accurately scaled map of the Earth's surface.
Photogrammetry	A method of obtaining accurate measurements and creating detailed maps of areas, typically collected through photographs taken from aircraft or drone.

Remote sensing	A method of capturing data with various devices typically from a distance and without contact using, for example, satellites, aeroplanes or drones. These devices can include, RGB cameras, radar, LiDAR thermal cameras, sonar etc.
RGB	Red-Green-Blue: refers to a colour imaging model for red, green, and blue bands of light that are captured to create true-colour images used to produce detailed visual products of landscapes or objects.
RPAS	Remotely Piloted Aerial System: A remotely operated aircraft without a human pilot on board and usually controlled autonomously.
RSF	Resource Selection Function: A statistical model used to analyse and predict the likelihood of an organism selecting specific habitat traits based on available environmental variables and observed behaviours.
UAV	Unoccupied Aerial Vehicle: Another term used for RPAS.

CHAPTER ONE
INTRODUCTION

1.1 Statement and background to the research problem

The steady decline in old-world vulture populations, including the critically endangered White-backed Vulture (WbVs), *Gyps africanus*, calls for urgent conservation efforts and a deeper understanding of their ecology (BirdLife International 2018). Suitable nesting sites are essential for the survival and reproduction of WbVs, yet information on their nesting requirements, especially related to tree physiognomy and spatial surroundings, is limited.

Existing studies suggest that WbVs exhibit species-specific nest tree preferences that vary regionally (Mundy *et al.* 1992; Monadjem *et al*. 2002; Anderson & Hohne 2007; Bamford *et al.* 2009c; Goodman & Worth 2018). However, traditional methods of measuring trees for avian research are labour-intensive and logistically challenging, making it difficult to gather precise data on tree structure and nesting sites (Avery & Burkhart 2015; Husch *et al.* 2003). The use of Light Detection and Ranging (LiDAR) technology offers a promising solution. LiDAR can provide detailed, high-resolution data on tree structure and spatial context (Lefsky *et al*. 2002; Anderson *et al*. 2006, Vierling *et al.* 2008; Davies & Asner 2014), which in turn enables researchers to enhance the efficiency and accuracy of their analyses of the relationship between vegetation structure and avian ecology (Choi *et al.* 2021; Davison *et al.* 2023; Shokirov *et al.* 2023). This study aims to leverage available LiDAR data and vulture nesting records from Karingani Game Reserve (KGR), Mozambique, to better understand WbV nesting habits and requirements.

Karingani Game Reserve is a recently protected area (established in 2008) situated in western Mozambique on the border of the Kruger National Park. The approximately 1 500 kilometre squared (km^2) reserve is a critical nesting area for WbVs with 115 known nesting sites (Goodman & Worth 2020. It is important to understand the relationship between tree structure and vulture nesting in KGR, particularly considering the potential threat posed by an increasing elephant (*Loxodonta africana*) population which may reduce the availability of suitable nesting trees (Goodman & Worth 2018). In anticipation of a resultant change in vegetation structure, a representative sample of the KGR landscape was surveyed to map the terrain and vegetation digitally using advanced LiDAR techniques. Combining LiDAR products with the existing vulture nest location data from KGR provides a unique opportunity to study the tree nest characteristics of WbVs. This can help characterise the nesting needs of WbVs in KGR and other savanna ecosystems. It can at the same time test whether using LiDAR technology in this way can provide a novel alternative to more traditional methods used to assess nest trees for various bird species.

This study thus aims to shed light on the specific nest site characteristics and preferences of WbVs within KGR and contribute to a broader understanding of vulture nesting selection across different environments, as well as evaluate whether LiDAR technology can advance or improve current methods of measuring trees for large bird ecological studies. Insights gained from this study could be crucial for developing models to identify and protect vegetation within KGR and elsewhere that possess traits important to WbVs for nesting.

1.2 Literature review

There are currently 23 extant species of vulture worldwide, 16 of them being old-world vultures that can be found throughout Africa, Europe and Asia (Mundy *et al.* 1992; Ogada *et al.* 2011). The other seven species are new-world vultures which are only found in North or South America (Ogada *et al.* 2011). As an obligate scavenger that feeds on both wildlife and livestock carrion (Mundy *et al.* 1992; Ogada *et al*. 2011; Kane *et al*. 2016), vultures are a keystone guild that play a vital role in ecosystem functioning. By devouring carcasses, they enhance nutrient cycling and dispose of animal carrion (De Vault *et al.* 2016; Craig *et al.* 2018; Plaza *et al.* 2020), lowering the risk of pathogen and disease outbreaks (Markandya *et al*. 2007; Craig *et al.* 2018; Plaza *et al.* 2020; Van Den Heever *et al.* 2021).

Old-world vultures have evolved several adaptations that assist with detecting and consuming carcasses, such as relying on keen eyesight and detection of other vultures in an area (Van Den Heever *et al.* 2021). Their large crop allows them to store enough food to last several days without eating (Botha *et al.* 2017) and their efficient soaring capabilities allow them to quickly reach carcasses, ensuring their swift removal (Van Den Heever *et al.* 2021). Moreover, strong stomach acid within the vulture's guts ensures that most pathogens and harmful bacteria are killed and unable to spread from the carcasses (Van Den Heever *et al*. 2021). In rural areas, declining vulture numbers creates an opportunity for an increased number of feral dogs and rats, which are well-known reservoirs for diseases such as rabies and bubonic plague (Baral *et al.* 2007; Marakandya *et al*. 2007; Ogada *et al.* 2011; De Vault *et al.* 2016). The transfer of these diseases to people is a particularly pertinent issue in many countries, such as India (Marakandya *et al.* 2013).

Vultures are also important from an economic and cultural standpoint by saving municipal money on expensive methods of animal carcass removal (Pomeroy 1975). In Uganda, for instance, vultures dispose of carcasses from abattoirs, saving local councils from having to use more sophisticated methods of carcass removal (Pomeroy 1975; Ogada *et al.* 2011). Vulture carcass disposal is also an important element of some religious practices that have now largely been lost due to the decline in vulture numbers, particularly in areas of Asia (Ogada *et al.* 2011). The Zoroastrian-practicing Paris community in India and Buddhists in Tibet would lay their deceased on “towers of silence” where they would rely on vultures to dispose of the human remains within minutes, a practice also known as sky burial (Subramanian 2008). A loss of vultures globally could lead to catastrophic ecological damage and threaten the direct health of humans. The increase in global epidemics and pandemics caused by zoonotic diseases (Morand & Walther 2018; Kilpatrick & Randolf 2012) heightens the need to protect and retain the ecosystem services provided by vultures to ensure a clean and healthy environment free of infected carcasses.

Of the 23 extant vulture species around the world, 14 are threatened with extinction (Ogada *et al.* 2011). The major drivers of these threats are anthropogenic such as poisoning, poaching, habitat loss, drowning in reservoirs, electrocution from power lines and, indirectly, climate change (Murn *et al.* 2002, 2017; Herholdt & Anderson 2006; Baral *et al.* 2007; Simons & Jenkins 2007; Murn & Anderson 2008; Bamford *et al.* 2009b, 2009c; Monadjem *et al.* 2012; Kane *et al.* 2016; Botha *et al.* 2017). In Asia, there has been a 95% loss of *Gyps* vulture species due to poisoning via diclofenac, a veterinary drug used as an anti-inflammatory for livestock (Ogada *et al.* 2011). The African continent has faced dramatic declines in vulture numbers too, with West Africa seeing a decrease of 95% in all vulture populations (except the Hooded Vulture [*Necrosyrtes monachus*]) in rural areas within the last 40 years (Ogada *et al.* 2011). In protected areas in Sudan, vulture numbers have fallen by 45% (Ogada *et al.* 2011) while East Africa has seen a decline of 70% in a three-year period in north-central Kenya (Ogada & Keesing 2010). The Masai Mara has also lost an average of 62% of its vultures over the past 40 years (Ogada *et al.* 2011).

Poisoning is considered the most significant driver for the decline of old-world vultures and includes both direct and indirect action. Indirect action refers to vultures being poisoned as a secondary result of farmers attempting to remove animals of conflict. These conflict animals include elephants that raid crops and carnivores that kill livestock in Africa, or wolves (*Canis spp)* and foxes (*Vulpes spp)* that interfere with human activities such as farming and hunting in Europe (Botha *et al.* 2017). Between 1992–2013, Spain recorded 185 000 animals poisoned, of which 34% were birds (Hernández & Margalida 2009; Botha *et al.* 2017), and from 1990–2007, Spain lost 294 Egyptian vultures (*Necrosyrtes monachus*) as a result of indirect poisoning (Hernández & Margalida 2009).

Direct poisoning is the result of vultures being the primary target of poisoning efforts. A significant contribution to the direct poisoning of vultures in southern Africa is ivory poaching (Roxburgh & McDougall 2012; Ogada *et al.* 2015). Vultures are valuable sentinels for anti-poaching units as their presence helps identify the location of poached animals (Roxburgh & McDougall 2012). Consequently, poachers will poison elephant carcasses to target vultures and remove them from the area to avoid carcasses being detected by law enforcement (Ogada *et al.* 2015). Ivory poaching has accounted for one-third of recorded vulture poisonings since 1970, and in 2013 alone, 1 642 vultures were recorded as poisoned due to ivory poaching-related incidents in 6 African countries (Ogada *et al.* 2015).

In many African countries where traditional medicine is still in high demand, vultures are poached for their body parts (Ogada *et al.* 2012; McKean *et al.* 2013; Ogada 2014; Botha *et al.* 2017; Mashele *et al.* 2021). Traditional healers use vulture heads, beaks, feet, vertebrae and hearts (Cunningham & Zondi 1991; McKean 2004), or a combination with plants, to make Traditional Medicine, that when ingested is believed to give clairvoyant abilities and promote good health and dreams (McKean *et al*. 2013; Mashele *et al.* 2021). In 2012, a total of 191 vulture carcasses were discovered around a single poisoned elephant carcass inside Gonarezhou National Park, Zimbabwe (Groom *et al.* 2013), all with the top half of their beaks removed. In South Africa, it is estimated that R1.2 million per year is generated through the illegal trade of vultures (Mashele *et al.* 2021).

Another concern for vulture populations, and in particular tree-nesting vultures, is the increasing number of elephants in protected areas (Vogel *et al.* 2014; Rushworth *et al.* 2018). WbV nests are mostly found in protected areas as they are sensitive to landscape change and anthropogenic pressure (Murn *et al.* 2002, 2017; Herholdt & Anderson 2006; Simons & Jenkins 2007; Murn & Anderson 2008; Bamford *et al.* 2009b, 2009c; Monadjem *et al.* 2012; Kane *et al.* 2016; Botha *et al.* 2017). Elephants are ecosystem engineers that shape and change vegetation structure, which in turn changes species composition and increases landscape heterogeneity (Vogel *et al.* 2014). An increase in elephant numbers is directly correlated with a decrease in large trees within protected areas (Shannon *et al.* 2008; Kalwij *et al.* 2010; Vogel *et al.* 2014; Cook *et al.* 2023; Nuttall-Smith & Parker 2023; O'Conner *et al.* 2023), with Asner & Levick (2012) finding that elephants are the main driver of tree fall rates in of savannas in Kruger National Park. This loss of large trees in protected areas decreases the number of available suitable nesting trees for WbVs (Rushworth *et al.* 2018).

The WbV is a tree-nesting vulture and is one of nine species of the old-world vultures found in southern Africa (Mundy *et al.* 1992). Although it is the most abundant and widely distributed of the vulture species in southern Africa, with an estimated 270 000 individuals surviving globally (Murn *et al.* 2002; Mundy *et al.* 1992; Bamford *et al.* 2009b; BirdLife International 2021), it is categorised as critically endangered on the International Union for Conservation of Nature (IUCN) red list and is in severe decline (IUCN 2021). Over the last 48 years, WbVs have experienced a 90% decline in numbers within unprotected landscapes in West Africa (Thiollay 2006b). The Masai Mara National Reserve in Kenya recorded a 52% decline of WbVs from 1988 to 2005 (Virani *et al*. 2011). In the Khwai and Linyati areas of north-central Botswana, there was a 53% decline in nesting pairs between 2006 and 2017 (Leepile *et al.* 2020). By the early 2000s, there were an estimated 40 000 WbV individuals left within southern Africa (Anderson 2004). McKean *et al*. (2013) suggest that if current levels of exploitation continue in South Africa, WbVs could become locally extinct by 2034 or sooner.

WbV activity and distribution are closely associated with their nesting behaviour as they spend most of the year near and around their nests (Mundy *et al.* 1992; Anderson 2004; Murn & Anderson 2008). Nests of WbVs are roughly 1 metre (m) in diameter and made of large sticks that are lined with grass and leaves (Mundy *et al.* 1992; Bamford *et al.* 2009b). WbV nests are typically found in large dry trees mostly of the *Senegalia* and *Vachellia* (formally *Acacia*) species (Mundy *et al.* 1992; Anderson 2004) and are known to nest in loose colonies (Mundy *et al.* 1992; Anderson 2004; Murn & Anderson 2008) with one nesting pair per tree. However, there have been observations of two nests in one tree (Bamford *et al.* 2009b). In southern Africa, nesting usually begins between May and June when one egg is laid, and the chicks fledge between late October to December (Mundy *et al.* 1992; Bamford *et al.* 2009b). White-backed Vultures can cover large distances to acquire food and resources, and have been recorded to travel up to 260 kilometres (kms) away from their nest in a single day when they do not have a nestling (Kane *et al.* 2016).

The quality and structure of the habitat play an important role in bird breeding site selection (William *et al.* 2007). Birds live and move in a 3D space, so the structure of vegetation influences all aspects of their ecology (Davies & Asner 2014). A review of 23 avian studies found a “positive relation between bird richness and abundance (including activity or occurrence) and canopy structural variability and complexity, vertical tissue distribution, and overall height” (Davies &

Asner 2014). However, these relationships can change across different habitat types, such as grasslands where taxonomic composition of vegetation plays a more important role for avian assemblages than the configuration and structure of vegetation (Rotenberry 1984).

Nest site selection is also related to vegetation structure, with the height at which birds nest and the foliage cover they choose to nest in playing an important role in the selection of preferred nesting sites (Walsberg 1985; Gōumark *et al*. 1995). Nesting high above the ground ensures the best possible chance of going undetected by predators (Gōumark *et al.* 1995). Selecting higher canopy cover and foliage density also increases nest site protection from wind and rain, which can limit heat loss during the night and protect against excessive heat radiation during the day (Walsberg 1985).

All birds, including WbVs must, however, face the consequences of their habitat and nest-site selection decisions (Jones 2001). Optimal foraging theory suggests that birds choose habitats with dense resources that provide heightened energy. The density of these resources means that the energy gained through foraging for resources outweighs the energy lost from the act of foraging itself (Stillman *et al.* 2000). Feedback for foraging decisions is generally immediate for birds, as they will quickly amend their course of action if their energy inputs and outputs become unbalanced. Typically, this means moving to a more suitable foraging site (William *et al.* 2007). In contrast, the feedback rate for breeding is much slower and bears much higher risk as the consequences for selecting an unsuitable breeding site will only be evident once breeding (or chick-rearing) has either failed or succeeded (Orians & Wittenberger 1991; Kristan *et al.* 2007). Information available to birds comes from past experiences or current cues of habitat quality, and future conditions about sites cannot be observed directly, such as predation or changes in food availability (William *et al.* 2007). Current cues of habitat suitability include information obtained via observation of conspecifics that have successfully occupied and nested in an area and thus formed colonies (Ahlering & Faaborg 2006).

WbVs show peculiar nesting behaviour with specific nesting sites and nest tree selection that varies regionally. For example, in southern Kruger National Park, Kemp & Kemp (1975) found that WbVs tend to favour *Senegalia nigrescens* for nesting. However, Monadjem (2003) compared tree species selected to the availability of tree species along rivers in Swaziland and found that *S. nigrescens* was not utilised. In more arid regions of South Africa, such as the Kgalagadi Transfrontier Park, WbVs tend to nest predominantly in *Vachellia erioloba* with a few nests recorded in *Albizia anthelmintica* to the north-east of Grootbrak, Botswana, where *Albizia* species were the tallest tree species in the area (Herholdt & Anderson 2006). White-backed Vultures have also been recorded to nest on top of electric pylons in the Kimberly area of the Northern Cape and Free State provinces of South Africa, as well as in Tsavo National Park, Kenya (Anderson & Hohne 2007). In KGR, just to the east of Kruger National Park and across the Lebombo mountain range in Mozambique, WbVs seem to favour mostly *Balanites maughamii* with some records of *Senegalia welwitschii* and *Senegalianigrescens* (Goodman & Worth 2018).

Literature on vulture nest site selection, such as those mentioned above, mostly focuses on the tree species selected and what surrounding variables affect vulture decision-making for the areas they choose to nest in over a wider scale (>1km), such as anthropogenic pressure or the availability of water and food (Bamford *et al.* 2009b, 2009c). Most literature suggests that WbVs tend to select the tallest trees in an area to nest in, which would make the height of a tree a significant variable when selecting nest sites and habitats. Chomba & Simuko (2013) recorded that WbVs in Lochinvar National Park on the Kafue flats in Zambia selected nest sites at a mean height of 16m and suggested that this could be to avoid predators or fires during the dry season. White-backed Vultures' selective nesting habits within different regions leave them vulnerable to the effects of habitat degradation and change from anthropogenic pressures and loss of suitable habitat (Bamford *et al.* 2009b, 2009c; Anderson & Hohne 2007). However, there appears to be some adaptive qualities that allow them to nest in man-made structures, such as the electric pylons (Anderson & Hohne 2007). Studies focusing on the direct structural attributes of selected WbV nesting trees have not been conducted, and literature discussing the immediate spatial characteristics (<1km) surrounding nesting trees is also lacking.

1.2.1 Existing relevant research for avian nest site selection

This study will analyse different structural traits of trees that may influence the decision-making of WbVs in their nest site selection. First, as discussed, multiple papers have suggested that the height of a tree is crucial for the nesting success and survival of large tree-nesting birds in Africa, including WbVs (Murn & Anderson 2008; Bamford *et al*. 2009a; Botha *et al.* 2017; Mundy *et al.* 1992; Anderson 2004). Many other large bird species rely on high trees for nesting such as the African Fish Eagle (*Haliaeetus vocifer*) and the Martial Eagle (*Polemaetus bellicosus*) (Brown *et al*. 1982). These raptors prefer tall trees because they offer strategic advantages, such as a broad field of view for spotting prey and early detection of potential threats (Sergio *et al*. 2003a). Elevated nests are also less detectable to ground predators, thereby increasing the chances of offspring survival (Blumstein 2006).

This study will explore the canopy area of potential nesting trees, as large canopies are essential for providing adequate shelter with their larger surface area and stronger support. This protects from harsh weather conditions, such as strong winds and heavy rains, ensuring the safety of nests and chicks (Stutchbury & Morton 2001). Larger canopies might also provide access for comfortable take-off and landing, accommodating WbVs' larger size and weight, as has been found for the Cinereous Vulture (*Aegypius monachus*) (Moreno-Opo *et al*. 2012; Martin & Li 1992).

The roughness of a tree's canopy, characterised by variation in height and density of the foliage and branches, is another important feature for nesting. Canopy roughness creates microhabitats that meet the specific nesting needs of different raptor species (Bradbury *et al*. 2005; Hughes 2011a). For example, the Verreaux's Eagle (*Aquila verreauxii)* often selects dense inner branches for better concealment from predators, while the African Harrier-Hawk (*Polyboroides typus*) seems to prefer more open, outer-branches that provide easier access to the nest (Hughes 2011b). This structural complexity also influences the microclimatic conditions within the nest, such as temperature and humidity, which are crucial for the proper development of eggs and chicks (Van Balen 1973). For example, the critically endangered Red-headed Vulture (*Sarcogyps calvus*) in Southeast Asia often selects nesting sites with dense foliage to protect the nest from extreme temperatures (Cuthbert *et al.* 2006).

Little research has been done on the location or position of raptor nests within the canopy of a tree in relation to exposure to potentially harmful environmental elements such as wind or radiation, hence its inclusion in this study. From the few studies available, it has been suggested that open nests on top of tree canopies tend to be situated on the side with most protection from prevailing winds or excessive sun in warmer environments (Mainwaring *et al*. 2015). Literature from other avian communities suggests that selecting specific areas within a tree's canopy can impact nesting success by influencing microclimatic conditions (Salaberria *et al*. 2014), predator protection (Kasprzykowski 2008), and the structural characteristics of the nesting habitat (Blumstein 2006; Sergio *et al.* 2003b; Newton & Marchesi 2003).

The distance to water from a nest is also important to consider as it directly impacts avian foraging efficiency and reproductive success. Proximity to water ensures that birds have easy access to essential resources such as food and hydration, which is vital for feeding their young and maintaining their own health during the breeding season (Smith & Reynolds 2007; Jones & Reynolds 2008). However, some birds choose to nest further away from water to avoid high densities of predators that are often more abundant near water sources (Chalfoun & Schmidt 2012; Fontaine & Martin 2006).

As with location of nests in tree canopies, little research has been conducted on the vegetation cover and height surrounding vulture nesting trees. However, existing studies of vegetation cover and height for other bird species suggests that the height of surrounding trees is a critical factor in avian habitat selection, nesting success, and predator–prey dynamics (Martin & Roper 1988; Dawson *et al*. 2005). Research for other species has found that birds have increased breeding success when selecting trees that have more coverage nearby (<100 m), such as Cinereous vultures (Moreno-Opo *et al.* 2014). Birds often choose nesting sites based on the vertical structure of vegetation, with taller trees offering significant advantages (Martin & Roper 1988). One such advantage is better nest concealment from ground predators and a strategic lookout point for spotting threats, allowing for early evasive action (Martin & Roper 1988; Lima 2009). Additionally, nesting in taller trees provides unobstructed flight paths to and from nests, aiding in avoiding collisions and enhancing escape responses (Bruderer & Boldt 2011).

Understanding how large tree-nesting birds interact with tree structure and the nesting tree's surrounding area helps researchers predict nesting preferences and habitat requirements for these species, aiding conservation efforts. For instance, identifying the characteristics of preferred nesting trees can inform habitat management practices, such as the preservation of specific tree species or the maintenance of savanna ecosystems that provide suitable nesting sites. In savanna ecosystems, the preservation of large, mature trees that can support the nesting requirements of species such as the WbV could prove essential (Monadjem *et al.* 2012). However, more information on the types of large trees selected, and whether characteristics of the surrounding area are also of consequence, is needed before detailed conservation planning can be implemented.

1.2.2 Current vegetation measurement methodology

Studying large raptor nesting characteristics involves a series of steps that require different approaches and tools depending on the type of nesting behaviour and nests constructed. In this instance, WbVs prefer to nest in trees (Mundy *et al.* 1992). Traditional methods used to measure tree structures such as canopy height, canopy area, and canopy roughness usually involve direct field measurements using various handheld tools (Smith *et al.* 2014; Parker *et al.* 2004; Avery & Burkhart 2015; Husch *et al.* 2003). To measure tree height, a clinometer is often used which allows users to measure angles from a distance, and by determining the angle to the top of the tree and the distance to the tree, height can then be calculated using trigonometric principles (Avery & Burkhart 2015; Van Laar & Akça 2007). Another method involves using a hypsometer or a measuring pole for smaller trees (Husch *et al*. 2003). These traditional methods are tried and tested, and may sometimes be the only method available to measure large trees. However, these methods also come with challenges and may cause inconsistencies through human error. As measuring tree height is vital in ecological study, finding new, easier, and more accurate means to gather these data will prove beneficial.

Canopy area is estimated by measuring the spread of the tree's branches. This process involves measuring the distance from the trunk to the edge of the canopy at several points around the tree and calculating the area, often approximated as a circle or an ellipse (Smith *et al.* 2014). An alternative method is using a rangefinder for more precise distance measurements (Husch *et al.* 2003). Canopy analysers and hemispherical photography can also be used for estimating canopy coverage and leaf area index, characteristics considered critical for understanding light penetration and photosynthesis (Welles & Cohen 1996).

Canopy roughness, referring to the variability in the height of the canopy surface, is usually assessed through visual inspection and detailed measurements of branch and foliage distribution. This might involve using ladders or climbing equipment to reach various parts of the canopy and record measurements (Spies *et al.* 1990) or noting visual estimations of canopy cover which could become subjective (Parker *et al.* 2004). Spherical densitometers can also be employed to estimate canopy cover and structure (Lemmon 1956).

These traditional methods, while providing foundational data for forest management, ecological research, and conservation efforts, are labour-intensive, time-consuming, and potentially dangerous. Measuring tree structures often involves climbing trees or using ladders, which poses significant risks to researchers (Avery & Burkhart 2015; Husch *et al.* 2003). The manual collection of data is also susceptible to human error and limited in spatial coverage, making it challenging to gather precise and comprehensive information on tree structure and nesting sites on a large scale (Larjavaara & Muller-Landau 2013). The introduction of advanced remote sensing technologies such as LiDAR and high-quality optical imagery have revolutionised this process by offering a safer, more efficient, and accurate means of collecting high-resolution data on tree structure and spatial context, thereby enhancing the effectiveness of ecology research and conservation efforts (Lefsky *et al.* 2002; Anderson *et al.* 2006; Hancock *et al.* 2017; Rudge *et al.* 2021; Allen *et al.* 2022).

1.2.3 LiDAR and photogrammetry

A LiDAR is a form of remote sensing that emits its own infrared light to measure the distance between the sensor and the target object (Davies & Asner 2014). Using a combination of a laser rangefinder, a global positioning system (GPS), and an inertial measurement unit (IMU) (Haugerud *et al.* 2003; Hodgson *et al.* 2003), it is possible to measure the precise spatial position of each laser pulse (Van Den Eeckhaut *et al.* 2006; Gold 2004). The combination of many such pulses creates a “point cloud” of data that can be converted into accurately constructed 3D models of terrain and vegetation across landscapes (Haugerud *et al.* 2003; Hodgson *et al.* 2003; Gold 2004; Davies & Asner 2014).

LiDAR has become an important method to measure landscape structure due to its consistent and reliable high-accuracy measurements within 3D space (Davies & Asner 2014). LiDAR has proven effective even in rainforest archaeological studies because the laser light can penetrate the dense forest canopy, reaching the ground beneath (Heckenberger *et al.* 2008; Dandois & Ellis 2010; Canuto *et al.* 2018). Such light penetration creates detailed topographical maps, allowing researchers to view hidden structures such as ancient roads, buildings and terraces that are usually covered by vegetation (Heckenberger *et al.* 2008). The high-resolution data generated helps archaeologists document sites with high accuracy and efficiency, revealing complex urban planning and extensive agricultural systems of ancient civilizations (Canuto *et al*. 2018).

The 3D structure of vegetation is an important attribute that drives animal community assemblage, behaviour and distribution (Dunlavy 1935; MacArthur & MacArthur 1961; Muller *et al*. 2010), and LiDAR measurements have been found to provide more accurate measurements of vegetation structure than most traditional methods (Ganz *et al.* 2019; Hancock *et al.* 2017). Because LiDAR products generate three-dimensional datasets of vegetative structures at large volumes, they are beneficial for understanding resource use and landscape-based decision-making of birds and mammals (Davies & Asner 2014). For instance, a study by Davies *et al.* (2019) integrated ground and helicopter nest surveys with high-resolution measurements of forest canopy structure using airborne LiDAR to understand orangutan nest site selection in the degraded forests of the Lower Kinabatangan region of Malaysian Borneo. Their findings showed that orangutans preferred nesting in areas with tall and uniformly high canopies. LiDAR was instrumental in providing detailed 3D models of the canopy, identifying gaps and emergent tree crowns, and facilitating multi-scale analysis.

Resource and habitat selection studies based on LiDAR products have been conducted for a wide variety of species over variable scales, ranging from birds (Goetz *et al.* 2007; Boucher & Davies 2023) to great apes (Davies *et al.* 2017, 2019) and lions (Davies *et al.* 2016). As such, LiDAR technology has proven invaluable in ecological research within African ecosystems. In African savannas, LiDAR combined with hyperspectral imagery has been utilised to map tree species distributions at ecosystem scales (Holmgren *et al.* 2017), achieving high accuracy by addressing challenges such as reflectance anisotropy and integrating pixel- and crown-level data. For example, Colgan *et al*. (2012) demonstrated the effectiveness of using LiDAR in combination with hyperspectral data as these technologies were able to identify a savanna tree's species with 76% confidence. This approach has enabled detailed mapping and monitoring of biodiversity and ecosystem functions, providing crucial data for conservation efforts.

Additionally, studies have shown how vegetation structure, assessed through LiDAR, influences predator–prey interactions. Davies *et al.* (2016) examined the effects of vegetation structure on the location of lion kill sites in African thickets. Their research highlighted that lions in denser vegetation areas selected different prey species compared to those in more open environments, underscoring the importance of vegetation structure in shaping ecological dynamics and predator–prey relationships. This study used high-resolution LiDAR data to map vegetation density and understand its impact on lion hunting behaviour, demonstrating the capability of LiDAR to provide insights into complex ecological processes.

Furthermore, LiDAR and hyperspectral data have been effectively used to estimate aboveground biomass in African tropical forests. Vaglio Laurin *et al*. (2014) integrated LiDAR and hyperspectral data to estimate aboveground plant biomass, which is critical for understanding forest structure and carbon storage. This research highlights the potential of LiDAR to contribute to global carbon cycle studies and forest management strategies by providing accurate measurements of forest biomass.

LiDAR data allows for the production of Canopy Height Models (CHM) to produce measurements of a tree's structure and surrounding spatial context. To produce a CHM, raw LiDAR data are first filtered to separate ground points from non-ground points using algorithms such as the Cloth Simulation Filter (Zhang *et al*. 2003). From these ground points, a Digital Terrain Model (DTM) is generated, representing the bare Earth surface (Chen *et al*. 2007). Simultaneously, a Digital Surface Model (DSM) is created using all the points, including buildings, vegetation, and other objects on the Earth's surface (Lefsky *et al.* 2002). The CHM is then derived by subtracting the DTM from the DSM, resulting in a model that depicts the height of vegetation above the ground (Popescu *et al.* 2002). Each pixel in the CHM grid represents a height value in metres, providing a detailed spatial distribution of vegetation height. The high-resolution LiDAR data ensures accurate height measurements by capturing three-dimensional information about terrain and vegetation (Anderson *et al*. 2006). CHMs are crucial for ecological and forestry applications, such as assessing forest biomass, monitoring vegetation health, and mapping habitat structures (Luck *et al.* 2020).

1.2.4 Orthomosaics

An orthomosaic is a detailed, geospatially corrected image created by combining multiple photographs taken from an aerial view, such as from drones. Orthomosaics are used in several industries including cartography, agriculture, and ecology to create accurate maps and analyse land use and features (Sona *et al*. 2014; Smith & Vericat 2015). Orthomosaics are particularly beneficial for ecological research as they offer detailed and accurate spatial information, which is essential for mapping habitats, monitoring vegetation health, and assessing land cover changes (Turner *et al*. 2015). The high resolution and true colour representation of RGB orthomosaics allows for precise identification of different vegetation types and assessment of ecological conditions over large areas, facilitating informed conservation and management decisions (Kerr & Ostrovsky 2003).

A series of steps must be followed to create an orthomosaic from aerial imagery to ensure accurate and georeferenced results. Initially, aerial images are captured using a camera mounted on an aircraft or drone, ensuring sufficient overlap between consecutive images to facilitate stitching (Haala *et al.* 2010). These images are then processed using photogrammetric software that aligns them by identifying common features and performing bundle adjustments to refine the camera positions and orientations (Colomina & Molina 2014). The next step involves generating a Digital Elevation Model (DEM) to account for terrain variations, which is crucial for rectifying image distortions caused by changes in topography (Remondino *et al.* 2014). Using the DEM and refined camera parameters, the individual images are orthorectified, correcting for any geometric distortions and ensuring uniform scale across the entire mosaic (Westoby *et al.* 2012). Finally, the orthorectified images are stitched together to form a seamless Red-Green-Blue (RGB) orthomosaic, providing a high-resolution, georeferenced map of the surveyed area (Leberl *et al.* 2010).

Seventeen circles with 2.5km radii that were evenly distributed across KGR for sufficient landscape representation were surveyed to map the terrain and vegetation digitally using advanced LiDAR and RGB sensors. Combining these LiDAR and RGB data with existing vulture nest location data provides a unique opportunity to study the nest tree characteristics of WbVs. This research can help characterise the nesting preferences of WbVs in savanna ecosystems while simultaneously testing whether using LiDAR technology in this way can provide a novel alternative to more traditional methods used to assess nest trees.

1.3 Significance of the research

WbV numbers are declining across the world due to a loss of habitat, poisoning by people, and other anthropogenic pressures (Murn *et al*. 2002, 2017; Herholdt & Anderson 2006; Simons & Jenkins 2007; Bamford *et al*. 2009b, 2009c; Monadjem *et al*. 2012; Kane *et al*. 2016). White-backed Vultures are the most abundant vulture species in southern Africa but have been categorised as critically endangered by the IUCN. This research can add valuable data to understanding vulture ecology and nesting behaviour, which will assist with identifying suitable habitats to prioritise for vulture conservation. Furthermore, this research will contribute to BirdLife South Africa's vulture database and, with the involvement of KGR management, the reserve can be listed as a vulture safe zone. Vulture safe zones are protected or private tracks of land that are dedicated to addressing the key factors that threaten vulture existence, such as using lead-free ammunition, modifying water reservoirs to prevent vultures from drowning, protecting breeding vultures from disturbance, banning poison used for conflict animal control, and creating visible electric pylons to avoid collision and electrocution, to name a few (BirdLife South Africa n.d.). This research project will be submitted as a publication of an article(s) in a peer-reviewed journal.

1.4 Research questions

1. What are the structural and taxonomic characteristics of trees used for nesting by WbVs in KGR and can this be determined using LiDAR and orthomosaic imagery?
2. What are the spatial characteristics of WbV nest locations across a range of spatial scales within KGR and can LiDAR and RGB imagery be utilised to answer this question?

1.5 Aims and objectives of the research

- To determine the structural and taxonomic features of trees utilised as nesting sites by White-backed Vultures in Karingani Game Reserve using LiDAR and RGB imagery.

- To determine the spatial characteristics of White-backed Vulutres nesting tree locations within Karingani Game Reserve at a range of spatial scales using LiDAR and RGB imagery.

CHAPTER TWO
METHODS AND MATERIALS

2.1 Site description

KGR is situated in south-western Mozambique (24°15'14.7"S 32°03'57.5"E) and shares a 75km boundary with Kruger National Park to its west, just south of Limpopo National Park (Fig 2.1). The system is semi open to Kruger national park, as the boundary fence between the two is severely damaged in some parts. It is the largest privately managed area in Mozambique and the Greater Limpopo Transfrontier Conservation Area (GLTFCA), covering 1 443.8km^2.

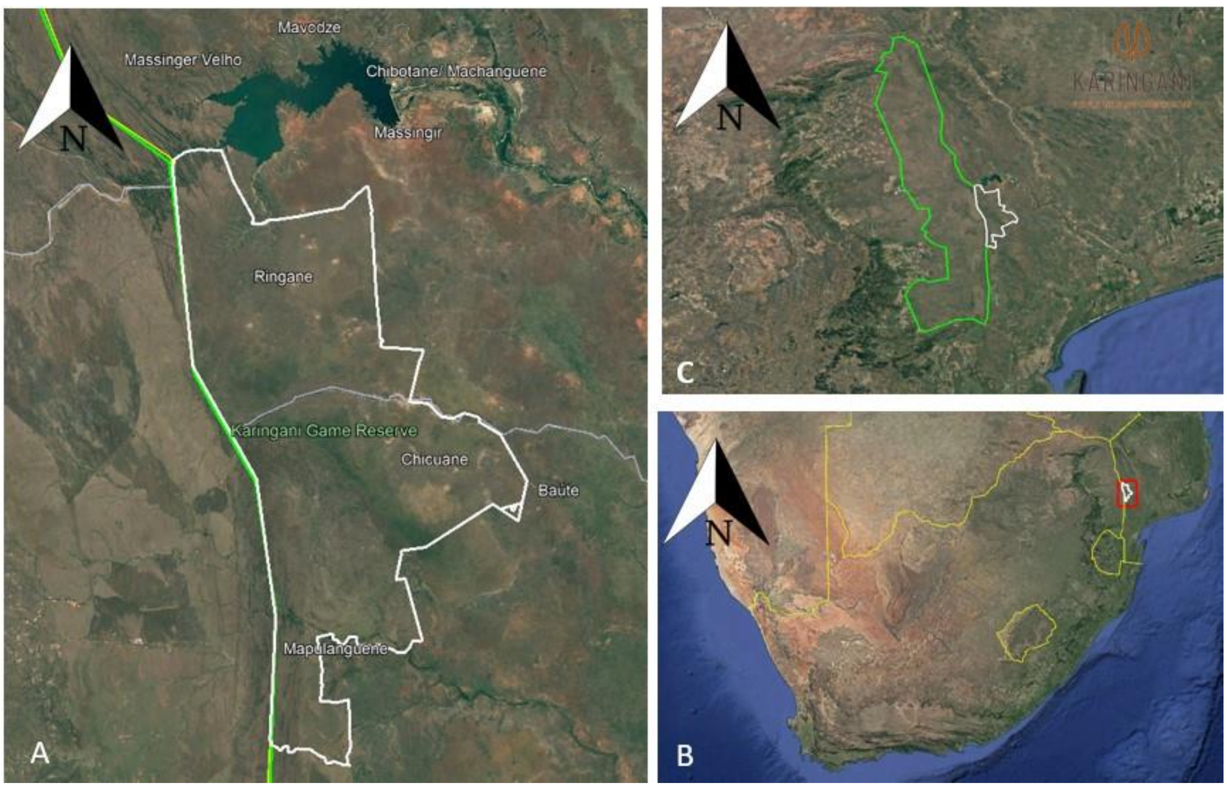

Figure 2.1: A represents the boundaries of Karingani Game Reserve in Mozambique (bright white line). The grey line running horizontally through the centre of the park represents the Gaza province (north) and Maputo province (south) divide. B shows the location of KGR within southern Africa, highlighted by a red rectangle represents the position of Karingani in relation to Kruger National Park in South Africa

KGR experiences a semi-arid climate with a dry season from April to October and a wet season from November to March. Eighty percent of the mean annual rainfall falls during the wet season, with the south-east receiving approximately 645 millilitres (mm) annually and the north-west approximately 486mm. Temperatures range between 14.5ºC to 38.2ºC throughout the year (Fig 2.2).

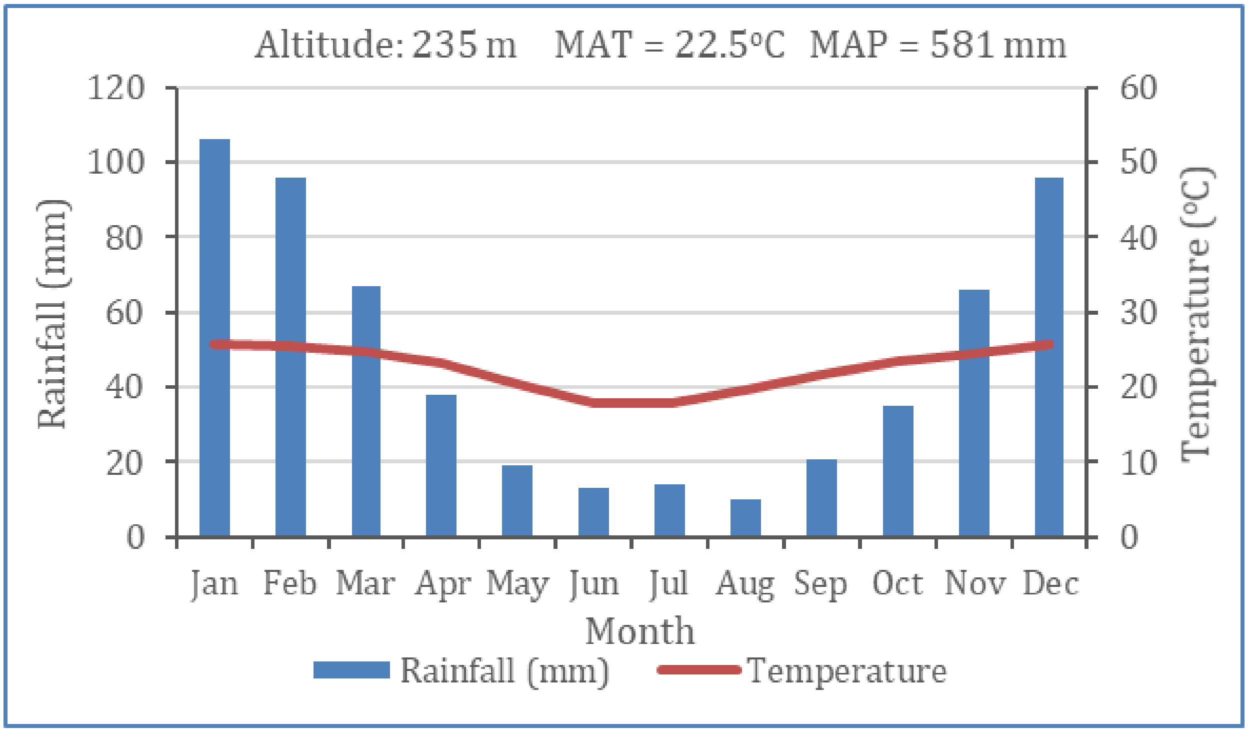

Figure 2.2: Average monthly rainfall and temperature for Karingani Game Reserve (Goodman & Worth 2020).

Approximately 62% of the park consists of fine, mostly white, aeolian sands that are well-drained and low in nutrients (Fig 2.3). Erosion has exposed calcareous gravel beds on about 18% of the surface, characterised by clay-rich soil with medium to high nutrient levels (Goodman & Worth 2020). Deeper erosion in valleys has revealed nutrient-rich mudstones with high clay content. The Lebombo Mountain Range on the western boundary of the park comprises 19% of the area and features volcanic rhyolites and basalts from the Karoo period, resulting in shallow, nutrient-rich clay soils on ridges and deep, dark clay soils on plains (Goodman & Worth 2020). Different soil types are often associated with certain vegetation structures and nutrient availability, which could influence the availability of suitable nesting trees or other habitat features (Bamford *et al*. 2009b).

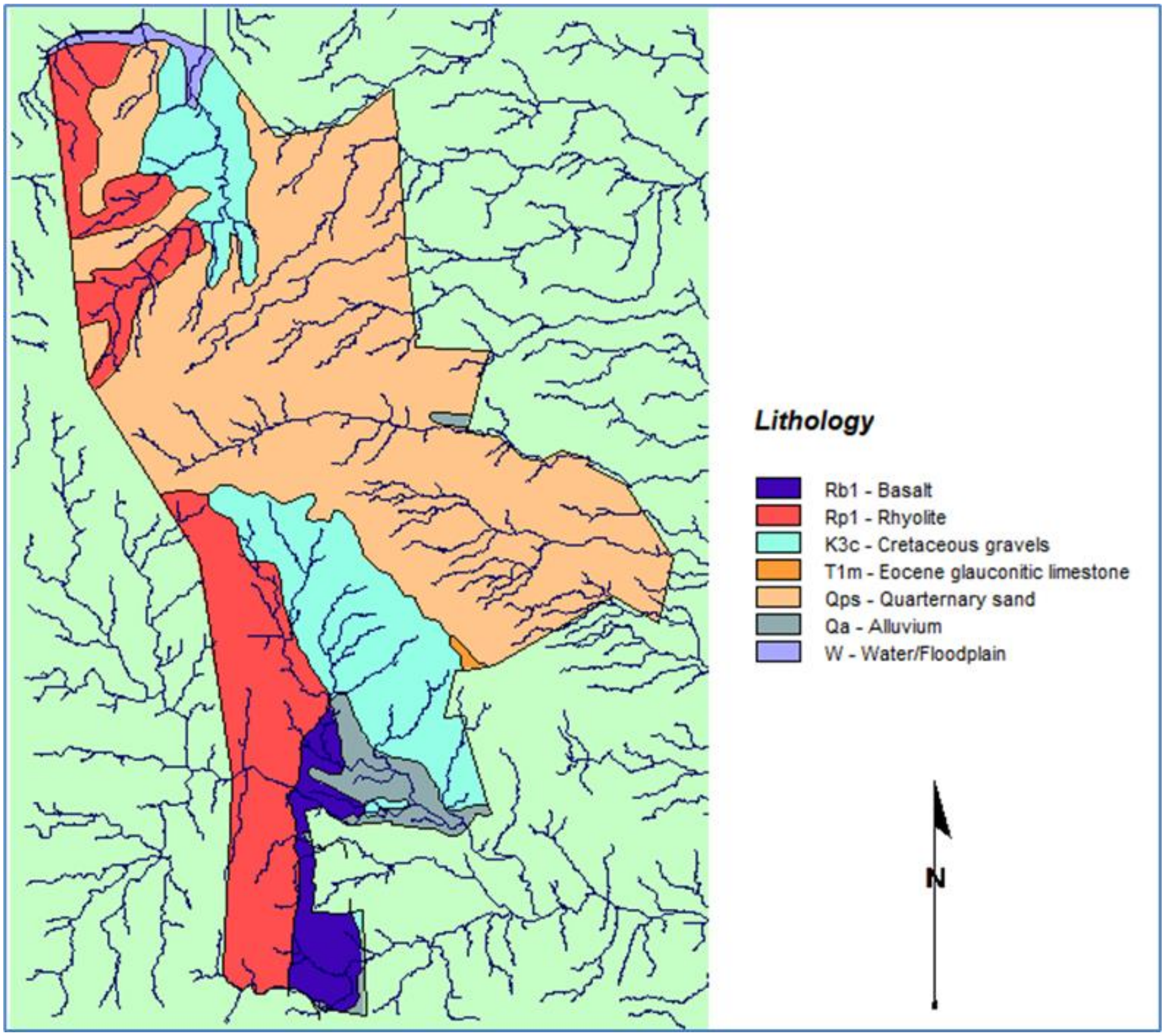

Figure 2.3: A map of the predominant geological soil distribution across Karingani Game Reserve and the perennial and non-perennial drainage lines in and around the reserve (Goodman & Worth 2020).

Phytogeographically, KGR falls on the boundary between the Zambezian Regional Centre of Endemism and the Maputaland-Pondoland Biodiversity Hotspot. Karingani Game Reserve's location along the tropical to subtropical climate gradient, combined with its variety of substrates, including rocky terrain, medium and fine sands, and heavy montmorillonite clays, has resulted in highly diverse vegetation (Fig 2.4), both in structure and species richness (Goodman & Worth 2020). The vegetation consists of, among others, savanna sandveld, pumbe sand thicket and shrub, mopane woodland, and open savanna.

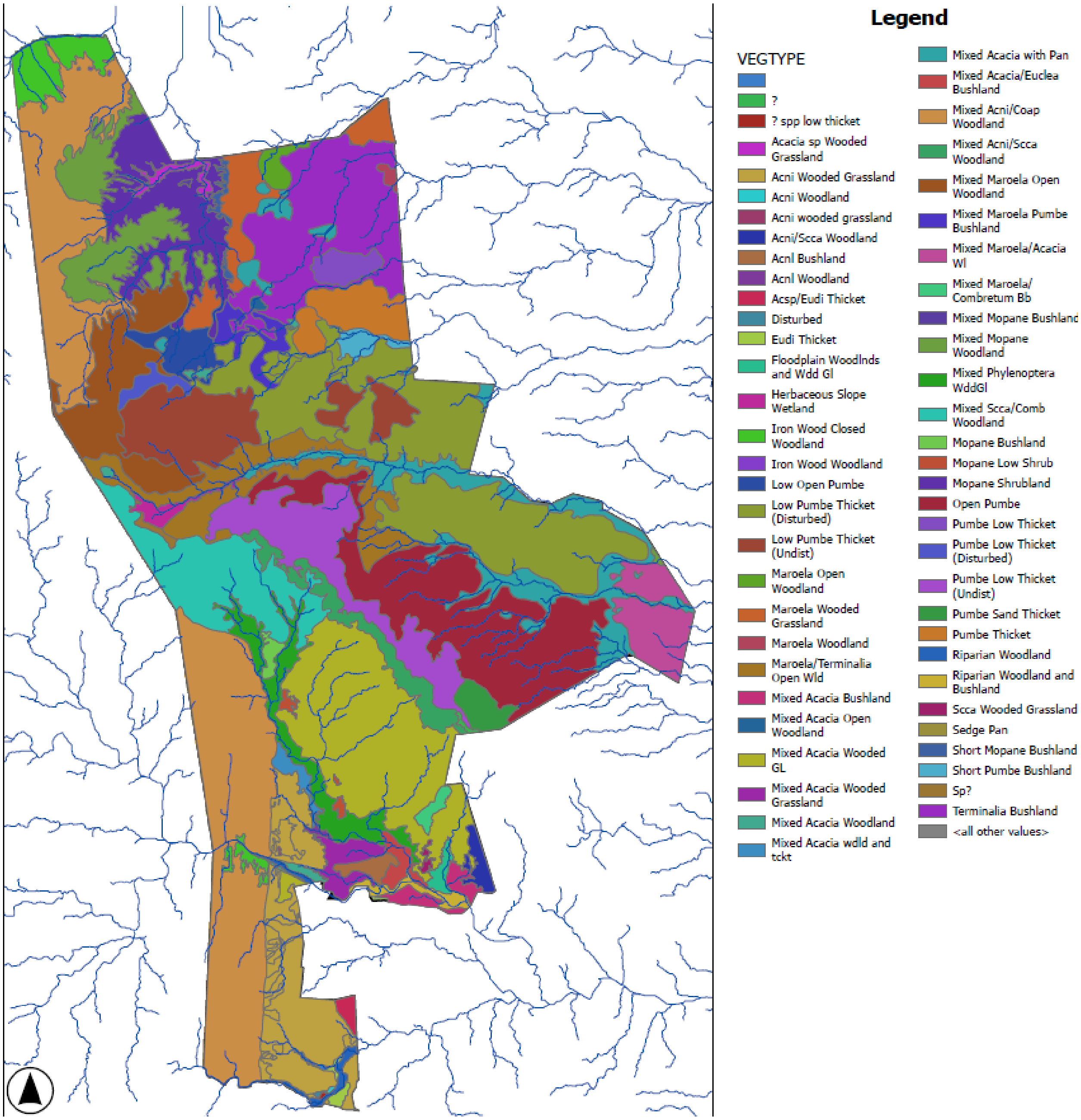

Figure 2.4: Map of vegetation types across Karingani Game Reserve (Goodman & Worth 2020).

Wildlife numbers in the park are comparatively low due to overharvesting during the Mozambique Civil War from 1977 to 1992. However, since establishment in 2008, KGR has seen a marked increase in the elephant population with a 2019 population estimate exceeding 360 individuals. These elephant numbers continue to rise annually at roughly 30% per annum (Goodman & Worth 2020). Sixty-five mammal species, including four large carnivores and 18 small to large herbivores available as prey have been recorded (Table 1).

Table 1: List of recorded large mammals in Karingani Game Reserve as of 2021 (from Goodman & Worth 2021).

Karingani Game Reserve, Large Mammal List (2021)		
Order	**Species**	**Common Name**
Hydracoidea 1	*Procavia capensis*	Rock Hyrax
Proboscidea 1	*Loxodonta africana*	Savanna Elephant
Tubulidentata 1	*Orycteropus afer*	Aardvark
Primates 4	*Papio ursinus*	Chacma Baboon
	Galago maholi	Southern Lesser Galago
	Otolemur crassicaudatus	Thick tailed Galago
	Chlorocebus pygerythrus	Vervet Monkey
Rodentia 4	*Hystrix africaeaustralis*	Cape Crested Porcupine
	Paraxerus cepapi	Smith’s Bush Squirrel
	Pedetes capensis	Southern African Springhare
Lagomorpha 1	*Lepus saxatilis*	Scrub Hare
Carnivora 25	*Proteles cristatus*	Aardwolf
	Civettictis civetta	African Civet
	Aonyx capensisa	African Clawless Otter
	Lycaon pictus	African Wild Dog
	Mungos mungo	Banded Mongoose
	Otocyon megalotis	Bat eared Fox
	Canus mesomelas	Black backed Jackal
	Caracal caracal	Caracal
	Acinonyx jubatus	Cheetah
	Helogale parvula	Dwarf Mongoose
	Genetta maculata	Large spotted Genet
	Panthera pardus	Leopard
	Panthera leo	Lion
	Atilax paludinosus	Marsh Mongoose
	Mellivora capensis	Honey Badger
	Leptailurus serval	Serval
	Canis adustus	Side striped Jackal
	Herpestes sanguineus	Slender Mongoose
	Genetta genetta	Small spotted Genet
	Crocuta crocuta	Spotted Hyena
	Ichneumia albicauda	White tailed Mongoose

	Felis silvestris *Ictonyx striatus*	Wildcat Zorilla
Pholidota 1	*Smutsia temminckii*	Ground Pangolin
Perissodactyla 3	*Diceros bicornis minor* *Equus quagga* *Ceratotherium simum*	Black Rhinoceros Plains Zebra White Rhinoceros
Cetartiodactyla 24	*Syncerus caffer* *Tragelaphus scriptus* *Potamochoerus larvatus* *Sylvicapra grimmia* *Tragelaphus oryx* *Hippopotamus amphibius* *Phacochoerus africanus* *Connochaetes taurinus* *Tragelaphus strepsiceros* *Aepyceros melampus* *Oreotragus oreotragus* *Cephalophus natalensis* *Tragelaphus angasii* *Hippotragus niger* *Raphicerus sharpei* *Giraffa camelopardalis* *Redunca arundinum* *Raphicerus campestris* *Nesotragus moschatus* *Kobus ellipsiprymnus*	African Buffalo Bushbuck Bushpig Common Duiker Common Eland Common Hippopotamus Common Warthog Common Wildebeest Greater Kudu Impala Klipspringer Natal Red Duiker Nyala Sable Antelope Sharpe's Grysbok Southern Giraffe Southern Reedbuck Steenbok Suni Waterbuck

KGR has few sources of permanent water. The most notable source is the Massingir Dam situated at the northern boundary of the park and the Nwanetsi River near the southern boundary (Fig 2.5). The northern and southern regions are drained by the Olifants and Nwanetsi Rivers respectively, while the central section of the park is drained to the east by various shallow valleys. The most prominent of these drainage lines is the Mazimechopes River which drains the centre of the reserve (Fig 2.5). Besides these rivers and streams, a dominant feature of KGR's hydrology is the numerous small internally drained pans associated with their respective ephemeral drainage lines.

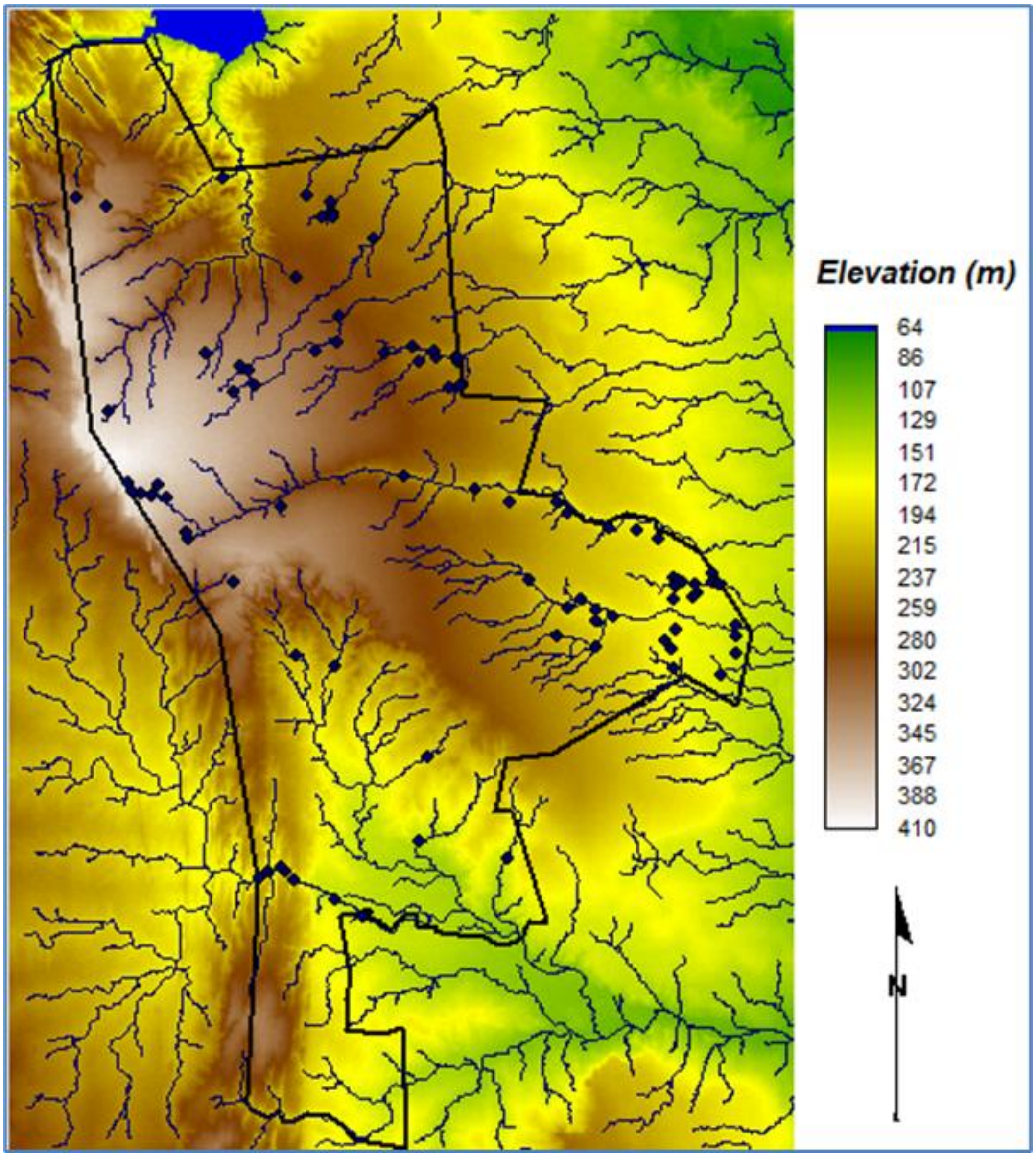

Figure 2.5. Topography (colour gradient from white, high elevation, to green, low elevation) and drainage (blue lines) map of primary drainage lines and ephemeral water points (blue dots) in Karingani Game Reserve (source: SRTM 30m DEM; Farr *et al.* 2007).

2.2 White-backed Vulture nests, LiDAR, and photogrammetry data collection

To describe the nest tree and nest site characteristics of WbVs in KGR, known nest site locations (hereafter referred to as “occupied” trees) that overlapped with LiDAR survey data were identified. LiDAR and RGB data of these nest sites and their immediate surrounding area were then processed to create Canopy Height Models (CHMs) and orthomosaics, respectively. These

LiDAR and RGB products were subsequently used to extract the following nest site characteristics: canopy height, canopy area, canopy roughness, distance to permanent water, distance to the nearest tallest tree, and other surrounding vegetation variables up to 100 m. The extracted characteristics were then compared to random non-nest trees with in the same LiDAR surveyed area (hereafter referred to as “unoccupied” trees) using a Resource Selection Function (RSF) analysis to determine whether there is a significant preference for specific nest tree and area traits by WbVs when selecting nesting sites and trees.

For this study, permission from KGR management for the use of all the vulture data from 2021 was acquired, as well as the LiDAR data collected with the HALO, which came from the Davies Lab of Harvard University. Ethical clearance was obtained from the relevant department of Cape Peninsula University of Technology to conduct this research (ethics ref: 212167944/10/2021).

2.2.1 Identification and mapping of WbV nesting sites

As part of routine landscape assessment surveys, KGR management has been collecting WbV nesting data since 2016. East–west transects one kilometre apart are flown annually during the month of October in an AS350 B-2 Squirrel helicopter carrying a team of five people composed of a pilot, recorder, and three observers. The survey helicopter flew at roughly 90 m aboveground level (agl) at a speed varying between 55–80 kilometres per hour (kph) along a survey grid comprising 60 transects (min 8.3km, max 33.3km in length) for a total sample effort of 1 457km. Observers scanned up to 500m on either side of the survey line for large mammals and raptor nesting sites (Goodman & Worth 2020).

When a raptor nest was sighted, the helicopter broke away from the survey line and moved closer to the nest; the distance from when the helicopter moved away from the transect line was recorded (Goodman & Worth 2020). The helicopter flew around the nest at a safe distance to record nest information without disturbing the nesting birds while taking a GPS coordinate. Consequently, only the approximate location of the nest is known. The exact nest tree location was then located using the RGB imagery and LiDAR data collected using the HALO, described below. The RGB provides a clear and detailed orthomosaic of the landscape where one can visually identify and see the nests within the tree (Fig 2.6).

Figure 2.6: Example RGB image of a White-backed Vulture nest identified within the RGB imagery captured by the Harvard Animal Landscape Observatory. This procedure was used to confirm the presence and location of White-backed Vulture nests in Karingani Game Reserve.

Nesting status was recorded as either active (parent bird sitting), active egg (egg present in the nest), active chick (chick or juvenile present in nest), active empty (nesting unsuccessful or juvenile already fledged), or not active. At the beginning of the nesting season, WbVs line their nests with leaves before they lay an egg. This lining (of grass and leaves) inside the nest is visible throughout the nesting season. If the nest was not being prepared for use or had not been used at the time of the survey, then this lining was not present. On that basis, these nests were scored as “not active” (Goodman & Worth 2020).

Nests were allocated to different bird species based on the direct visualisation of nesting birds or the structure and placement of the nests. Marabou storks (*Leptoptilos crumenifer*) and Bateleurs (*Terathopius ecaudatus*), White-headed (*Trigonoceps occipitalis*) and Lappet-faced vultures (*Torgos tracheliotos*) also nest within KGR. However, other vulture species’ nests are larger and more tightly packed, flat nests, built on top of the flatter crowned *Vachellia* species such as *V. tortilis,* and are easily distinguishable from WbV nests (P. Goodman *pers comms.*).

2.2.2 LiDAR and RGB data collection

In May 2021, an integrated LiDAR, RGB, and thermal camera remote sensing system, the Harvard Animal Landscape Observatory (HALO) was attached to a FreeFly Alta X unmanned aerial vehicle (UAV) (Fig 2.7) and used to survey parts of KGR to provide the reserve with baseline data on vegetation structure. The aim of the surveys was to monitor vegetation change in response to the increasing elephant population. The LiDAR and RGB imagery together with the vulture nest site location information provided the data from which the WbV nest tree and nest sites characteristics were extracted.

Figure 2.7: The Harvard Animal Landscape Observatory (HALO) attached to the Free Fly Alta X unoccupied aerial vehicle used to survey Karingani Game Reserve.

The LiDAR sensor used was a Riegl VUX-1LR, capable of collecting up to 750 000 measurements per second. The mounted RGB camera was a modified (for lightweight) 24.3-megapixel Sony A6000. The thermal camera used was a modified FLIR Tau 2, which can measure object temperatures within 1.5 and 3ºC of truth on structured and unstructured surfaces. The LiDAR unit, RGB camera, and thermal camera were integrated into one unit to communicate directly with a centralised navigation computer, which utilised a high precision Micro-Electro-Mechanical Systems Inertial Measurement Unit (Sensonor STIM300) and integrated GPS for collection of each data product (Boucher *et al.* 2023). The sensor types were integrated into a single remote sensing system (the HALO) by Phoenix LiDAR Systems, USA. The HALO was then attached to a Free Fly Alta X remotely piloted aircraft system (RPAS). To improve data spatial accuracy, a StoneX S900 Global Navigation Satellite System (GNSS) receiver base station was used to collect differential GNSS reference data used to correct the UAV's trajectory in post-processing.

In 2021, roughly 350km^2 of KGR was surveyed with the HALO system by the Davies Lab for baseline vegetation sampling and to scope sites for KGR future development. An additional 110km^2 was flown to gather supplementary data specific to this study. In total, the surveyed area used for this study was roughly 460km^2 (31% of KGR total area). A large portion of this total data was collected via flights that were conducted over 17 circles with a 2.5km radius, flown in north–south or east–west (wind dependent) transects (Fig 2.8). The 2.5km radius circle survey areas were determined by consideration of the limitation of the RPAS system as the ALTA X UAV has a 2.5km signal connection range from its ground control station. The 2.5km radius polygons were spread as evenly as possible across the area of KGR to maximise cover and representation of the protected area while staying within the safe operating parameters of the ALTA X. Another portion of the total surveyed area was collected for development purposes but could still be used for baseline vegetation samples for the broad project mentioned previously. These areas were supplied to the Davies Lab by KGR management and adjusted accordingly to align with the ALTA safe flying parameters and accessibility. For the purposes of this study, two additional survey areas were recorded and included in the total surveyed area to ensure adequate inclusion of occupied vulture nests in this study, as the existing data from the Davies Lab did not include enough occupied vulture nests to draw accurate conclusions.

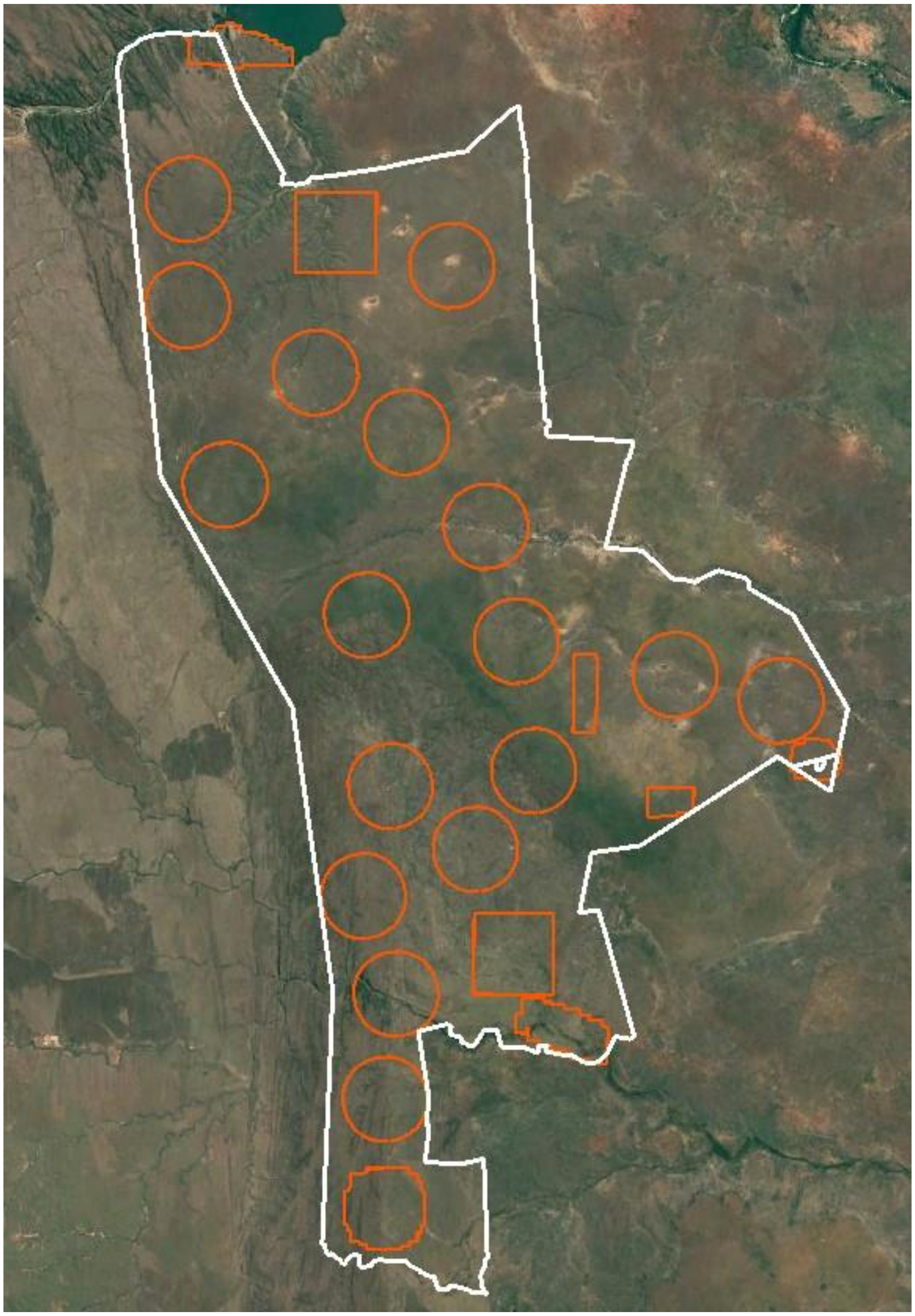

Figure 2.8: All representative samples (orange polygons) surveyed by the Harvard Animal Landscape Observatory (HALO) within the perimeter of Karingani Game Reserve (white outline).

All flight plans were created in the ALTA_QGround_Control (QGC) desktop application (*Freefly custom version of the QGroundControl App for Alta X [v1.3.x*]). A pre-made polygon of 2.5km radius circles (made in QGIS V3.16) was imported into the flight planning page of QGC. The QGC program automatically created a flight plan that consisted of a take-off location, flight paths in the form of transects, and a landing location. In this case, the landing location was at the same point as the take-off. Flight parameters were entered into the appropriate tabs as follows:

- Flight height AGL (aboveground level): 150 m
- Flight speed: 10 metres per second
- Line spacing: 147m

This flight plan was then uploaded onto the RPAS.

The LiDAR unit was set to the following:

- Pulse frequency: 820 kilohertz
- Laser power: 100%
- Scan rate: 93 lines per second (lps)
- Field of view (FOV): 109 degrees

The settings were determined in the RiPARAMETER (V2.2.0.5408 x68bit) desktop application. The process requires the user to enter settings into the program and adjust the setting until the desired results are achieved. In this case, the objective was to ensure that the point cloud achieved >150 points per metre at a 65% overlap while flying at 150 m agl (for safety reasons). The data collected were stored onto a 512GB SanDisk SD card.

2.2.3 LiDAR and photogrammetry data processing

Metrics for vegetation structure were derived from the classified and denoised LiDAR point clouds involving multiple different proprietary software programs. The following program suites were used to convert the raw LiDAR data into products that could be used to extract the required measurements for the study (CHMs and RGB orthomosaics):

- **StaticToRinex**: Used to convert the raw .DAT navigation file from the STONEX S900 ground-based GNNS GPS into a .O rinex file, which was then uploaded to AUSPOS (https://gnss.ga.gov.au/auspos) to further refine the precise coordinate positions of the sensor during flight for post-processing trajectory correction of the LiDAR data.
- **Inertial Explorer 8.80:** Used to refine the flight line trajectories using the AUSPOS report.
- **Spatial Explorer 6.0.8**: Used to filter out any noise points and select only the required flight lines that contained LiDAR data needed for the study, as well as to create a “clean”

point cloud, which was extracted into a .LAS file for further processing in MicroStation CONNECT.

- **TeraScan (V19), TeraMatch (V19), TeraPhoto (V19):** Used with MicroStation CONNECT to continue the refinement of the trajectories and LiDAR points, and for final generation and exportation of the required products such as the CHM, DTM and orthomosaic.

2.2.4 Canopy height model

The CHM was extracted at the final step of the LiDAR data processing workflow using the program TeraScan in MicroStation. A horizontal 10-centimetre (cm) resolution CHM was selected as the base layer for value and measurement extraction.

2.2.5 Orthomosaic

An orthomosaic was produced using TeraPhoto in MicroStation. Multiple images taken during the flight were overlaid and stitched together to create a continuous image of the entire area flown, giving the viewer a top-down, or "bird's-eye view" of the survey area. A 10 cm resolution for the RGB was used for this study. No further corrections were made as this study did not do any spectral analysis, as the orthomosaic was only used to confirm the location of the nests in the trees.

2.2.6 Merging of WbV nest sites and remote sensing data

Upon the completion and production of the CHM and orthomosaic, the products were imported into the QGIS v3.16 along with the GPS points of each recorded WbV nest supplied by KGR management. QGIS is an open-source software application used for viewing, editing and analysing geospatial data. By using this software, the GPS points of the vulture nests were visible over the CHMs and orthomosaics. As the helicopter was not able to hover directly over the nests, the GPS point recorded was off set from the nesting tree. I then used the othromosaic to identify which tree had a nest present in it closest to the recorded GPS point and manually move the GPS point to the correct position of the nesting treel.

2.2.7 Random tree generation

An RSF was implemented to determine the preferred nesting characteristics of WbVs. To conduct this analysis, unoccupied trees within the survey areas that were not used for nesting were identified, which were then compared to the occupied trees used for nesting within the same areas. Random trees were generated using the *random point in polygon* tool in QGIS. Random points with a maximum distance of 300 m apart were created in the polygons, which represented the survey areas used for in the study, to ensure an even spread and representation within each survey area (Fig 2.9). in total for this study, 30 occupied and 184 unoccupied nests were used for the RSF analysis. Since the random generated points did not always fall directly on trees and were sometimes positioned on the ground, they were manually adjusted to the nearest tree to ensure comparability between occupied and unoccupied trees.

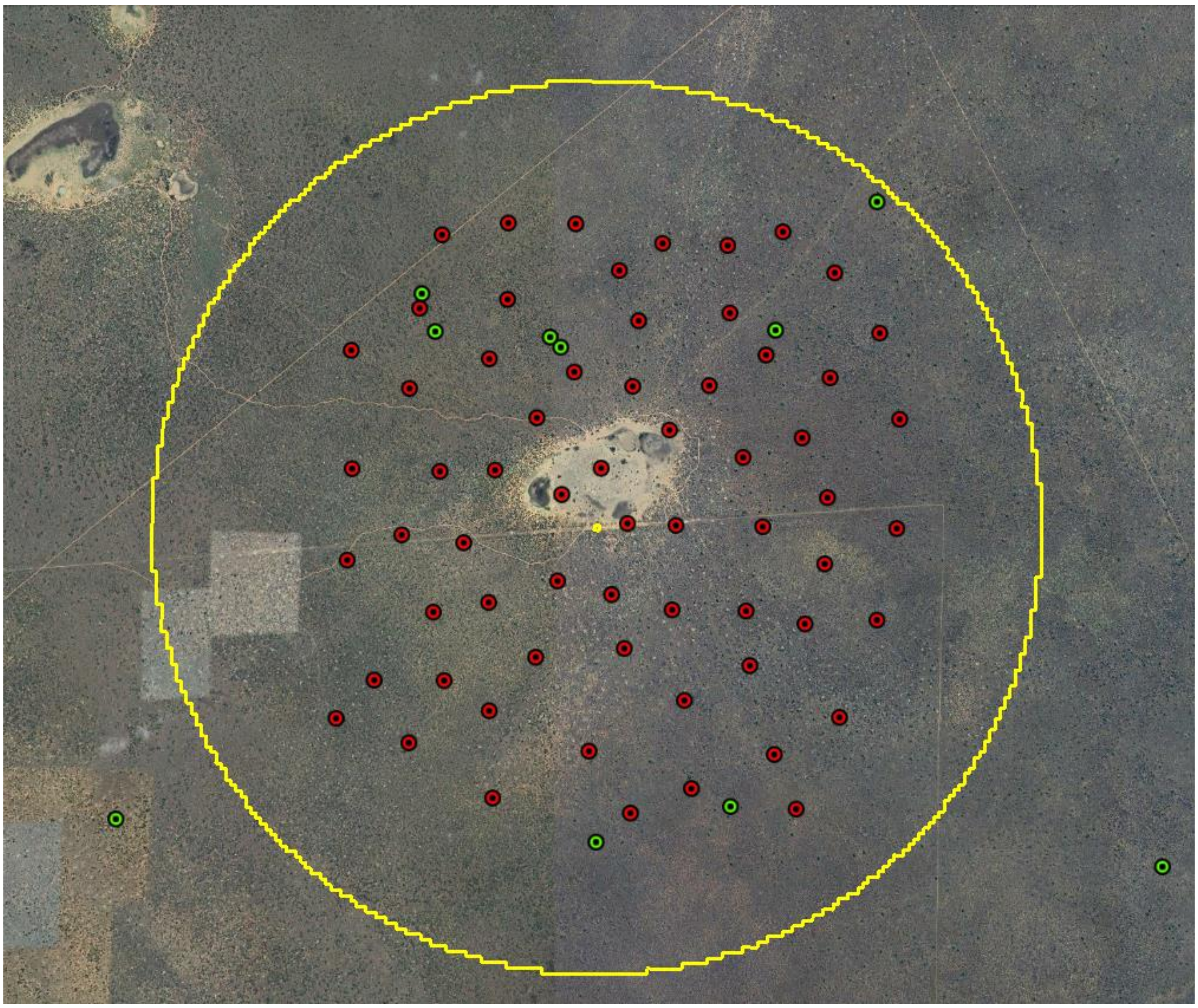

Figure 2.9: An example of one of the survey areas (yellow circle) showing random trees (red dots) and known nesting trees (green dots) in Karingani Game Reserve, Mozambique.

2.3 Tree measurements and variable extraction

The measurements extracted from the occupied trees and their immediate surroundings were duplicated for the randomly selected trees, except for nest orientation as there were no nests present in the randomly selected trees. Table 2 lists the measurements and variables used for this study, followed by detail on how they were extracted and calculated.

Table 2: Variables measured for this study.

Variable	**Description**
Tree variables	
Tree species	Species of tree in which the nest is present
Canopy height	Height of tree from base of trunk to highest point of canopy
Canopy area	Total area of canopy in m^2
Canopy roughness	The variation of height and compactness of branches within the canopy area
Nest orientation	Placement of where the nest is on top of the canopy
Distance to water	Distance to nearest permanent water from tree
Surrounding tree variables	
Surrounding woody plant percentage and canopy roughness ≥ 3 m within a 50 m radius	Woody cover percentage and canopy roughness ≥ 3 m, within a 50 m radius of an occupied or unoccupied tree

Surrounding woody plant percentage and canopy roughness ≥ 3 m within a 100 m radius	Woody cover percentage and canopy roughness ≥3 m, within a 100 m radius of a tree
Surrounding woody plant percentage and canopy roughness ≥10 m within a 50 m radius	Woody cover percentage and canopy roughness ≥10 m, within a 50 m radius of a tree
Surrounding woody plant percentage and canopy roughness ≥10 m within a 100 m radius	Woody cover percentage and canopy roughness ≥10 m, within a 100 m radius of a tree
Nearest tallest tree	Tallest tree from the selected tree within a 50 m and 100 m radius

2.3.1 Tree variables

2.3.1.1 Tree species identification

The tree species for the occupied trees was identified visually during the routine landscape assessment helicopter surveys by KGR management, and recorded alongside the nesting status on the data sheet used at that time. Tree species for the unoccupied trees were not identified in this study, as the orthomosaic layer was not reliable enough to identify the tree species.

2.3.1.2 Canopy height, canopy area, canopy roughness

To facilitate measurement extraction of canopy height, canopy area, and canopy roughness, polygons were drawn around each occupied and unoccupied tree visible in the CHM layer, following the outer edge of the canopy shape using the *New Shapefile Layer* QGIS tool and selecting “polygon” as the geometry type. Each pixel in the CHM represents a height value in metres, which allows the user to have a detailed spatial distribution of vegetation height. The *Zonal Statistics* tool in QGIS was employed to extract various tree metrics, including maximum height above ground (which represents canopy height), area in square metres (which represents canopy area), and standard deviation of canopy height (which represents canopy roughness).

The standard deviation, denoted by **s**, was used to quantify and represent the canopy roughness of the tree canopy. A higher standard deviation indicated greater variation in the pixel heights within the polygon that covered the tree canopy surface, reflecting more unevenness or roughness in the canopy structure. The higher the standard deviation, the greater the canopy roughness, while a lower standard deviation represented a lower canopy roughness.

2.3.1.3 Nest orientation

Nest orientation represents the position of the nest within the canopy peripherals (outer edge of canopy to the centre of the canopy) and its azimuth relative to North. An orthomosaic of the survey areas was created with the Teraphoto MicroStation application from the RGB imagery obtained with the HALO. These orthomosaics were used to pinpoint the exact location of the nests within the tree canopies. The position of each nest relative to the centre and outer edge of the canopy, as well as the nest azimuth, was noted. The following values were assigned to the nest position within the canopy (Fig 2.10):

- **Nest position:** 0 – Centre; 1 – Closest to the centre; 2 – Within the middle region of the canopy; 3 – Near the outer edge of the canopy.
- **For nest azimuth:** 0 – Tree centre, no clear direction; 1 – North; 1.5 – North-East; 2 – East; 2.5 – South-East; 3 – South; 3.5 – South-West; 4 – West; 4.5 – North-West.

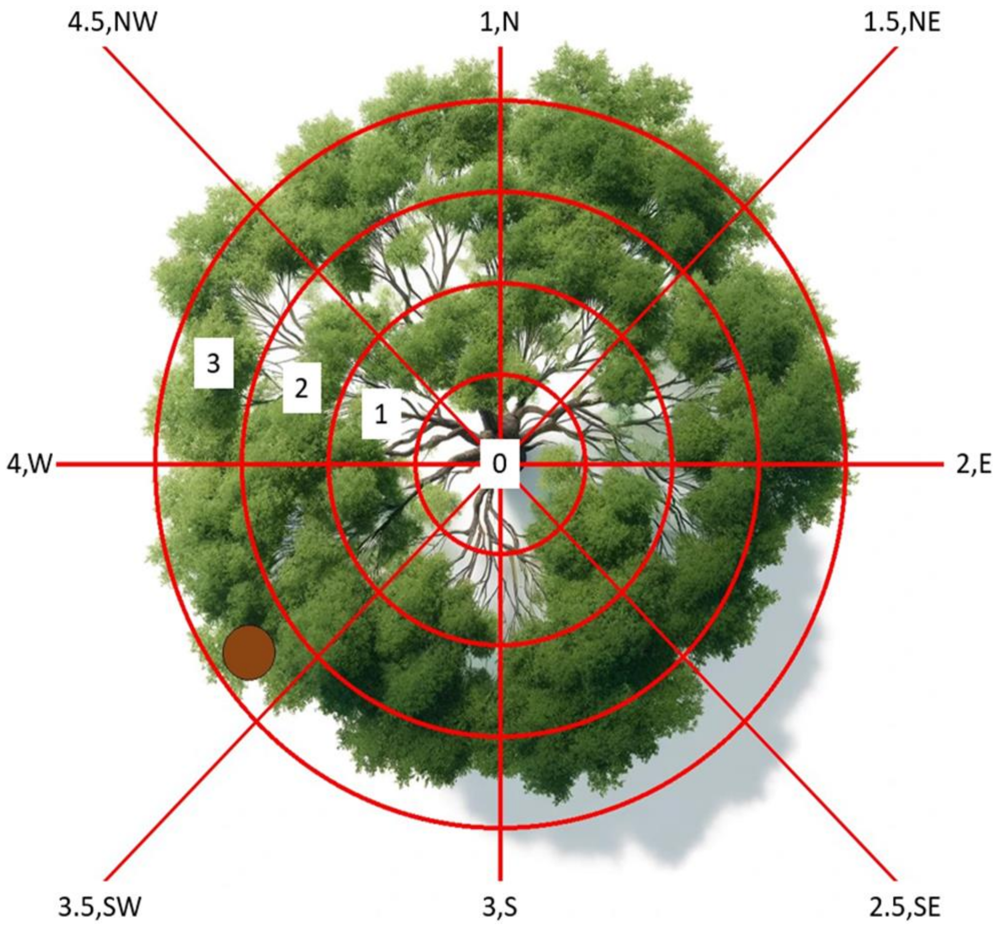

Figure 2.10: Representation of how each occupied tree was segmented to assign a value to each nest location and azimuth. Nest position: 0 – Centre; 1 – Closest to the centre; 2 – Within the middle region of the canopy; 3 – Near the outer edge of the canopy. For nest azimuth: 0 – Tree centre, no clear direction; 1 – North; 1.5 – North-East; 2 – East; 2.5 – South-East; 3 – South; 3.5 – South-West; 4 – West; 4.5 – North-West. Brown circle is an example of a nest position which would read as: nest position 3, nest azimuth 3.5.

2.3.1.4 Distance to water

KGR management recorded all the permanent water sources within the reserve in 2020 (Goodman *pers coms*). These locations were imported into QGIS and overlaid onto the boundary of KGR. For the purposes of this study, a raster heat map in which each pixel value was associated with a distance in metres from the nearest permanent water source was used. All 115 recorded occupied trees from the 2020 survey were then overlaid onto the heat map to determine the distance from the nearest permanent water within KGR for each occupied tree. New additional 115 random points were then generated specifically for this comparison, over the entire extent of the surveyed area of KGR to compare. The average distances for occupied and unoccupied trees were then compared to find significant results regarding whether WbVs were selecting nest sites closer to water.

2.3.2 Surrounding tree variables

To identify whether the vegetation characteristics surrounding a tree influenced the selection of specific trees within the landscape for WbV nesting, the vegetation height, variation and percentage cover were calculated within a 50 m and 100 m buffer from the occupied and random unoccupied trees (Fig 2.11).

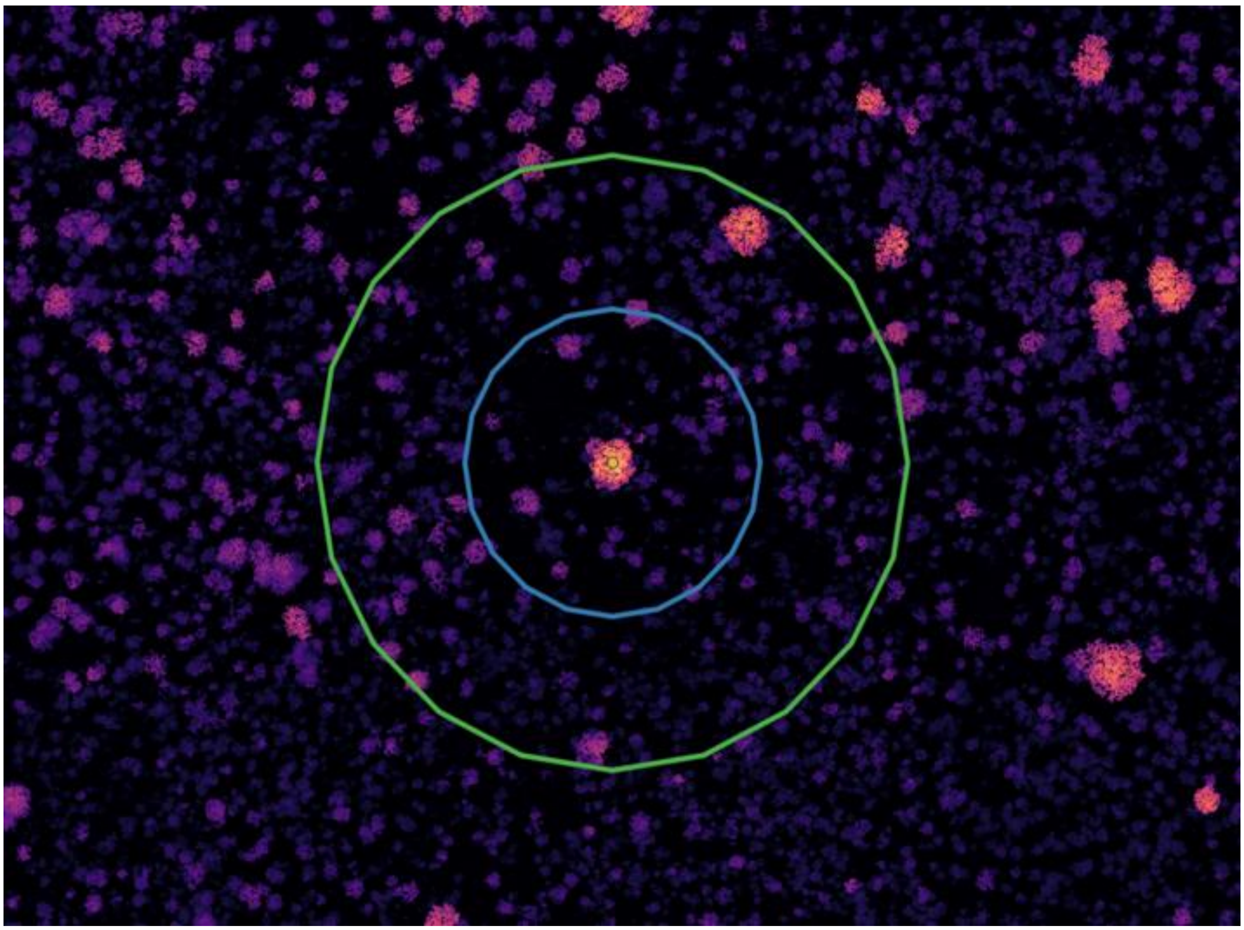

Figure 2.11: Visual representation of a tree (yellow dot) with the 50 m buffer (blue ring) and 100 m buffer (green ring) overlaid onto the CHM.

2.3.2.1 Surrounding woody vegetation canopy roughness

Surrounding woody vegetation canopy roughness was calculated at 50 m and 100 m buffers for the selected occupied and unoccupied trees. The variation in woody vegetation canopy roughness was calculated as the standard deviation of canopy roughness using the *Zonal Statistics* tool in QGIS. A higher or lower standard deviation value indicated a higher or lower canopy roughness of vegetation across the buffer zones, respectively. Canopy roughness was calculated for the surrounding area of both the occupied and unoccupied trees.

2.3.2.2 Surrounding woody plant percentage cover

Surrounding woody vegetation cover percentage was also calculated at 50 m and 100 m buffers for the selected occupied and unoccupied trees. This was done in R version 2023.06.0. The relevant CHM was imported into R and, using the required code, a new CHM was created in which all vegetation below 3 m was removed, leaving only the pixels that measured from 3 m and above. The same procedure was performed for vegetation below 10 m in height. Percentage cover of woody vegetation above 3 m and above and 10 m and above, was then calculated within 50 m and 100 m buffers for each occupied and unoccupied tree.

2.3.2.3 Nearest tallest tree

The nearest tallest tree within a 50 m and 100 m buffer was identified by locating the tallest pixel of the CHM within each buffer (50 m or 100 m) and extracted using the *Zonal Statistics* tool in QGIS. These data showed whether or not the occupied or unoccupied tree was the tallest tree within a 50 m and 100 m vicinity, or if there were taller trees within that same vicinity.

2.4 Statistical analysis

Two separate sets of variables related to WbV nests were measured: variables that characterised an individual occupied tree, and variables that represented the immediate surroundings of the individual occupied tree at a 50 m and 100 m radius.

2.4.1 Analysis of tree variables

An aim of this study was to determine which individual tree variables or measurements of relevance to vulture nesting could be extracted from the LiDAR and RGB data, and if these variables had a significant effect on WbV decision-making when selecting a tree to nest in.

2.4.1.1 Canopy height, canopy area, canopy roughness

To determine if there was a significant difference in canopy height, canopy area, and canopy roughness between occupied and unoccupied trees, a Welch's two sample t-test was conducted on the distribution of each variable between the two classes of trees. The Welch's t-test was chosen over the standard Student's t-test because it does not assume equal variances or equal sample sizes between the compared groups (Quinn & Keough 2002). In this case, the number of occupied trees (30) fell short of the number of unoccupied trees (184).

2.4.1.2 Nest orientation

To test whether nest position in a tree was uniformly distributed or exhibited a preferred direction, a Rayleigh's test for non-uniformity was used. This test is particularly suitable for circular data, such as nest azimuth, because it assesses whether the data exhibits a preferred mean direction rather than being uniformly distributed around the canopy (Jammalamadaka 2001). A resultant length value closer to 1 suggests a stronger clustering in one direction, while a value closer 0 indicates uniform distribution (Jammalamadaka 2001). Additionally, a Chi-squared test for goodness of fit (Quinn & Keough 2002) was employed to assess if there was a preference for nest position relative to the centre of the tree. This test evaluated whether the distribution of nests between central and peripheral locations within trees was random or indicated a significant preference.

2.4.1.3 Distance to water

A Student t-test was conducted to examine whether a significant relationship between the distance to water and occupied tree existed. The dependent variable was “occupied” (1 for occupied, 0 for unoccupied) indicating whether a tree was used for nesting, and the independent variable was “DTW” (distance to water).

2.4.2 Analysis for surrounding tree variables

In addition to differences between occupied and unoccupied trees, this study also aimed to observe how ecological characteristics surrounding trees influenced the probability of a WbV selecting a tree to nest in.

2.4.2.1 Surrounding vegetation percentage cover

This analysis quantified whether the percentage of vegetation cover in the immediate vicinity of the occupied trees, at a 50 m and 100 m radii, influenced nest tree selection. For each radius, vegetation percentage cover at 3 m and 10 m and aboveground level was assessed using a Welch's two sample t-test.

2.4.2.2 Surrounding canopy height

A Welch's t-test was used to determine if the mean canopy height in the immediate vicinity of occupied trees (at 50m and 100m) differed from the mean canopy height around the unoccupied trees. Each occupied tree and random unoccupied tree in the 50 m and 100 m buffers were run with the *Zonal Statistic* tool to extract the standard deviation of canopy height within each buffer. The standard deviation of canopy height represented the amount of variation in the height of the vegetation within the buffer. A higher value represented a larger variation and a low consistency of vegetation height within the buffer, and a low value represented smaller variation and more consistent/homogeneous height of vegetation within the buffer.

2.4.2.3 Nearest tallest tree

To determine if trees containing WbV nests were taller than surrounding trees within a 50 m and 100 m radius of the occupied tree, a binomial test (Quinn & Keough 2002) was used to compare the height of selected nest trees to the height of the tallest tree in the surrounding buffers.

2.5 Predictive modelling

Resource Selection Functions (RSFs) were used to identify key environmental factors, at an individual tree level and for the immediate surrounding area, influencing habitat preferences of WbVs (Boyce *et al*. 2002). By integrating habitat data, such as LiDAR and RGB in this study, and species location data, vulture nests in this case, RSFs facilitate the assessment of habitat characteristics and the impact of environmental changes on wildlife (Johnson *et al*. 2006). Given that the response variable “occupied” was binary (0 or 1), a logistic regression model GLM with a binomial distribution was used, which is appropriate for modelling the probability of occupancy when comparing the features of occupied and unoccupied trees (McCullagh & Nelder 1989).

To identify collinear variables that needed to be removed or combined for the RSF, Spearman correlations were used (Dormann *et al*. 2013) to assess the strength and direction of the relationship between the various tree variables (Mukaka 2012). As the data were not normally distributed (tested using Kolmogorov-Smirnov test and visually with Quantile-Quantile plots), Spearman correlations, which are more robust to outliers and non-linear relationships compared to Pearson correlations (Myers & Well 2003), were used. Unlike Pearson correlations that measure the linear relationship between two variables and are sensitive to outliers, Spearman correlations assess the monotonic relationship between variables, ranking the data and thus reducing the impact of outliers (Myers & Well 2003). This is particularly important in ecological studies where data can often be skewed or contain extreme values, which could distort results if Pearson correlations are used (Conover 1999).

Variables were also scaled (standardised) before including them in the model as many had different ranges and units (Gelman & Hill 2007). Standardisation to a common scale made it easier to compare the coefficients and allowed for better interpretation of the effects of the predictors in terms of standard deviations from the mean (Schielzeth 2010).

After implementing the logistic regression, odds ratios were calculated to measure the association between predictors and the response variable. In logistic regression, odds ratios represent the change in odds of the outcome (nest occupation in this case) for a one-unit increase in the predictor. An odds ratio greater than 1 indicated increased odds, while an odds ratio less than 1 indicated decreased odds. For scaled variables, this represented the change for a one standard deviation increase (Hosmer *et al.* 2013).

To ensure the validity of the logistic regression model, residual checks were conducted using the DHARMa package in R, which simulated residuals from the fitted model to create readily interpretable residual plots (Hartig 2020). This approach helped verify model assumptions and diagnose potential issues. This included using QQ plots to check if the residuals (differences between observed and predicted values) followed a normal distribution, residual versus fitted plots to check for consistent variance (homoscedasticity), and tests for overdispersion to assess whether the observed variability was greater than expected (Cameron & Trivedi 1990).

Tree-level variables and surrounding tree variables at 50 m and 100 m radii were analysed using Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) to ensure a good balance between model fit and complexity, ensuring that overfitting did not occur. Lower AIC and BIC values indicated better model quality (Burnham & Anderson 2004). In logistic regression, pseudo-R-squared measures such as McFadden's R-squared show how much variance the model explained, with values between 0.2 and 0.4 considered an excellent fit (Barlett 2014). Additionally, higher log-likelihood values indicate a better model fit (Menard 2002).

CHAPTER THREE

RESULTS

A total of 115 WbV nests were recorded during KGR management's annual biodiversity survey in 2020. Of those nests, 30 fell within the survey areas flown by the HALO system, and as such were chosen for analysis in this study. All 30 occupied trees were of the species *Balanities maughamii,* identified by KGR management during the survey. In addition, 184 random unoccupied trees were generated to compare against the occupied trees (Fig 3.1). The 184 random unoccupied trees were not identified to species level, as the RGB imagery could not produce a confident enough image to identify all the random tree species.

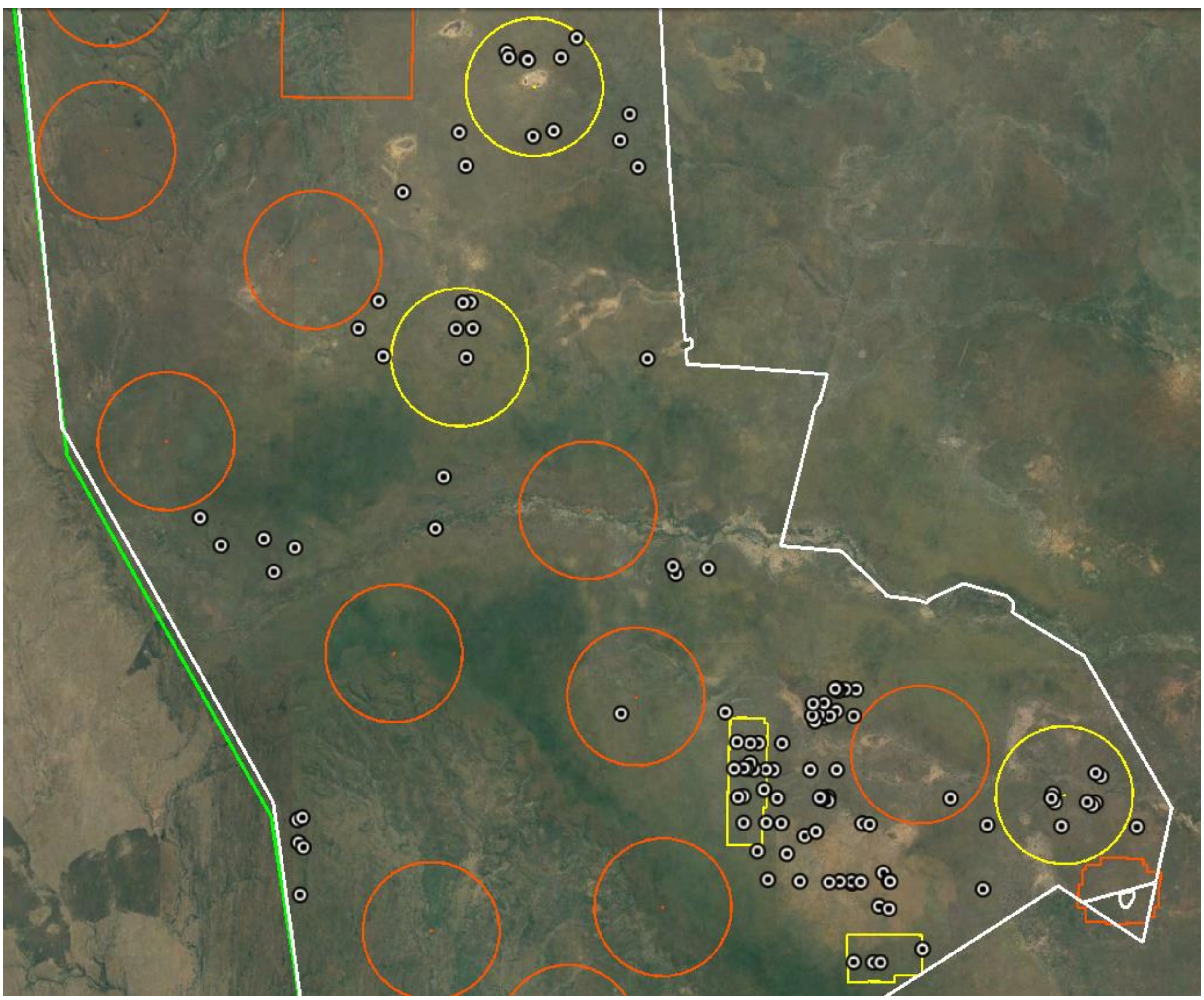

Figure 3.1: Map of the located White-backed Vulture nesting sites (white dots) and the survey areas that were analysed (yellow polygons) for this study. The orange polygons are other areas surveyed with the Harvard Animal Landscape Observatory, but not used in this study.

3.1 Tree-level variable results

3.1.1 Canopy area

There was a significant difference in the canopy area of the occupied versus unoccupied trees ($p =< 0.001$, $t = -8.3$, $df = 38.95$). The average canopy area for occupied trees (161.58m²) was significantly greater than for random unoccupied trees (49.25m²) (Figure 3.2).

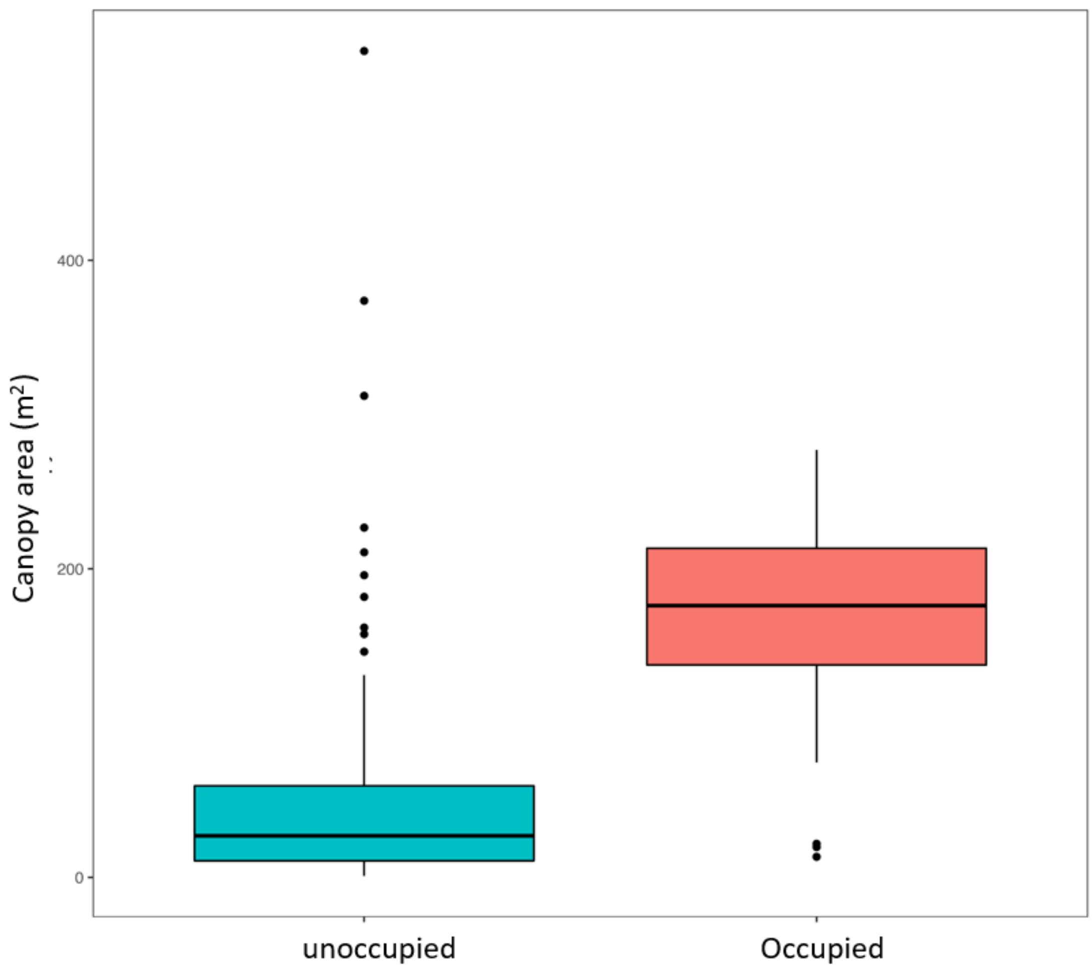

Figure 3.2: Box plot showing the distribution of canopy area for unoccupied trees (blue) and occupied (with nests) trees (red) with outliers in the data represented by black dots.

3.1.2 *Canopy roughness*

There was a significant difference in the canopy roughness of the occupied versus unoccupied trees ($p= <0.001$). The average canopy roughness for occupied trees (4.04**s**) was significantly greater than for random unoccupied trees (1.96**s**) (Figure 3.3)

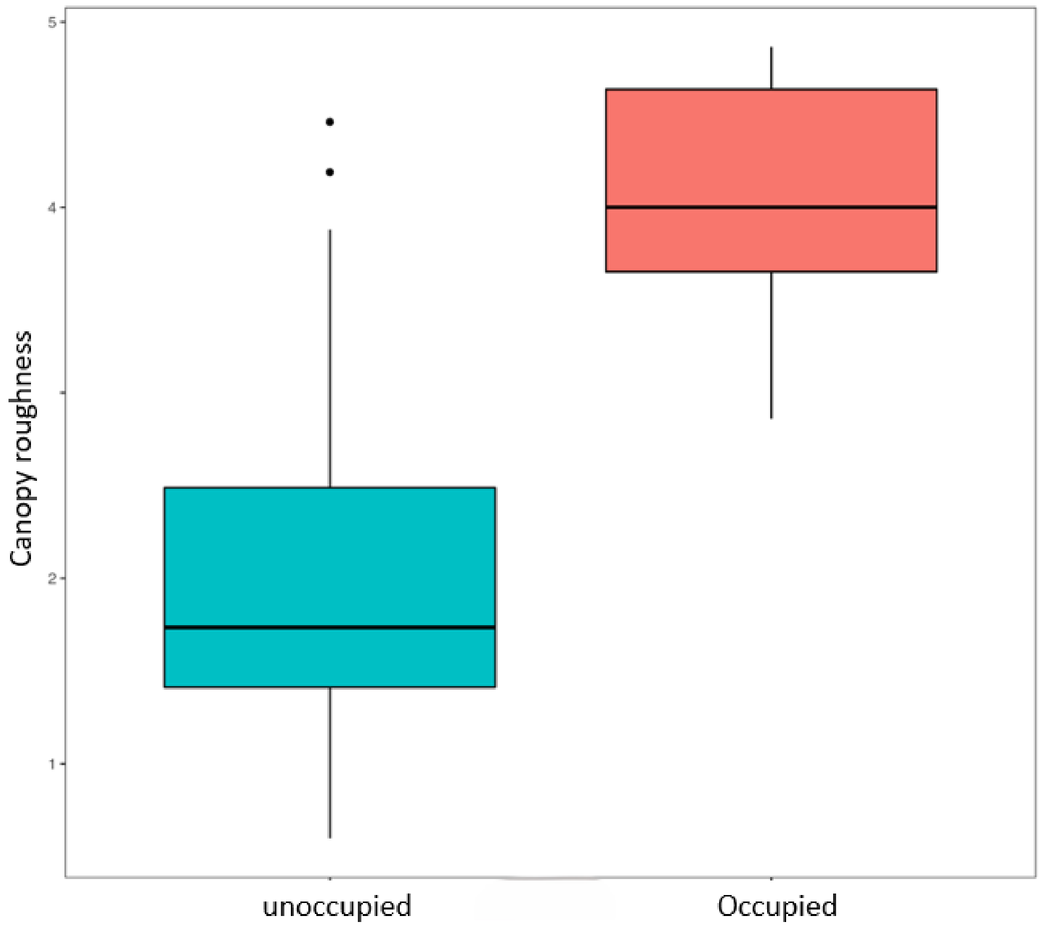

Figure 3.3: Box plot of the distribution of canopy roughness for unoccupied trees (blue) and occupied trees (red) with outliers in the data represented by black dots.

3.1.3 Canopy height

There was a significant difference in the canopy height of the occupied versus unoccupied trees (p=<0.001). The average canopy height for occupied trees (14m) was significantly higher than for random unoccupied trees (7.38m) (Figure 3.4)

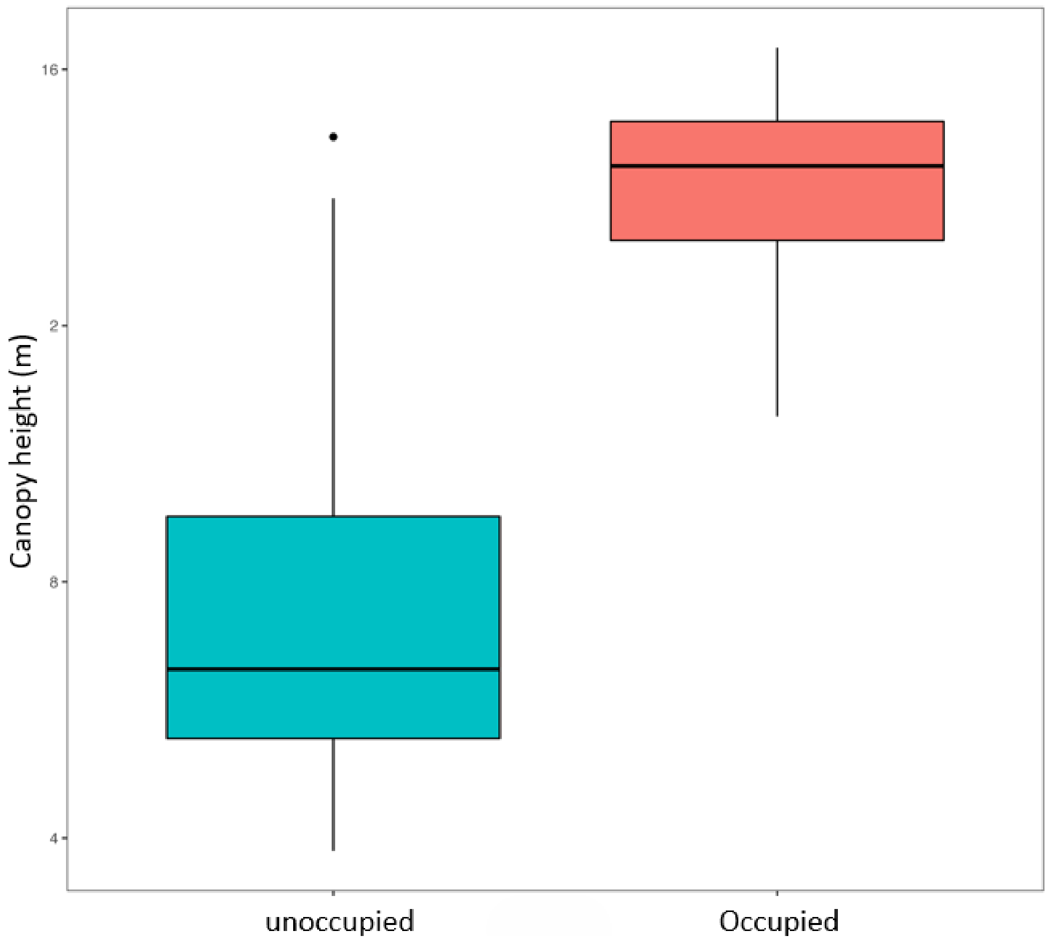

Figure 3.4: Box plot of the distribution of canopy height for unoccupied trees (blue) and occupied trees (red) with outliers in the data represented by black dots.

3.1.4 Nest orientation and azimuth

Results showed slight preference for nest orientation towards the North (Fig. 3.5). The Rayleigh test indicated resultant length of 0.75 (indicating the data falls in one direction) and a mean cardinal directional preference of 10.86, indicating a preferred nesting position on the northern side of the tree. Additionally, a Chi-squared test for goodness of fit to a uniform distribution indicated no significant preference for central or peripheral nest locations ($\chi^2 = 0.60$, $p = 0.741$), and the effect size was small (Fei = 0.10, 95% CI [0.00, 1.00]). These findings suggest that WbVs in KGR prefer to nest on the northern side of the tree canopy but have no preference for central or peripheral location within the canopy.

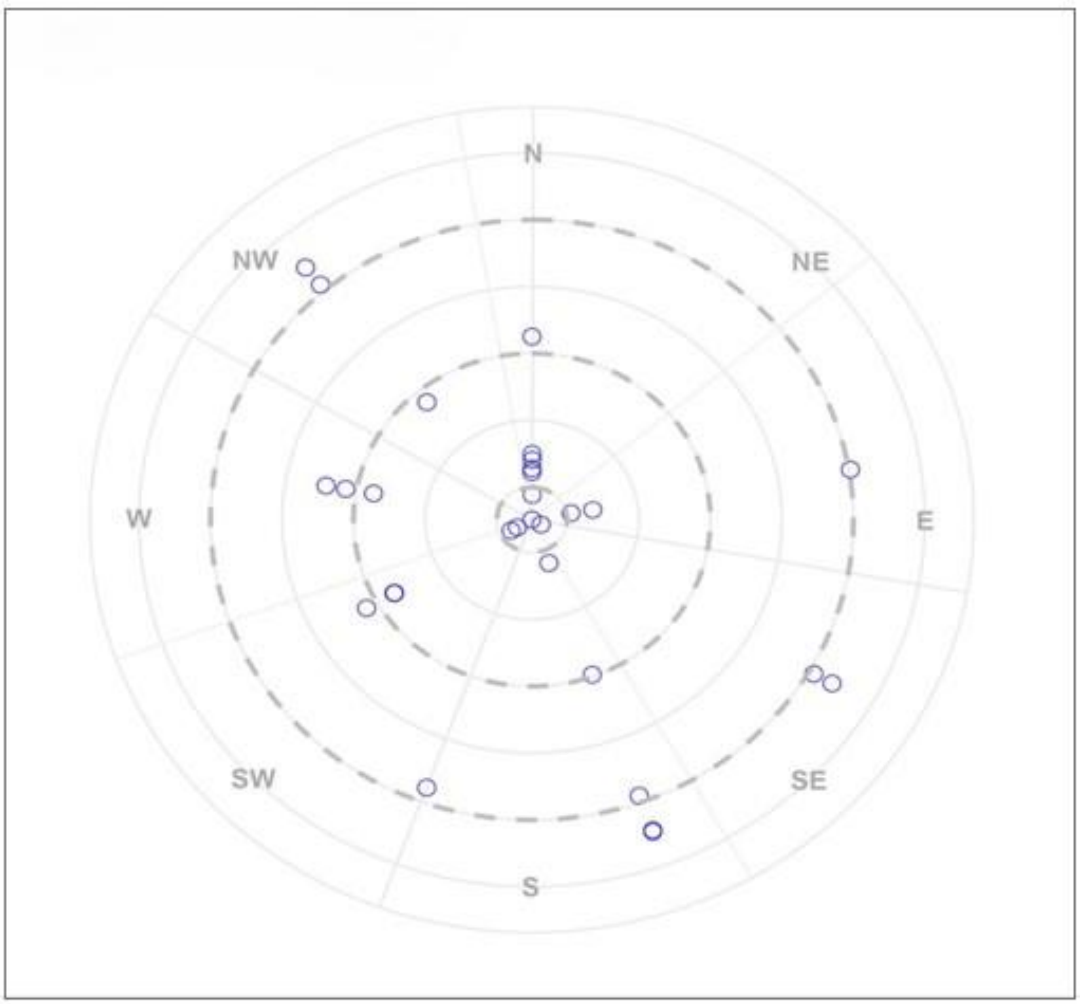

Figure 3.5: Visual representation of all 30 occupied nests chosen for study from Karingani Game Reserve, Mozambique, in relation to the canopy of the occupied tree. Blue rings represent the position of the nest,

letters represent the cardinal and intercardinal directions, and dotted lines represent the peripheral zones of the canopy.

3.1.5 Distance to water

All 115 recorded nests (i.e., not just those within the HALO survey areas) from the routine survey by KGR were used, and an additional 115 random unoccupied trees were also included in the Student t-test of how distance to water affected the selection of nest trees. The average distance to water for occupied trees (13.77km) was slightly greater than for unoccupied trees (13.01km) but was not statistically significant ($p = 0.324$). This result suggests that there is no preference for WbV nests in relation to proximity to water sources.

3.1.6 Correlation analysis for tree-level variables

Significant and strong correlations were found between several variables (Fig 3.6). First, there was a strong positive correlation between canopy roughness and canopy height ($r = 0.908$, $p < 0.001$). Second, a positive correlation was observed between canopy height and canopy area ($r = 0.537$, $p < 0.001$).

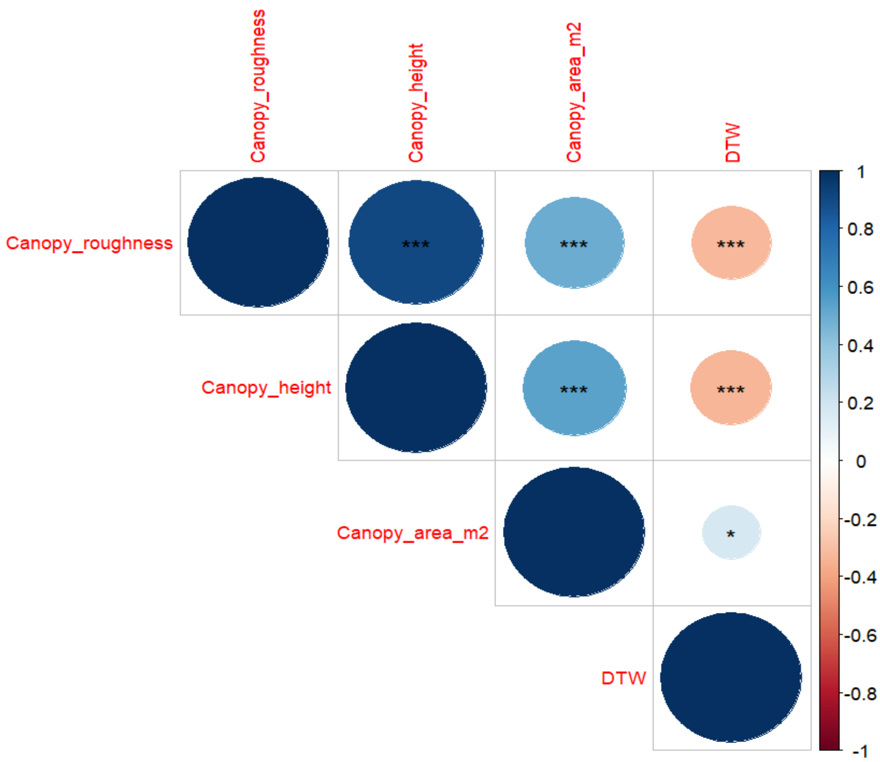

Figure 3.6: Correlation plot of the tree level variables for occupied nesting trees of White-backed Vultures in Karingani Game Reserve, Mozambique. The size and colour intensity of the circles represent the strength of the correlation, with blue circles indicating positive correlations and red circles indicating negative correlations. Larger circles represent stronger correlations, and smaller circles represent weaker correlations. The statistical significance of these correlations is indicated by stars: no stars for not significant, one star (*) for $p < 0.05$, two stars (**) for $p < 0.01$, and three stars (***) for $p < 0.001$.

Due to the strong correlation between canopy roughness and canopy height ($r = 0.908$, $p < 0.001$), two separate GLMs were fitted to compare their effects on vulture occupancy. Both models included canopy area and distance to water as additional predictors to determine which variables well best suited going forward with the analysis.

The canopy height model resulted in a lower AIC (59.80) and BIC (73.26) compared to the canopy roughness model (AIC = 61.56, BIC = 75.02). Additionally, the canopy height model had a higher pseudo-R-squared (0.701) and log-likelihood (-25.90) compared to the canopy roughness model (pseudo-R-squared = 0.691, log-likelihood = -26.78). Therefore, the canopy height model was selected for further analysis.

A logistic regression model was fitted to assess the relationship between nest occupation and three predictor variables: canopy height, canopy area, and distance to water (Fig 3.7). The model indicated that canopy height was a significant predictor of nest occupation (estimate = 3.90, SE = 0.75, $z = 5.22$, $p < 0.001$). A one standard deviation increase in canopy height was associated with 49.58 times increase in the odds of nest occupation. Distance to water was also significant (estimate = 1.27, SE = 0.55, $z = 2.32$, $p = 0.021$) with a one standard deviation increase associated with 3.57 times higher odds of occupation. Canopy area was not a significant predictor of nest occurrence within a tree (estimate = -0.55, SE = 0.43, $z = -1.29$, $p = 0.196$).

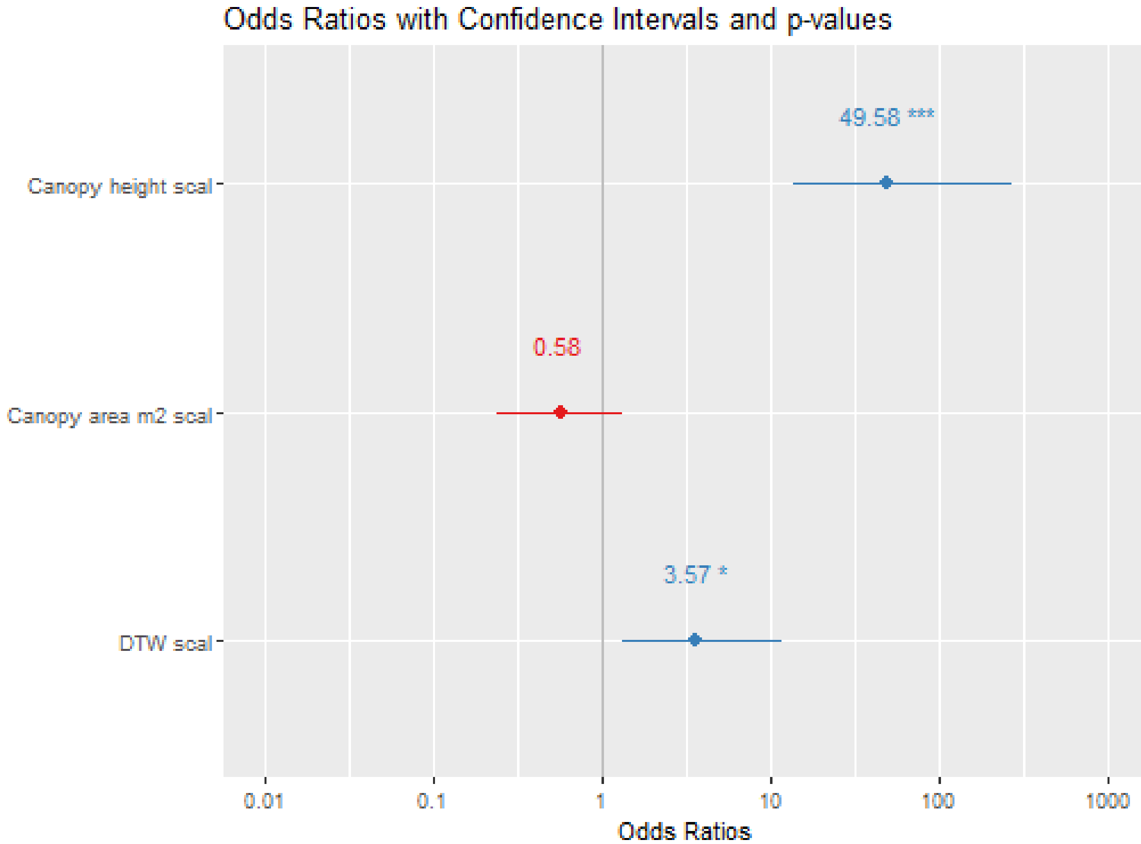

Figure 3.7: Odds ratios and 95% confidence intervals for the predictor variables in the logistic regression model assessing White-backed Vulture nest occupation in Karingani Game Reserve, Mozambique. Positive odds are shown in blue and negative ones in red. The model includes canopy height (scaled), canopy area (scaled), and distance to water (scaled). Statistically significant predictors are denoted by asterisks: ***$p < 0.001$, *$p < 0.05$. The x-axis is on a logarithmic scale to accommodate the wide range of odds ratios.

The goodness of fit was evaluated along with assumptions of the GLM using the DHARMa package for residual diagnostics. The QQ plot showed that the residuals were approximately normally distributed. This was confirmed by the Kolmogorov-Smirnov (KS) test with a $p = 0.144$, indicating no significant deviation from normality. The dispersion test ($p = 0.528$) suggested no significant over-dispersion, and the outlier test (p = 1) indicated no significant outliers. Additionally, the residuals versus predicted values plot showed random scatter around zero with no discernible pattern. These diagnostic tests and plots confirmed that the model fits the data well, with no major issues in the residuals.

3.2 Surrounding tree variable results

3.2.1 Correlation analysis for surrounding tree-level variables

Spearman correlations showed significant and strong (r > 0.5) correlations among some variables used to describe the area surrounding occupied and unoccupied trees (Fig 3.8).

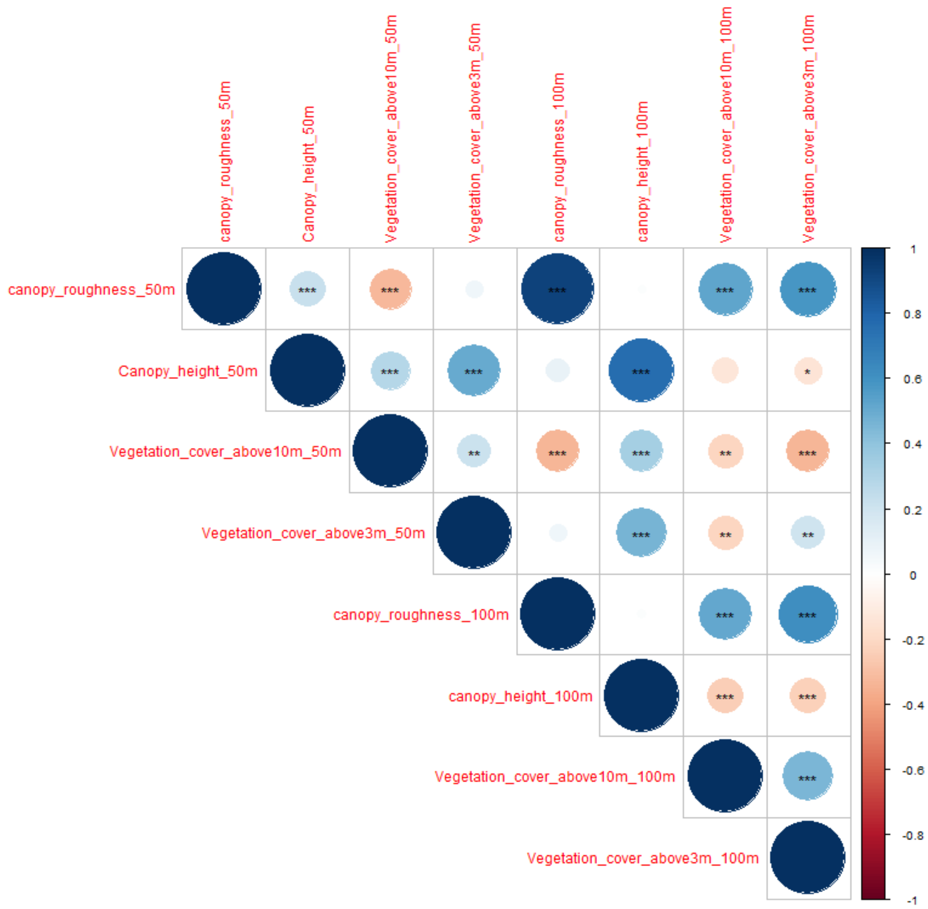

Figure 3.8: Correlation plot showing the correlations among measurements of variables surrounding occupied and unoccupied trees. The size and colour intensity of the circles represent the strength of the correlation, with blue circles indicating positive correlations and red circles indicating negative correlations. Larger circles represent stronger correlations and smaller circles represent weaker correlations. The statistical significance of these correlations is indicated by stars: no stars for not significant, one star (*) for

$p < 0.05$, two stars (**) for $p < 0.01$, and three stars (***) for $p < 0.001$.

3.2.2 Generalised linear models

Due to correlation in environmental characteristics between the 50 m and 100 m buffers, two separate GLMs were fitted to compare their effects on nest occupancy. Both models included canopy height, canopy roughness, and vegetation cover at either 50 m or 100 m surrounding the tree as predictors.

3.2.3 Model selection

The 50 m buffer model was more parsimonious with a lower AIC (105.17) and BIC (122.00) compared to the 100 m buffer model (AIC = 145.18, BIC = 162.01). Additionally, the 50 m buffer model exhibited a higher pseudo-R-squared (0.451) and log-likelihood (-47.58) than the 100 m buffer model (pseudo-R-squared = 0.221, log-likelihood = -67.59). Therefore, the 50 m buffer model was selected for further analysis.

3.2.4 Model outcomes

The logistic regression model indicated significant effects of surrounding canopy height on tree selection for nesting by WbVs ($\beta = 2.54$, SE = 0.45, $z = 5.64$, $p < 0.001$) with an odds ratio of 12.66, suggesting a strong positive impact on nest site selection (Fig 3.9). In contrast, canopy roughness showed no significant effect on nest site selection ($\beta = 0.63$, SE = 0.51, $z = 1.23$, $p = 0.091$).

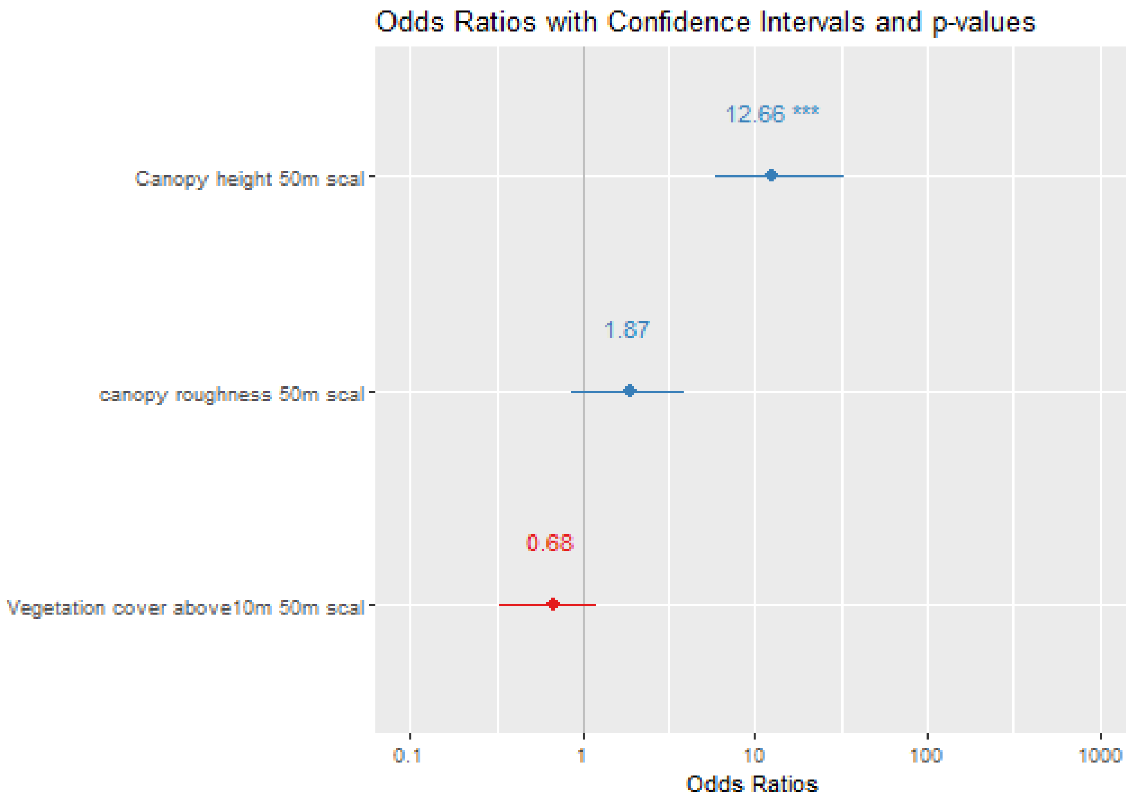

Figure 3.9: Odds ratios and 95% confidence intervals for the predictor variables in the logistic regression model assessing WbV nest site selection in Karingani Game Reserve, Mozambique. Positive odds ratios are shown in blue and negative ratios in red. The model includes canopy height (scaled), roughness (scaled), and vegetation cover (scaled). Statistically significant predictors are denoted by asterisks: ***p < 0.001, *p < 0.05. The x-axis is on a logarithmic scale to accommodate the wide range of odds ratios.

3.2.5 Residuals versus predicted values

The QQ plot showed that the model residuals were approximately normally distributed, which was confirmed by the KS test with a p-value of 0.31706, indicating no significant deviation from normality. The dispersion test ($p = 0.624$) further suggested no significant over-dispersion, and the outlier test ($p = 1$) indicated no significant outliers. Additionally, a plot of the residuals versus predicted values showed a random scatter around zero with no discernible pattern. These diagnostic tests and plots confirm that the model fit the data well, with no major issues in the residuals.

3.2.6 Nearest tallest tree

Within a 50 m buffer, 22 of the 30 nests were in the tallest tree within the buffer (73.33%) (p = 0.008). Similarly, within a 100 m buffer, 21 out of 30 (70%) selected occupied trees were the highest (p = 0.021) in the surrounding vegetation. The binomial test results strongly suggests that WBVs prefer to nest in the tallest trees available with in an area (Fig 3.10).

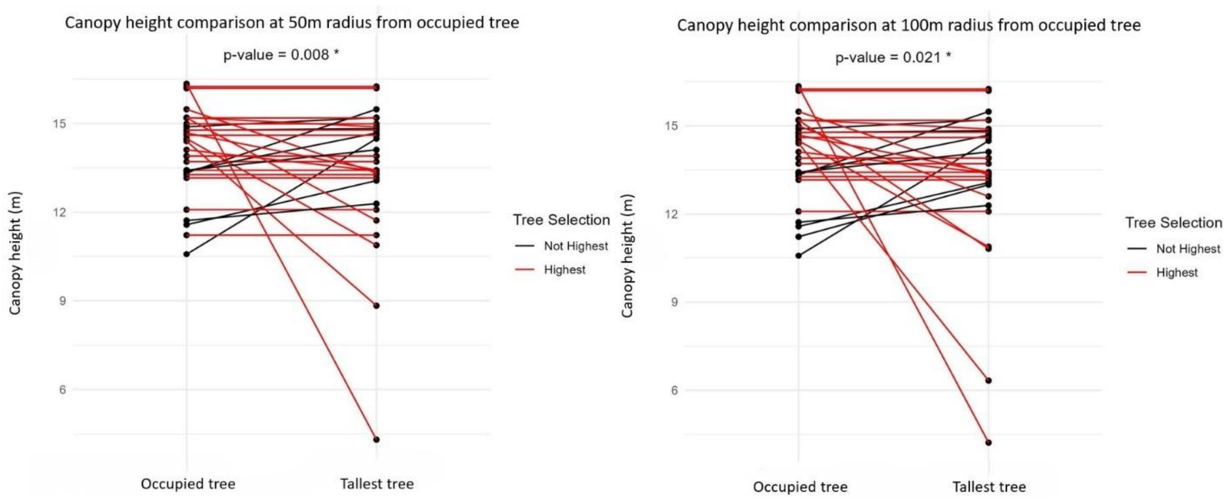

Figure 3.10: Paired comparison plot of occupied nesting trees for White-backed Vultures in Karingani Game Reserve, Mozambique, to the tallest tree within a 50 m radius (left) and 100 m radius (right). The red lines represent trees that are the tallest within the 50 m or 100 m radii. Most of these lines are horizontal or nearly horizontal, indicating that these occupied trees are consistently among the tallest in the area. The black lines represent trees that are not the highest within the 50 m or 100 m buffers. These lines slope upward when moving from occupied trees to tallest trees, indicating that the occupied nest trees were shorter than the highest canopy height within the buffer.

CHAPTER FOUR

DISCUSSION

With the LiDAR data collected by the HALO, this study was able to attain and describe the structural attributes of trees occupied and a random selection of unoccupied trees by WbV nests within KGR. It was also able to quantify vegetation metrics surrounding trees with and without WbV nests. However, it was not able to classify or identify the species of trees occupied due to insufficient resolution of the RGB.

WbVs in KGR nest in trees that are taller, wider, and have a greater canopy roughness than surrounding trees within the landscape. There was a significant difference in the canopy height of occupied versus unoccupied trees, with occupied trees averaging 14m in height compared to 7.38m for unoccupied trees. These findings are consistent with previous research suggesting that taller trees provide essential advantages for WbVs when selecting nesting sites (Jones 2001; Bamford *et al*. 2009b). Taller canopies could offer strategic vantage points for surveillance, allowing WbVs to detect potential threats and food sources from a greater distance. Additionally, elevated nests could be less accessible to ground-based predators, increasing nest security and improving chick survival rates. This preference for taller trees is likely an adaptive strategy to optimise the safety of nests and thereby reproductive success for WbVs. Consequently, the conservation of taller trees in KGR is vital for supporting the nesting success of these critically endangered vultures. This is particularly important considering potential habitat disturbances from elephant activity, which can reduce the availability of large trees for nesting (Asner & Levick 2012; Asner *et al*. 2016; Davies & Asner 2019).

There was a significant difference in the canopy roughness of occupied versus unoccupied trees, with occupied trees having an average canopy roughness of 4.04**s**, compared to 1.96**s** for unoccupied trees. This result suggests that WbVs preferentially select trees with greater canopy roughness for nesting in KGR. Canopy roughness, which reflects the variability in canopy structure, provides several ecological advantages. Studies suggest that a more complex canopy can offer numerous small perches and secure anchor points for constructing nests, and better concealment protecting large raptors from both predators and environmental factors such as wind or intense sunlight (Davies & Asner 2014; Moreno-Opo *et al*. 2012). For example, Bamford *et al.* (2009c) found that WbVs in southern Africa often select trees with dense and irregular canopies such as *Vachelia spp., Senegalia spp.,* and *Colophospermum mopane*. In KGR, WbVs similarly select *B. maughamii* trees, which have rough canopies. These rougher canopies may be preferred by WbVs as they limit a predator's access to nesting sites or slow down their movement, making it less energy-efficient to pursue prey in such environments (Smith *et al.* 2014).

The Welch's two sample t-test analysis revealed a significant difference in the canopy area between occupied and unoccupied trees, with occupied trees having an average canopy area of 161.58m² compared to 49.25m² for unoccupied trees. These findings align with existing research suggesting that broad-canopied trees such as *Adansonia*, *Vachelia,* and *Senegalia* are preferred nesting trees for WbVs in savanna regions of southern Africa (Mundy *et al*. 1992). A larger canopy may offer increased structural support for the vultures' sizable nests, which require stable, expansive branches (Moreno-Opo *et al.* 2012). From a predation perspective, a large canopy can also increase nest concealment, providing a natural barrier from predators.

However, other factors not considered in this study may also influence nest site selection. These factors could include tree health, branch structure, surrounding habitat quality, and human disturbance. For example, trees with large canopies might be avoided if they are unhealthy, unstable, or located in a highly disturbed area (Bamford *et al.* 2009a). In some cases, trees with smaller canopies could potentially be favoured in certain situations, particularly when they are in optimal areas with minimal disturbance and abundant food resources nearby. These findings highlight the importance of considering multiple factors in conservation strategies.

Nest azimuth appeared to be important for WbVs in KGR as there was a significant preference for nesting on the northern side of the nesting tree. Previous studies have mentioned a preference for nest positions in the canopy from aerial surveys, such as Murn *et al.* (2012) who observed a preference for vultures to nest in the southern sides of canopies and suggested that this was for protection from prevailing winds or direct sunlight throughout the day. The findings from this study suggest that WbVs in KGR often choose to nest on the northern side of the tree, potentially supporting wider findings that suggest a preference for nest position to protect nests from prevailing winds (Mainwaring *et al.* 2015). This is particularly important during WbVs' breeding season in KGR, as winds come from a South to South-East direction. However, WbVs in KGR do not appear to prioritise specific nest position according to placement around the peripherals of the canopy.

With relation to distance to water there was no significant difference in the distance between occupied and unoccupied trees, with occupied trees averaging 13.77km from water sources compared to 13.01km for unoccupied trees. This observation is in contrast to previous studies that have found WbVs to prefer nesting along rivers in riparian vegetation with a preference for *Sengalia* and *Vachellia* species (Kemp & Kemp 1975; Houston 1976; Whateley 1986). However, the large number of endorheic pans and ephemeral drainage lines within KGR may minimise WbVs' preference for nesting near water. Since their breeding season begins in October, coinciding with the arrival of seasonal rains, WbVs likely prioritise tree canopy structure over distance to water. During this time, the availability of water in the environment is already abundant, potentially reducing the need to nest near permanent water sources.

The results of this study show that WbVs select the tallest trees in surrounding vegetation for their nests, with 22 of the sampled 30 nest trees being the highest trees within a 50 m radius around the occupied tree, and 21 of the sampled 30 trees being the highest trees within in a 100 m radius. Selection for the tallest tree within an area may facilitate easier take-offs and landings for WbVs, as the open space beneath and around the canopy provides unobstructed flight paths to and from the nest (Newton 1979). Nesting in the tallest tree within an area may also be beneficial for predator identification from further distances. White-backed Vultures generally utilise passive defence strategies, relying on nesting in high, inaccessible trees rather than engaging in direct aggression toward threats to the nests (Mundy *et al*. 1992; Houston 1976), so they likely benefit from having easy access to escape ambush or surprise predators. Although adult WbVs can easily flee from danger, their eggs cannot. As such, WbVs may also choose taller trees to confer protection for eggs and chicks from ground predators.

Part of this study was to investigate if the use of LiDAR and photogrammetry could aid or improve WbV nesting research. The LiDAR data successfully extracted accurate measurements of canopy height, canopy area, canopy roughness, and various surrounding tree variables such as woody vegetation cover and height. The LiDAR data also made the extraction of the measurements easy and time-efficient compared to traditional methods. Once the trees were identified and selected, it took only a matter of minutes to extract the measurements for all trees in the study. These data were then able to be stored and backed up immediately onto a server, rather than being manually written down on paper and potentially lost or incorrectly recorded due to human error. Using the HALO system also proved to be much safer for the individual collecting data, as the HALO was flown from one spot for each survey area, reducing the risk of encounters with dangerous animals or being exposed to harsh weather conditions such as extreme heat or wind while climbing trees. These advantages enabled the type of RSF analysis that was conducted, as many other trees that were unoccupied needed to be measured, which would have been incredibly time-consuming and difficult to execute manually.

The RGB imagery used to create the orthomosaics was crucial for accurately locating and confirming the nests within the occupied trees. Without this imagery, it would have not been possible to pinpoint the specific trees and collect the necessary data. Therefore, unless the precise GPS coordinates of the nesting trees are known, this study can conclude that RGB orthomosaics are crucial for accurately identifying WbV nests using this approach. The imagery also allowed for better identification and quantification of the exact position of the nest within the canopy, which appears to be a new possibility for study of WbV nests at this spatial scale.

Surrounding vegetation metrics such as woody cover percentage and roughness, as well as height, were also extracted using the LiDAR data. This data extraction technique proved effective and beneficial in terms of accuracy and time. With LiDAR data, researchers are able to create horizontal cross-sections of canopy height, enabling for increased detail of canopy strata information of the woody vegetation from the ground up. This could prove beneficial for future research that requires in-depth information of canopy structure at different heights.

Despite the measurable benefits of the LiDAR data, which introduced more accurate, time-efficient and effective ways of measuring trees for WbV research, there were some shortcomings that could pose challenges to others that would like to adopt this method. LiDAR devices, especially the one used for this study, are expensive to purchase. There are also multiple different programs that require paid subscriptions to process resulting data, as well as dedicated training on how to use the programs to process and analyse the data. Additionally, the RGB orthomosaic was notably limited in reliably identifying tree species. Finally, the UAV and flying component of this data collection can be challenging as many countries require professional UAV-licensed pilots to operate drones for commercial or scientific use. This limits researchers from being able to conduct the LiDAR surveys and forces many to hire dedicated professional UAV pilots for these projects, increasing cost and logistic constraints.

CHAPTER FIVE
CONCLUSIONS AND RECOMMENDATIONS

WbVs face a multitude of threats to their existence and need ongoing support and intervention to ensure their future. Understanding their nesting preferences is a crucial factor in WbV preservation and, as such, this study aimed to identify and characterise the structural and taxonomic features of trees used as nesting sites by WbVs in KGR while determining the effectiveness of a new approach for data collection and analysis by using remote-sensing technology: LiDAR and RGB imagery. Karingani Game Reserve is an ideal location to add valuable WbV ecology data as there is a strong breeding population present with 115 known nesting sites as of 2020, with an 18% increase per annum (Goodman & Worth 2020).

From the data collected, this study found that WbVs in KRG prefer nesting in tall trees (>14m) with larger canopies (mean of 161.58m²) and increased canopy roughness (averaging 4.04**s**). WbVs in KGR or seemed to prefer nesting on to the North side of the canopy. Distance to water and was not found to be significant variables in WbVs' nesting preferences. White-backed Vultures also most often selected the tallest tree within a 100 m buffer, but no significant pattern was found in favour of choosing nesting trees in relation to surrounding vegetation density or roughness at or above 3 m and 10 m in height.

These findings suggest two outcomes; First, WbV conservation efforts in KGR should focus on preserving trees with higher and more inconsistent (i.e., rough) canopies to support WbV nesting preferences, ensuring the protection of tree species (especially *B. maughamii)* known for their complex canopy structures. Maintaining the health and integrity of these trees is also essential. Understanding vulture nesting preferences will inform knowledge on habitat suitability and contribute to WbV conservation generally by guiding management actions. Moreover, understanding the nesting preferences of WbVs can provide valuable insights for the conservation of other large raptors. Maintaining a diverse array of large-canopied trees within a habitat can help support a variety of raptor species, each with its specific nesting requirements. This approach can enhance biodiversity and ecosystem stability, ensuring the survival of these important bird species (Thiollay 2006a).

Second, although there are some limitations with access to the remote-sensing equipment needed and expertise required to collect and process the data to conduct such measurements for this research, this study found that technology that enables the collection of LiDAR and RGB data can indeed enhance surveying power for future studies of raptor ecology and conservation. Traditional methods of measuring trees and nesting sites for raptors that nest in large trees are time-consuming, hazardous to human safety, inaccurate and ineffective over large areas. This study employed advanced technologies to capture nesting data and analyse WbV nesting preferences in KGR with great effect. The precision of these data and their concurrence with existing literature suggests that LiDAR and RGB can be employed effectively in future data capture and analysis of large raptor research.

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