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# The Gnu Frontier:
# Deploying machine learning and open-source electronics for the study of ungulate movement in the Anthropocene

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# Abstract

The Anthropocene epoch has ushered in unprecedented and irreversible changes in many biomes, resulting in the disruption of ecological functions and processes. These changes are largely driven by the increased human footprint on a planetary scale and global warming. Consequently, various impacts have been documented, including the extinction of flora and fauna, modification of ecosystems into more homogeneous covers (e.g., farmlands), increase in human-dominated landscapes, disruptions of animal migrations, species range shifts, invasions leading to the extermination of native species, and encroachment of protected areas. These widespread ecosystem changes have become a primary concern for researchers and policymakers who must maintain a delicate balance between the persistence of species and their habitats and the promotion of sustainable development. Furthermore, the rate at which these changes are occurring outpaces the evolutionary response of many species. Consequently, gaining insight into how species respond to various ecological disruptions, both within and outside protected areas, is imperative. However, a thorough understanding of animal behaviour and their responses to rapid ecosystem changes remains challenging due to the lack of robust tools for collecting fine-grained data.

To address this methodological gap, I first use camera trap data to demonstrate how migratory species in the Serengeti ecosystem are spatially distributed in relation to human activities occurring in the immediate landscapes adjoining protected areas. The results reveal that the species tend to avoid areas transitioning into human-dominated landscapes as opposed to those bordering buffer zones. The results hold significant conservation value and illuminate population-level responses to anthropogenic disturbances. However, camera trap data does not provide individual-level behavioural insights. Consequently, it remains unclear which additional factors and social cues animals may be observing when traversing across habitats

with varying threat levels and how these factors influence their behaviour. Camera traps and telemetry tools such as GPS alone cannot provide data required to answer such questions; therefore, a different set of tools is necessary. Leveraging the capabilities of open-source electronics, I present a low-cost system for automated and repeated observation of collared animals. This system consists of a GPS collar, a long range network (LoRa) radio transmitter, and a commercially available low-flying unmanned aerial vehicle (UAV), taking advantage of its built-in capacity to track a stream of GPS points. The system was tested on a small group of ponies and demonstrated its efficacy and performance by collecting data on focal individual as well as information about its nearest neighbours.

Furthermore, automated tracking system collects data in bursts of approximately 20 minutes, aligning with the flight time capacity of a fully charged battery. As such, obtaining behavioural data for longer periods is difficult which necessitates a different approach. Given the rapid ecological changes, it is crucial to understand animal behaviour and its perception of the immediate surroundings. For instance, where do animals spend more time being vigilant as opposed to engaging in other restorative activities like resting? Such areas could be regarded as risky from an animal's perspective. In this study, I developed a near real-time animal behaviour classifier using low-cost open-source electronics, a low-power long-range wide-area network (LoRaWAN) for connectivity, and edge machine learning. The custom-designed animal tracking system records behavioural data, preprocesses it, and classifies it into four classes: grazing, lying, standing, and walking. The predicted behaviour classes are transmitted to the end-user via servers in near real-time. The tracking tool was tested on Serengeti wildebeest and demonstrated its performance by sending both behavioural classes alongside positional data of the collared animal.

In this study, I have demonstrated the utility of existing remote tracking tools as well as their limitations in addressing evolving ecological questions in relation to animal behaviour and response to ecosystem perturbations. The methodological approaches presented here have the potential to greatly enhance our understanding of animal ecology. Importantly, the application of novel technologies will empower scientists to enhance existing tools, generate complementary data streams, improve data resolution and quantity, and enrich their overall capabilities to study complex questions. For instance, it improves our ability to collect behavioural and positional data, monitor focal individuals, and track nearest neighbours, and potentially opens up other avenues for scientific applications. The application of open-source electronics creates an opportunity for other researchers to customise the tools as an alternative to commercial devices to address specific questions and potentially result in other valuable innovations.

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# Declaration

I, Cyrus Mutunga Kavwele, hereby affirm that all the information presented in this report is accurate, truthful, and valid. Any external information used, which I do not own, has been appropriately cited and referenced.

# Co-authorship statement

Chapter 1

Author contributions: Cyrus M. Kavwele wrote the chapter with inputs from both supervisors.

Chapter 2

Author contributions: Cyrus M. Kavwele, Colin J. Torney, J. Grant C. Hopcraft and Thomas A. Morrison designed the study. J. Grant C. Hopcraft, Thomas A. Morrison, Joseph Masoy and Majaliwa M. Masolele collected data. Cyrus M. Kavwele, Colin J. Torney, Sidney Fulford, Thomas A. Morrison and J. Grant C. Hopcraft analysed data. Cyrus M. Kavwele, Colin J. Torney and J. Grant C. Hopcraft wrote the paper with input from all authors. All authors gave approval for the publication of the final manuscript.

Chapter 3

Author contributions: Cyrus M. Kavwele, J. Grant C. Hopcraft and Colin J. Torney conceptualized the study design. Cyrus M. Kavwele and Colin J. Torney developed the code and 3D housing. Cyrus M. Kavwele collected data with help from Colin J. Torney, Grant C. Hopcraft, Dennis Minja, Majaliwa Masolele and Deborah Davy. Colin J. Torney developed the computer vision model for data extraction. Cyrus M. Kavwele analysed data and drafted the manuscript with inputs from all authors.

Chapter 4

Author contributions: Cyrus M. Kavwele, J. Grant C. Hopcraft and Colin J. Torney designed the study and collected model training data. Cyrus M. Kavwele cleaned the training data and developed the model. Cyrus M. Kavwele, J. Grant C. Hopcraft and Colin J. Torney deployed the LoRa collar in Serengeti. Cyrus M. Kavwele analysed the near real-time behaviour data and drafted the manuscript which received inputs from all the authors.

Chapter 5

Author contributions: Cyrus M. Kavwele wrote the chapter with inputs from supervisors.

# Chapter 1

# Introduction

## 1.1 History of the Anthropocene

The history of the earth's system is marked by geologists according to stratigraphic changes that record the major biotic compositions (Aunger, 2007; Bardi, 2016). The recent geological epoch strongly characterised by the human activity with profound influence on the global environment suggests that we are currently in the ***Anthropocene epoch*** (Crutzen, 2006; Zalasiewicz et al., 2011). The start of the Anthropocene epoch is a subject of debate, with proposals suggesting its onset in 1850, a period that aligns with the commencement of global-scale industrial expansion (Ruddiman, 2013). The influence of humans on the Earth began to appear strongly toward the end of the ***Pleistocene epoch***, during which certain "megafauna" such as the sabre-toothed cats in North America and the woolly mammoths (*Mammuthus primigenius*) of Siberia disappeared.

Although some megafauna species still exists in other parts of the world such as Africa and Asia, they are facing threats attributable to human activities (Zalasiewicz et al., 2011). For instance, land cover conversion through agriculture, development of infrastructure, hunting for animal products and their derivatives have contributed to the global decline of flora and fauna. Since the coining of the term Anthropocene, its usage both within academia and outside has increased rapidly (Dalby, 2013) and there has been a surge in popularity following the publication of two influential papers about two decades ago (Crutzen, 2002, 2006).

To contextualise the Anthropocene and its defining characteristics, there are several geological human actions that impact negatively not only the Earth's major biogeochemical cycles but also the evolution of life. The epoch is characterized by a substantial increase in human impact on the global environment, beginning around 1945 and continuing to the current era, a period that has been referred to as the ***Great Acceleration*** (Hibbard et al., 2006). After slow and uneven population growth, the abundance of humans increased to 2.5 billion by 1950. Future projections estimate the world's population will reach 8.9 billion by 2050 (Bongaarts, 2009). The exponential human population growth has had significant ramification on the environment and will continue to exert more pressure unless human consumption patterns change to support and facilitate ecological resilience and recovery. The use of fire by early humans is considered one of the earliest significant environmental impacts, as evidenced by the presence of fossil charcoal dating back to the early Pleistocene Epoch (Glikson, 2013; Lewis and Maslin, 2015; Roebroeks and Villa, 2011). Since then, anthropogenic activities, coupled with advances in technology, have continued to change the face of the Earth in many spheres. For example, the rise of atmospheric carbon dioxide ($CO_2$) as shown in figure 1.1c has lead to global warming resulting in de-iced polar oceans, rising of sea levels (Shepherd et al., 2010; Stroeve et al., 2007), and ocean acidification (Doney et al., 2009). Similarly, the global nitrogen (N) cycle has been disrupted by processes such as nitrogen fixation and fossil fuel combustion, leading to an increase in the concentration of the greenhouse gas nitrous oxide ($N_20$). The increase in human-caused N inputs have resulted in eutrophication of water bodies causing algae blooms and consequently, threatening aquatic life (Vitousek et al., 1997).

The rapid explosion of the modern human population has been a direct driver of urbanization, leaving a visible mark of mankind's imprint on the planet. This phenomenon is closely linked with the industrial revolution and has had a profound impact on the environment. For instance, about 30%-50% of the planet's surface has been modified by activities such as clearing forest, draining swamps as well as building dams and changing river courses to provide food and power for modern industries (Crutzen, 2016; Zalasiewicz et al., 2011). The Anthropocene has witnessed a decline in Earth's biodiversity, particularly the loss of megafauna, which aligns with the global expansion of human activities (Johnson, 2009; Malhi et al., 2016; Sandom et al., 2014) as shown in figure 1.1a,b. As such, the global patterns of rapid loss has been in regions that have experienced sudden arrival of *H. sapiens* (Malhi et al., 2016; Sandom et al., 2014; Surovell et al., 2016) and not climatic variation (Sandom et al., 2014) with exception of Europe (Barnosky et al., 2004).

The extinction of megafauna during the Anthropocene epoch has significant implications, particularly for terrestrial ecosystems. These megafauna play vital roles, such as shaping the physical structure of ecosystems through browsing, tree breakage, and trampling, as well as mediating the competitive balance between herbaceous and woody vegetation (Bakker et al., 2016), diversity and composition of vegetation community (Malhi et al., 2016) thus accelerating ecosystem biogeochemical cycling (Hobbs, 1996; Malhi et al., 2016). The current geological epoch is also typified by ongoing state of collapse of the Earth's entomofauna (van der Sluijs, 2020) a phenomoenon posing a great risk to insect mediated ecological processes and functions such as nutrient cycling, biological pest control, pollination services which are crucial for survival of other species (Daily and Karp, 2015; van der Sluijs, 2020). For example the decline of beetles, months and caddisflies has been well document in the Netherlands (Hallmann et al., 2020). Given the immense human-induced pressures, coupled with global warming, the equilibrium of Earth's systems will be disrupted. This includes a shift in critical balances, such as greenhouse gas concentrations, the energy received from the sun and radiated back into space, nutrient cycling, precipitation, evapotranspiration, and others. These imbalances can lead to social-economic instability and environmental unpredictability, ultimately resulting in a biodiversity crisis. For example, local or regional flora and fauna that cannot adapt to a rapidly changing environment may face extinction.

## 1.2 Animal movement in the Anthropocene

Movement, which entails spatial relocation of the whole individual in time (Nathan et al., 2008) spans a wide range of spatial and temporal scales, from just a few cms in protozoans to thousands of kilometers exhibited by larger vertebrates like whales, terrestrial mammals, and birds. This phenomenon occurs on various scales, from local to regional and global

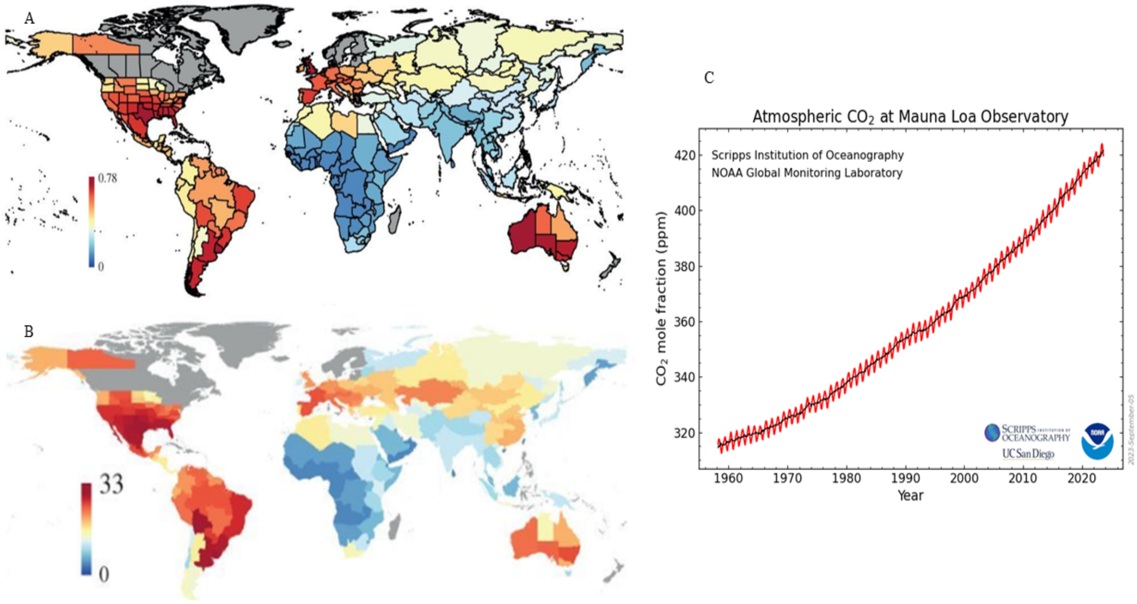

Figure 1.1: *(a)* The proportion of extinct large mammal species (more than or equal to 10kg body weight) in each Taxonomic Databases Working Group (TDWG) country during the last 132,000 years, only counting extinctions earlier than 1000 years BP.*(b)* The cumulative number of extinct large mammal species occurring in each Taxonomic Databases Working Group (TDWG) country. *(c)* Atmospheric carbon dioxide mole fraction (ppm) between 1960-2023 downloaded on 05th September 2023 measured at Mauna Loa Observatory, Hawaii,USA (website:`https://gml.noaa.gov/ccgg/trends/mlo.html`). The figure (*a* and *b*) are adapted from (Sandom et al., 2014)

(Hansson and Åkesson, 2014). It is a fundamental trait that occurs in various life stages, whether in the air, water, or on land, either passively or actively. It plays a crucial role as it is the link between various ecological processes ranging from individual fitness, species interaction, population structure and dynamics to the evolution and diversity of life (Abrahms et al., 2021; Nathan et al., 2008; Questad and Foster, 2008). In a dynamic world, animals must track the spatial-temporal configuration of the resource landscape (typically in response to phenological waves) in order to acquire the resources they need to survive. This leads to the emergence of animal movement patterns such as migration (Abrahms et al., 2021; Armstrong et al., 2016). As such, the movement at an individual level can be categorised into a framework with four mechanistic components, namely: the internal state of the animal, motion capacity, navigation capacity and external factors as shown in figure 1.2a. Each of these components result in a distinct movement path, such as the movement patterns of wildebeest and elephant illustrated in figure 1.2b and c.

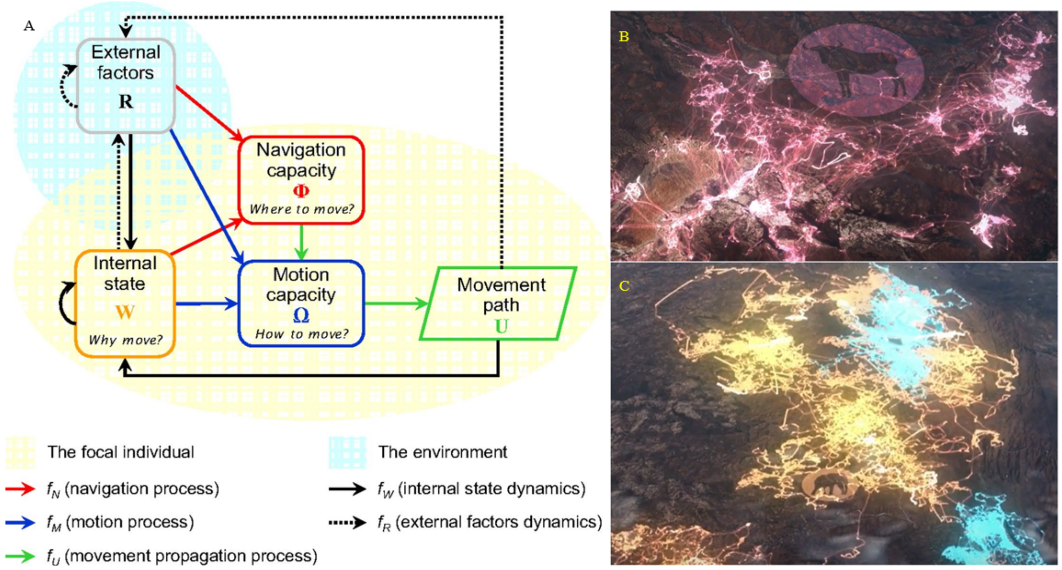

Figure 1.2: *(a)* The conceptual framework of components that drive movement at an individual level and their relationship adapted from (Nathan et al., 2008). *(b)* and *(c)* depicts simulated movement path of wildebeest and elephant in the African savanna sourced from Movebank (website:`https://www.movebank.org/cms/movebank-main`).

The external component consisting of both abiotic and biotic factors has become a major focus in study of animal movement. In the realm of abiotic factors, climate change stands as a prominent manifestation of humanity's significant impact on the planet(Kauffman et al., 2021; Steffen et al., 2011). The irregular disruptions in environmental predictability, such as variations in green-up and other significant events such as seasonality, have implications for animal migration and movement patterns (Riotte-Lambert and Matthiopoulos, 2020). For instance, in migratory species, the start of migration is timed to coincide with the onset of spring and arrival on summering grounds when resources are abundant. As such, environmental predictability of seasons is crucial alongside animal ingrained behaviours and other cues. However, if rapid anthropogenic activities continue to drive climate change and disrupt seasonal patterns in the process, it may lead to the creation of ecological traps for animals, ultimately making migration in the Anthropocene a costly and challenging endeavor. A classic example occurs when migratory species leave and arrive either too late or too early in their summering grounds, thus missing important phenological phases and leading to the use of suboptimal habitats. (Riotte-Lambert and Matthiopoulos, 2020; Robertson et al., 2013). A case in point is the Olive-sided Flycatchers (*Contopus cooperi*) a disturbance-dependent species whose nesting success has been affected by human activities that mimic natural perturbations such as forest thinning (Robertson and Hutto, 2007). In this instance, the movement of the bird species is triggered by changes in the environment driven by human activities, as opposed to natural factors. Large ungulates in South Africa, such as African elephants (*Loxodonta africana*), plains zebras (*Equus quagga*), and blue wildebeest (*Connochaetes taurinus*), migrate in response to water availability. However, due to erratic rainfall patterns, the populations of some species have declined (Owen-Smith and Ogutu, 2012), providing a clear example of how climatic variability is affecting animal movement.

A global comparative study on animal movement in the Anthropocene has revealed that increased human presence tends to reduce the distances animals move. This change in movement patterns could be attributed to behavioural responses to the human footprint, such as increasing farmlands that provide unintentional supplemental feeding (Tucker et al., 2018) and can result in human wildlife conflict (e.g., crop raiding by African elephants (Troup et al., 2020) and Asian elephants (*Elephas maximus*) Naha et al. (2020)). Furthermore, in regions where there are significant interactions between humans and wildlife, which often leads to the persecution and hunting of animals, other behavioural changes and adaptations can occur in animals. For instance, the animal may forgo crucial behaviours such as grazing at the expense of vigilance and walking/running as a response to the anthropogenic disturbances to the detriment of reproduction, health and survival (Ciuti et al., 2012).

The long-distance movement of ungulates in large numbers, commonly termed as migration, is a spectacular natural phenomenon that captivates the interest of scientists and non-scientists alike. However, movement in the context of animal migration between key isolated habitats has been affected by anthropogenic activities. Most of these aggregated terrestrial mammal migrations are extinct or declining largely due to increasing human activities leading to habitat destruction,loss, fragmentation, erection of barriers such as fences, excessive exploitation, and climate change (Wilcove and Wikelski, 2008).

A global audit by Harris et al. (2009) revealed that 6 mass migrations in Africa alone have gone extinct or have unknown status due to insufficient data about them. For example, the Cape springbok (*Antidorcas marsupialis*) that used to roam in millions at the Karoo landscape in South Africa were driven to extinction by hunting, diseases and fencing around the end of the 19th century. The migration of black wildebeest (*Connochaetes gnou*) native in Namibia and South African has also gone extinct (Berger, 2004; Gasaway et al., 1996). Other species whose migrations have been lost include the scimitar-horned oryx (*Oryx dammah*) that was once wide spread in West Africa and the quagga (*Equus quagga*) (Harris et al., 2009). In Kenya, land use changes, such as mechanized agriculture driven by market opportunities, have disconnected the wet season ranging area in Loita Hills from the Mara ecosystem. This disruption has affected the northern Serengeti-Mara ecosystem wildebeest migration, which has now collapsed; the subpopulation is now largely resident (Serneels and Lambin, 2001). Moving forward, animal movement in the Anthropocene faces increasing complexities and a multitudinous threats, pushing this natural phenomenon to the brink even in regions where migrations persist. A case in point is the Mongolian gazelles (*Procapra gutturosa*) and Khulan (*Equus hemionus*) whose habitat is undergoing fragmentation and loss due to creation of barriers (Ito et al., 2013). For instance, the Ulaanbaatar–Beijing Railroad has impacted the movement of Mongolian gazelles (Ito et al., 2005) while international fencing between Mongolia and China has hindered movement of Khulan (Kaczensky et al., 2011).

Given the ongoing changes in various landscapes, there is a high risk of losing the remaining migrations unless we address both the continued perturbation of ecosystems and the restoration of degraded ones. One of the major concerns is the potential ecological collapse that may occur following the cessation or reduction of ungulate migration. Terrestrial animal migrations play a significant role in influencing various direct and indirect processes, such as nutrient flow and nitrogen mineralisation, ultimately leading to increased grassland productivity (Bauer and Hoye, 2014; Harris et al., 2009; Torney et al., 2018a). Similarly, the loss of migration could pose significant challenges, especially in regions where tourism plays a vital socioeconomic role. This loss may potentially prompt changes in land use regimes, such as shifts towards agriculture and livestock farming, to compensate for dwindling sources of income, which could, in turn, lead to the eradication of natural vegetation (Harris et al., 2009).

In the context of changing landscapes, scientists' desire to understand *when*, *how* and *why* movement occurs has greatly benefited from valuable telemetry technology, which serves as a crucial tool for tracking animals and advancing the study of movement ecology across various species in both space and time.

## 1.3 Animal tracking and challenges

On-foot animal tracking is a difficult and strenuous activity, especially when dealing with species that are shy, timid, cryptic, can cover vast distances, and can outrun human beings. As such, collecting substantial volumes of data across various habitats spanning multiple seasons to answer subtle questions is impractical. Therefore, data generated through this approach are also very limited in applications, and only a narrow range of ecological questions can be explored.

Since the revolutionary invention of biotelemetry such as the use of radio collars pioneered by the Craighead brothers in the 1960s (Craighead, 1979), its adoption by ecologists world wide has led to exciting discoveries and unprecedented insights beyond what the pioneers envisioned (Hebblewhite and Haydon, 2010). The first technology ever deployed to track free-ranging animal, was a Very High Frequency (VHF) radio tag which dates back to the early 1960s (Cochran and Lord Jr, 1963; Lord Jr et al., 1962). Radio collars are now lightweight and small, which extends the range of species that can be tracked. (Jin et al., 2023; Kays et al., 2011). However, they have some serious limitations. They are labour-intensive because the operator needs to search potential target areas to establish strong signal receptions, often covering several kilometres. For instance, when an animal cannot be seen directly or is cryptic, its location can only be established through triangulation, which involves determining the bearing of the animal from different locations and calculating its exact position. Furthermore, the scale of data collected is very small, typically less than 50 data points collected in a day (Tremblay et al., 2017). These limitations led to the development of automated radio-telemetry (ARTS) (Kays et al., 2011) which needs relatively less labour but requires multiple receiving stations and multiple receivers per station (Jin et al., 2023). However, through continuous development and collaborative efforts an automated radio-telemetry for instance, the motus wildlife tracking system (MOTUS) (`https://motus.org/`) has been designed to facilitate landscape-scale research of migratory animals. The platform has been used to track monarch butterflies (*Danaus plexippus*) and common green darner dragonflies (*Anax junius*) migrations between southern Ontario, Canada and into the United States (Knight et al., 2019) demonstrating its usefulness.

The development of the Argos systems in the 1980s using *Collecte Localisation Satellites* (CLS) (`https://tinyurl.com/4xkt96dh`) became a crucial tool for large-scale tracking of vertebrates on both land and in water (Witt et al., 2010) such as, caribou (*Rangifer tarandus*) (Tamstorf et al., 2005) and camelids (*Camelus dromedarius*) (Grigg et al., 1995). An animal equipped with CLS is geolocated using a combination of radiotransmitters called Platform Transmitter Terminal (PTTs) and the satellite-borne receivers. The encoded signal is transmitted to the satellites passing overhead (Witt et al., 2010). Argos PTTs broadcast a signal at 406.65MHz, which is detected multiple times by individual polar-orbiting satellites. These signals are then relayed to a ground-based processing station, where the location of the tracked object on the Earth's surface is determined using the Doppler effect principle. Locations are categorized into several levels of accuracy, denoted as location classes (LC) LC3, 2, 1, 0, A, B, and Z. (Fancy et al., 1988). LC-3 has an error of less than 150 meters, LC-2 ranges between 150 meters and 350 meters, LC-1 ranges between 350 meters and 1000 meters, LC-0 has an error greater than 1000 meters, while LC-A, LC-B, and LC-C do not have error estimates, and data are stored on the satellite, minimizing battery power requirements (Costa et al., 2010). Further details can be found in the CLS ARGOS system user manual (`https://tinyurl.com/y8jfbaak`).

A significant limitation of the Argos-derived locations is their low spatial accuracy, especially for collared animals that spend considerable time submerged, or for terrestrial animals that inhabit dense forests and subsequently obscure overhead satellite signals (Hays et al., 2001; Vincent et al., 2002). Despite these challenges, Argos systems can be useful in cases where no other means of retrieving data is possible as well as in situations where the cost and weight of the tag in relation to the animal to be collared are major considerations (Dubinin et al., 2010). Due to the evolving nature of the system, its applications have expanded into other fields. For example, it is now used in smart agriculture, including livestock tracking and pollution monitoring. It also plays a role in collecting in-situ data to enhance ocean protection, among other applications. The system has become useful in tracking species that move vast distances through inaccessible habitats where applicability of the traditional VHF radio tracking is impractical.

To fulfil scientific requirements that go beyond what could be achieved using the Argos system, such as addressing low spatial resolution challenges when monitoring animals that inhabit dense forests, alternative approaches to rapidly and accurately ascertain animal's location are necessary. One such development is the global positioning system (GPS) a satellite-based navigation system. GPS uses a trilateration process to determine the location of a point on Earth's surface. A GPS receiver is programmed to receive radio signals from GPS satellites and determine its location by measuring the time it takes to receive signals from at least four satellites (El-Rabbany, 2002). GPS systems are more accurate as well as repeatable compared with ground-based VHF triangulation techniques or even Argos satellite Doppler-based positioning (Coelho et al., 2007), VHF tracking form aircraft or Argos system (Soutullo et al., 2007). Additionally, they enable automated tracking at set time intervals with minimal observer bias and have the potential to collect large sets of GPS data (Dodd et al., 2007).

GPS top-level precision was initially reserved for military use. However, it was intentionally degraded for non-military use, a practice referred to as selective availability, which began in March 1990 (Tomkiewicz et al., 2010). The non-military degraded GPS had a precision of approximately 100 meters. In response, commercial users developed differential GPS (DGPS) as an independent approach to minimize the selective availability (SA) error (Moen et al., 1997; Rempel and Rodgers, 1997; Tomkiewicz et al., 2010). In principle, the observed errors of a receiver at a location are established, then applied as a correction factor to the other GPS receiver to obtain their 'true' positions (Tomkiewicz et al., 2010). However, by May 2000 selective availability was suspended and permanently decommissioned in September 2007. The early GPS receivers required 10-30 minutes to acquire satellites, and even with a 'warm start,' the minimum time to first fix (location) was still lengthy before a location could be acquired. Therefore, to use GPS in animal tracking, minimizing the time to first fix was crucial since they are programmed to periodically turn on and off to manage power consumption and extend longevity of use. However, modern GPS receivers' time to first fix is about 30 seconds or less, especially if they have a good antenna and a clear view of the sky. This development is attributable to a complete satellite constellation, with backup that is more constant and predictable (Tomkiewicz et al., 2010).

Integrating GPS technology into animal telemetry marked the beginning of a new era of animal biologging, with some early applications in tracking of sea turtles (Godley et al., 2008), investigation of spatial distribution of marine predators as a function of sea-surface temperature (Grémillet et al., 2008), moose (*Alces alces*) response to road network (Laurian et al., 2008), mapping of foraging pathways of the king penguin (*Aptenodytes patagonicus*) (Trathan et al., 2008) just to mention a few. This was followed by efforts to reduce power consumption, develop long-life batteries, and acquire fine temporal resolution tracking data, which has significantly advanced our understanding of various ecological themes (Kays et al., 2015). For example, long-term tracking of migratory raptors has revealed when and where their mortality occurs (Klaassen et al., 2014), functional connectivity as enhanced by large frugivorous birds, which move seeds from one patch to another(Mueller et al., 2014), testing leadership in flocking pigeons using light weight GPS devices (Nagy et al., 2010), intergroup contests in Capuchin monkey (*Cebus capucinus*) social groups of varying sizes (Crofoot et al., 2008), corridor and connectivity mapping (LaPoint et al., 2013; Roever et al., 2013), and energy expenditure in Pumas (*Puma concolor*) (Williams et al., 2014).

The continuous development in telemetry technology has undeniably revolutionised the field of movement ecology, enabling researchers to uncover a wealth of impressive discoveries, such as migratory patterns and behaviour in unprecedented detail, offering profound insights into the natural world. However, animal tracking faces challenges largely due to the increasing complexity of ecological questions, often fueled by the overarching goal of understanding how animals respond to a rapidly changing environment. For instance, off the shelf GPS tracking device offer very limited programmability inhibiting customisation by the end user hence limited modification can be incorporated. Additionally, in instances where the option to alter sampling frequency to address specific need is provided, longevity of use is compromised because of power issues. Although GPS technology has reduced the human resources required for manual tracking of animal, the associated costs are still high (Hebblewhite and Haydon, 2010). An example of this is when a GPS collar for ungulates includes extra features such as two-way satellite communication for data retrieval, adjustable sampling schedules, larger batteries, and near-real-time data transmission for geofencing applications. These additional features can significantly increase costs, resulting in challenges such as small sample sizes, limited population-level inference, and a limited range of ecological applications (Hebblewhite and Haydon, 2010). Consider the example of the Serengeti wildebeest collar, where a unit with a drop-off mechanism costs approximately €2,000, along with a €30 subscription fee. Additionally, an extra fee is incurred if any GPS unit acquires more than 100 fixes in a month, equivalent to four fixes in a day (*personal communication*). Given the circumstances, continuous innovation and the adaptation of novel technologies are essential to push the boundaries of our comprehension of the nuances of animal behaviour and movement in its changing environment.

## 1.4 Application of novel technologies in wildlife studies

Researchers' attempts to follow animals in their natural environment have come a long way and have benefited substantially following continuous advances in technology. Such novel technologies have made it possible to track animals in the air, water, and terrestrial ecosystems (Costa-Pereira et al., 2022) facilitating detailed insight into species interaction (King et al., 2018; Strandburg-Peshkin et al., 2017; Torney et al., 2018b) even on a lifetime scale (Nathan et al., 2022).

Remote sensing has become a viable tool for monitoring animals and their environment and it entails acquisition of data about a target without being in contact with it (Duporge et al., 2021). Several technological innovations have led to the production of various devices that can acquire data remotely or in combination with others, thereby offering complementary streams of data. A case in point is where ecologists are able to link animal movement trajectories to phenological waves by combining GPS data and satellite imagery (Bohrer et al., 2014; Thorup et al., 2017). However, satellite imagery can be used as stand alone to answer other ecological questions such as monitoring human footprint, assessing habitat productivity, classification of land cover types, surface temperature among others.

As a monitoring tool, the application of satellite imagery is advantageous because it covers a large spatial extent and revisits a specific point on Earth at short intervals, allowing for reassessment (Duporge et al., 2021). For example, GeoEye-1 temporal resolution (revisit time) is less than a day, spatial resolution of 1.24m at nadir and swath width of 13.1km (`https://earth.esa.int/eogateway/missions/worldview-3`). The availability, albeit commercial, of high spatial resolution data, generally less than 10 meters paired with ample spectral information, offers new possibilities for differentiating objects of interest from the background (Wang et al., 2010). Thanks to these properties, remote sensing products have been employed to track animals from space where the background is uniform such as seascapes. This approach has been used to detect whales in known calving, breeding and feeding sites (Abileah, 2002; Cubaynes et al., 2019), to estimate colony size of Adélie penguins (*Pygoscelis adeliae*) (LaRue et al., 2014), count elephant seals (McMahon et al., 2014) and wildebeest (Wu et al., 2023). The application of remotely acquired satellite imagery to detect objects outside monochrome or homogeneous environments has advanced, as exemplified by Duporge et al. (2021), who have demonstrated the efficacy of high-resolution satellite imagery and deep learning to detect and count elephants in heterogeneous environments.

However, the application of remote sensing satellite imagery in detecting objects is limited in the sense that its reliability is influenced by the size of the object, the complexity of the background, and the contrast between the object and the surrounding environment (Duporge et al., 2021). For example, species that live in dense forests or canopies can be difficult to detect although thermal remote sensing could be an alternative. The data volume can also be substantial, depending on the desired spatial and temporal resolution, necessitating the use of powerful processors. Furthermore, the end user typically lacks the ability to modify the operations of a remote sensing platform.

Camera traps have become indispensable tools for biodiversity surveys due to their ability to cover extensive areas when deployed in large arrays compared to direct observation. They are less invasive due to their ability to record data remotely and offer logistical advantages in field research (Caravaggi et al., 2017) such as long term monitring without neec for direct observation and require minimal maintenance. The imaging methods include high speed-camera, three dimensional (3D) videography, thermal infrared imaging, multi-camera videography, and imaging sonar (Hughey et al., 2018). The decreasing cost of this equipment, driven by market competition (Rowcliffe, 2017; Tobler et al., 2008b), versatility (Rovero et al., 2013) and ongoing technological advancements, has led to the availability of high-quality cameras and sensors. As a result, their popularity is expected to continue on an upward trajectory (Caravaggi et al., 2017). Camera traps record high-definition images or videos of animals detected at specific sites, using each site as a sampling unit. The recorded images can be matched with other information, such as the date, time, greenness index value, number of individuals detected together, among other things, facilitating the study of social and ecological interactions (Caravaggi et al., 2017; Hughey et al., 2018). Some examples of application of camera trap include species diversity estimation (Tobler et al., 2008a), relative abundance (Carbone et al., 2001), population dynamics (Karanth et al., 2006; Rowcliffe et al., 2008), site occupancy by cryptic animals (Linkie et al., 2007). Stationary imaging has also been used to study collective behaviour for example Cavagna et al. (2008) used fixed a camera on top of a building to record individual positions and movements of starlings (*Sturnus vulgaris*) in large flocks. Furthermore, the complexity of ecological questions addressed using camera trap data is evident. For instance, activity patterns of agouti (*Dasyprocta punctata*) and ocelot (*Leopardus pardalis*) (Suselbeek et al., 2014), bush rat (*Rattus fuscipes*) antipredator responses (Carthey and Banks, 2016), animal travel speed (Rowcliffe et al., 2016) among other applications.

While the use of camera trap as monitoring tool offers a range of benefits, their inherent operation from a fixed position is a drawback. For instance, imaging from a fixed position in a laboratory setting is possible when the entire region of interest is within the field of view, enabling the capture of sufficient details. However, tracking the movement of individuals within groups is challenging in the natural world, where moving animals often occlude one another

(Hughey et al., 2018). One technological advancement to address this challenge would involve designing a miniaturised camera (animal welfare concerns) with GPS capability and the ability to run image detection models although the occlusion problem would persist. This would ensure that each distinct record of a given coat pattern associated thin an individual is geo-tagged (Nichols et al., 2011), and the information which often reached terabytes of data (Fennell et al., 2022) can be extracted to reconstruct movement trajectories.

Remote animal tracking using GPS technology began in the early 1990s (Tomkiewicz et al., 2010) and has progressively advanced to offer a high-spatial resolution data. As such, improvement in the technology such as, smaller GPS receivers that operate at lower voltages hence with power consumption and extended longevity of use has led to the emergence of new scientific questions in the field of animal ecology and conservation (Cagnacci et al., 2010; Hebblewhite and Haydon, 2010; Kays et al., 2015). The precise temporal and positional data from the GPS collars are crucial and intuitively allow ecologists to relate an animal to its environment. For example, migrations across landscapes are hypothesised to respond to spatial variations in resources, especially for migratory ungulates (Boone et al., 2006; Leimgruber et al., 2001). As such, by combining high-resolution spatiotemporal data with resource 'maps' from satellite platforms like the Moderate Resolution Imaging Spectroradiometer (MODIS), clear evidence of migration as a function of seasonal resource pulses has been generated. This achievement would have been unimaginable without GPS technology (Hebblewhite and Haydon, 2010). Thus, the technology is crucial in helping us decipher species and ecosystem interactions that are fundamental for overall fitness.

Over the decades, GPS technology has advanced to address some key concerns such weight of the fully assembled collar in relations to the target species. GPS technology was first used to track large herbivores such as, elephants (*Loxodonta africana*) (Douglas-Hamilton, 1998), moose (*Alces alces*) (Edenius, 1997) and bears (*Ursus arctos*) (Schwartz and Arthur, 1999). However, following miniaturisation of GPS collars to reduce impacts on study subjects and animal welfare (Kays et al., 2015) their has expanded. They have also become more affordable and lighter making them useful for tracking small-bodies animals (Dore et al., 2020). Incorporating solar panels for battery charging extends deployment duration (Kays et al., 2015). Similarly, the success and adoption of the technology in ecological studies have necessitated the development of robust and sophisticated quantitative techniques (Morales et al., 2004) designed to address issues such as spatially correlated datasets (Fieberg et al., 2010), among other concerns.

Cagnacci et al. (2010) argues that, given the significant costs involved and the potential influence of the collar on animal interactions and behaviour (Tomkiewicz et al., 2010) , the data collected should have a lasting impact on scientific research and be used to address additional ecological questions beyond its initial purpose. While GPS technology has provided valuable insights into animal movement ecology, its application to address more complex questions is limited by small sample sizes, which can compromise robust population-level inferences (Lindberg and Walker, 2007). For instance, in collective behaviour studies where groups are cohesive, it is possible to fit all individuals with a collar. However, this becomes unfeasible if the group is large due to cost implications and fission-fusion dynamics (Couzin, 2006). As a result, using GPS collars alone implies that other social cues that an animal may be observing are not recorded.

Technological advances aimed at addressing conservation challenges have ushered the field into a new era of innovation. An example of this innovation is the utilization of low-cost autonomous unmanned aerial vehicles (UAVs), commonly known as drones, for biodiversity monitoring (Weissensteiner et al., 2015). Typically, a UAV system includes the platform called an unmanned aerial vehicle, a control system (ground control station), a payload (imaging system), and personnel necessary to control the operations of the the UAV (Gupta et al., 2013). Due to the inherent benefits that UAVs afford to users, such as the ability to cover inaccessible rough terrain (Fust and Loos, 2020; Hughey et al., 2018), their application in various areas has seen increased use (Baena et al., 2017; Castellanos-Galindo et al., 2019; Hardin et al., 2019). Outside of their use for military operations (Orfanus et al., 2016), the application of UAVs has expanded to other fields such as search and rescue techniques for emergency services (Goodrich et al., 2008), precision agriculture (Librán-Embid et al., 2020), habitat mapping and delineation (Padró et al., 2019), animal detection and counting (Hamilton et al., 2020; Spaan et al., 2019; van Gemert et al., 2015) among others.

Additionally, UAVs offer flexibility in various aspects, allowing for the use of multi-spectral sensors. This enables users to collect data in diverse weather conditions. Thermal or infrared sensors can be employed in areas with dense canopies or poor lighting conditions (Yang et al., 2022). Furthermore, remote control has been optimized to the extent that camera angles can be adjusted on the fly from several kilometers away by the operator (Hughey et al., 2018). Owing to such flexibility, UAVs have been used to remotely track group-living species to quantify movement and behaviour in the wild (Koger et al., 2023). In the study by Koger et al. (2023), a DJI Phantom 4 Pro drones (DJI) was flown at 80m height above the ground surface and manually adjusted the position of the drone to keep all herd members in frame. They also stopped filming whenever animals appeared disturbed by their presence or other cues. As such, the UAV operator had to maintain a minimal distance without compromising the quality of data.

Another case, demonstrating the flexibility and limitations of using UAVs, is based on personal experiences from conducting a pilot study on Serengeti wildebeest collective behaviour in April 2023, where I employed a slightly different protocol, with further studies to be undertaken in the future. Here, together with the crew members, the co-pilot, and observers, we approached an opportunistically sighted herd of wildebeest at 5km/h and stopped approximately 100 meters away to minimise any potential disturbance. A relatively flat area with short grass (<4cm) was identified as a launching and landing site, then a UAV landing pad was set. Once ready, the UAV was launched and climbed at an angle of 45° away from the herd to minimise any potential disturbance up to a height of 120m from the ground. Once airborne, the UAV camera was tilted to record nadir footage, then flown forward and stopped when the individuals at the front of the herd were positioned within the center of the frame. Filming started and stopped when all the individuals exited the frame or incase any potential danger was reported (e.g., birds of prey that attacked the UAV), and the position of the UAV was adjusted. The pilot study exercise was conducted for 10 consecutive days, resulting in 40 hours of tracking footage.

Filming from a static point was necessary because manual tracking from the UAV pilot's point of view is difficult. For instance, it is challenging to keep track of the focal individual since wildebeest have homogeneously coloured coats. There is the possibility of reacting to slight adjustments in position by a given focal individual, which are insignificant. Conversely, abrupt changes in direction could be difficult to track, which could introduce instability in the video frame, necessitating additional processing to compensate errors such as distinguishing foreground and background movements.

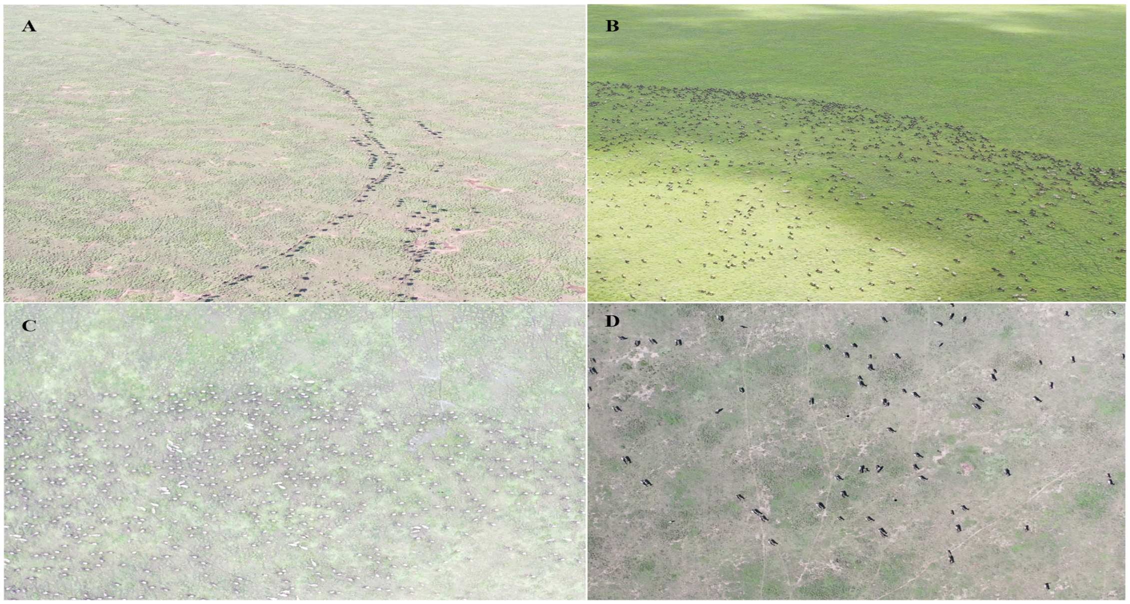

Figure 1.3: Aerial photos of collectively navigating Serengeti wildebeest taken with DJI Mavic 2 Pro UAV depicting various aggregation patterns: *(a)* shows a linear structural formation of moving wildebeest, *(b)* shows a pressure ridge, *(c)* shows an ordered behavioural state of moving wildebeest, and *(d)* shows a disordered state of grazing wildebeest. *Photo credits: Cyrus M. Kavwele, J.Grant C. Hopcraft, and Colin J. Torney.*

While the application of UAVs in tracking animal movement is innovative, there are a number of issues such as data processing and handling which need to be addressed as the technology continues to evolve. For instance, robust modelling techniques such as, machine learning are necessary for managing the voluminous data generated and for extracting relevant information for analysis. The distribution of the extracted data does not conform to classical statistical model assumptions, such as homoscedasticity and normality. Therefore, quantitative techniques capable of handling such non-conformity are necessary. Additionally, this approach is limited in the sense that tracking a particular individual within a group context across seasons, habitats, or along a disturbance gradient is impractical. This methodological limitation necessitates the automation of animal tracking, integrating it with other components, and leveraging UAV features to eliminate the need for manual operation, thereby reducing errors. Such consideration will enable scientists to repeatedly observe a particular individual within the group, improving data quality and broadening the range of ecological questions that can be addressed.

The continuously evolving technology has revolutionized the remote measurement of animal physiology, behaviour, and ecology in the wild, thanks to the production of a multitude of animal-borne sensors. Such inexpensive and miniature animal-borne sensors include accelerometers, magnetometers, temperature sensors, humidity, pressure sensors, heart rate sensors, and acoustic recorders (Hughey et al., 2018; Wilmers et al., 2015). The sensors can be used individually; however, when combined, they become a powerful tool capable of generating complementary streams of data. This presents another promising frontier for understanding animal behaviour and energy expenditure in relation to the environment (Hernandez-Pliego et al., 2017; Patterson et al., 2019).

Animal movement involves various activities such as grazing and vigilance, which are difficult to distinguish when using GPS positional data. As such, since their use in late 1990s (Brown et al., 2013) accelerometers have become arguably the most widespread sensors used to obtain animal activity budgets (Berlincourt et al., 2015; Brown et al., 2013; Patterson et al., 2019), crucially advancing our knowledge in relation to animal behaviour along its trajectory paths (Grémillet et al., 2004; Mendez et al., 2017; Ryan et al., 2004). Accelerometer sensors measure acceleration in 3-dimensional planes namely: forward-back, $x$-axis, side-side, $y$-axis, and up-down, $z$-axis (Shepard et al., 2008) at user defined frequency, typically >1Hz (Brownscombe et al., 2018). The measurement units of acceleration are $g$, which correspond to the force of gravity in air, approximately $9.81\text{m/s}^2$. This value represents both static component which is accelerometer's incline with respect to gravitational force and dynamic component which is the total acceleration which represents change in velocity as result of body motion (Lennox et al., 2023; Shepard et al., 2008). The voluminous accelerometer data are translated into specific behavioural classes via use of algorithms trained to recognise inherent patterns (Brown et al., 2013; Shamoun-Baranes et al., 2012; Tatler et al., 2018).

To leverage the capabilities of accelerometers, advancements, such as the incorporation of solar charging for batteries to provide sufficient power for extended periods, miniaturization of components, on-board data storage, and the utilization of microprocessors for data analysis through edge machine learning, need to be explored. In the context of rapidly disturbed ecosystems, the establishment of a framework for data transmission, either in real-time or near real-time depending on the objectives is of fundamental importance. For example, the intrusion of protected areas by poachers is likely to trigger deviations in animal behaviour from the norm, making real-time data transmission crucial as a sentinel measure (de Knegt et al., 2021). This approach underscores the remarkable potential and power of accelerometers, particularly in cases where access to real-time animal behavioural data is required within a short period to aid decision making.

Animal-borne tracking technologies have contributed to exciting discoveries in the realm of animal ecology with profound implications for conservation science. Tracking tools such as GPS collars have allowed ecologists to gather information about the spatial ecology of animals over varying scales and in harsh conditions (Cagnacci et al., 2010), while solving the problem of observer's influence on the target animal (Cain and Cross, 2018). While commercial animal trackers offer numerous benefits (Kays et al., 2015; Wilmers et al., 2015), the cost per unit is exceptionally high for small projects (Clark et al., 2006; Foley and Sillero-Zubiri, 2020; McGranahan et al., 2018) especially where application of such tools is a prerequisite. For instance, cost per unit could range between \$2000-\$8000 (Cagnacci et al., 2010; Cain and Cross, 2018) excluding cost for other features such as data download, battery size, programmability, and satellite communication (Cagnacci et al., 2010). By comparison, the development of an Arduino-based lightweight GPS tracker could cost between \$40-\$820.

The development and production of open-source single-board microcontroller (widely used for DIY engineering projects) by platforms such as Arduino `https://www.arduino.cc/`, Raspberry pi `https://www.raspberrypi.com/`, and Micropython `https://micropython.org/` is a promising and feasible alternative to expensive commercial tracking tools for researchers. Several companies manufacture open-source electronics and compete for market share by offering programming examples and guides, ultimately contributing to cost reduction (Foley and Sillero-Zubiri, 2020). The application of open-source electronics offers several benefits. For example, users can customise devices to collect data that meets their requirements, tailor structural designs to fit different species, gain technical skills, and even commercialise their products. Therefore, exploring readily available open-source electronics has the potential to transform and innovate wildlife remote tracking by automating processes such as data collection, pre-processing, and transmission.

The application of novel technologies has revolutionised studies of animal movement and collective behaviour to unprecedented levels. However, the data collected are often large and multi-dimensional, requiring robust quantitative techniques for inference. Therefore, to fully exploit the potential of these novel tools in wildlife studies, the development of quantitative techniques to pre-process and extract intricate patterns from the data is crucial.

## 1.5 Role of machine learning and application in wildlife research

The integration of cutting-edge technological tools within the domain of ecological research to investigate complex patterns and process has yielded extensive and intricate data sets (Kays et al., 2015; Tomkiewicz et al., 2010). Such multi-dimensional data include remotely acquired imagery, audio, videos, acoustic data, social networks, and data generated by animal-borne sensors, such as accelerometers and magnetometers. Despite the valuable contribution of high-dimensional data to gaining unprecedented ecological insights, making inferences can be a daunting task (Borowiec et al., 2022). This is attributable to inherent features of such complex data sets such as failure to conform to the assumptions of classical statistical models and non-linear relations among variables across multiple scales (Valletta et al., 2017). Therefore, extraction of relevant information requires robust mathematical models capable of recognizing intricate patterns embedded in the data.

Machine learning, which was introduced in 1950 (Turing, 1950), is a modeling technique capable of addressing limitations of classical statistics (Valletta et al., 2017), to process and perform complex data analysis such as speech recognition, text recognition, object detection, and other complicated tasks. It is an interdisciplinary field that encompasses mathematics, statistics, and computer science (Jordan and Mitchell, 2015). Machine learning can be broadly categorized into two groups: supervised and unsupervised learning (Tarca et al., 2007). Under the category of supervised learning, attributes and features are used to make predictions using methods such as, artificial neural network (Lek et al., 1996), support vector machine (Drake and Lodge, 2006), and classification and regression trees (De'ath and Fabricius, 2000). In the unsupervised learning category, the objects of interest do not have predefined labels (Tarca et al., 2007; Willcock et al., 2018) hence the goal is to reveal patterns in the data.

Over the decades, machine learning has progressed well and found practical application in various fields such as computer vision, speech recognition, natural language processing, robot control, as well as others (Jordan and Mitchell, 2015). In ecology, machine learning has been used to address a number of challenges such as counting wildlife from aerial surveys (Torney et al., 2019; Wu et al., 2023), model population trends of birds using citizen science data (Fink et al., 2023), facial recognition of individual whales (Patton et al., 2023), and seasonal bird movements (Fuentes et al., 2023).

Based on the above examples, it is evident that machine learning is efficient and effective in processing and analysing complex data that would otherwise be time-consuming and laborious if done manually. As such, its application will not only enhance our understanding of intricate ecological processes but also open new avenues for innovation and the application of novel technologies. It has the potential to revolutionize animal ecology, providing unprecedented insights and data-driven solutions.

## 1.6 Introduction to the Serengeti ecosystem and threats

The Serengeti-Mara ecosystem shown in figure 1.4 is a transboundary conservation area comprising the Masai Mara ecosystem located in southern Kenya and the Serengeti ecosystem in northern Tanzania, covering an extensive area of 25,000km$^2$ which is managed for protection of biodiversity and ecological processes (Thirgood et al., 2004; Veldhuis et al., 2019). The habitat types in Serengeti ecosystem are broadly categorised into two: treeless short-grass plains in the southern regions while the northern region is dominated by tall-grass and woodlands (Holdo et al., 2009). The rainfall in this region follows a bimodal pattern. Short rains occur in November and December, while long rains fall between March and June and increases gradually from 500 in the south east to 1300mm/year in the north west (Holdo et al., 2009). Soil fertility varies across the region, with the lowest levels in the northwest and the highest in the southeast. The temperature ranges from a minimum of 15°C to a maximum of 30°C , with an average of 22°C (Holdo et al., 2009; Morrison et al., 2019). The ecosystem is dominated by woody species such as, *Acacia tortilis*, *A. robusta* while other sub-dominant species include *A. drepanolobium*, *A. gerardii*, *A. senegal*, *Commiphora africana*, and *Balanites aegyptiaca* (Rugemalila et al., 2016; Sinclair et al., 2009). It is also rich in faunal diversity and numerically dominated by the sheer numbers of wildebeest and plains zebra that migrate throughout the year tracking resources and in return drive virtually all other ecological process (Harris et al., 2009; Holdo et al., 2009). The wildebeest migration patterns is as shown in figure 1.5

The Serengeti National Park (SNP) which is the core conservation area is surrounded by multiple buffer areas that form "soft" edges and human dominated landscapes that form "hard" boundaries. To the southwestern are the Maswa, Grumeti and Ikorongo Game Reserves, to the southeast lies the Ngorongoro Conservation Area and the Loliondo Game Controlled Area, while to the north, it adjoins the Masai Mara National Reserve and a series of adjoining communal wildlife conservancies in Kenya (Kavwele et al., 2022; Thirgood et al., 2004). In terms of land use, both the Loliondo Game Controlled Area and the Ngorongoro Conservation Area Authority permit livestock, while the game reserves allow for trophy hunting and tourism but not livestock.

Globally, many protected areas face significant pressures from both internal and external factors, primarily driven by anthropogenic activities such as hunting, poaching, land conversion for agricultural purposes, grazing, conflicting conservation goals, and those of indigenous people. The Serengeti ecosystem is facing a number of threats which may potentially result in wide ranging ecological ramifications. For instance, the economic endeavours such as tourism activities are intended to stimulate economic growth and sustain the operations of conservation areas. Nevertheless, when mismanaged, these activities can have a negative im-

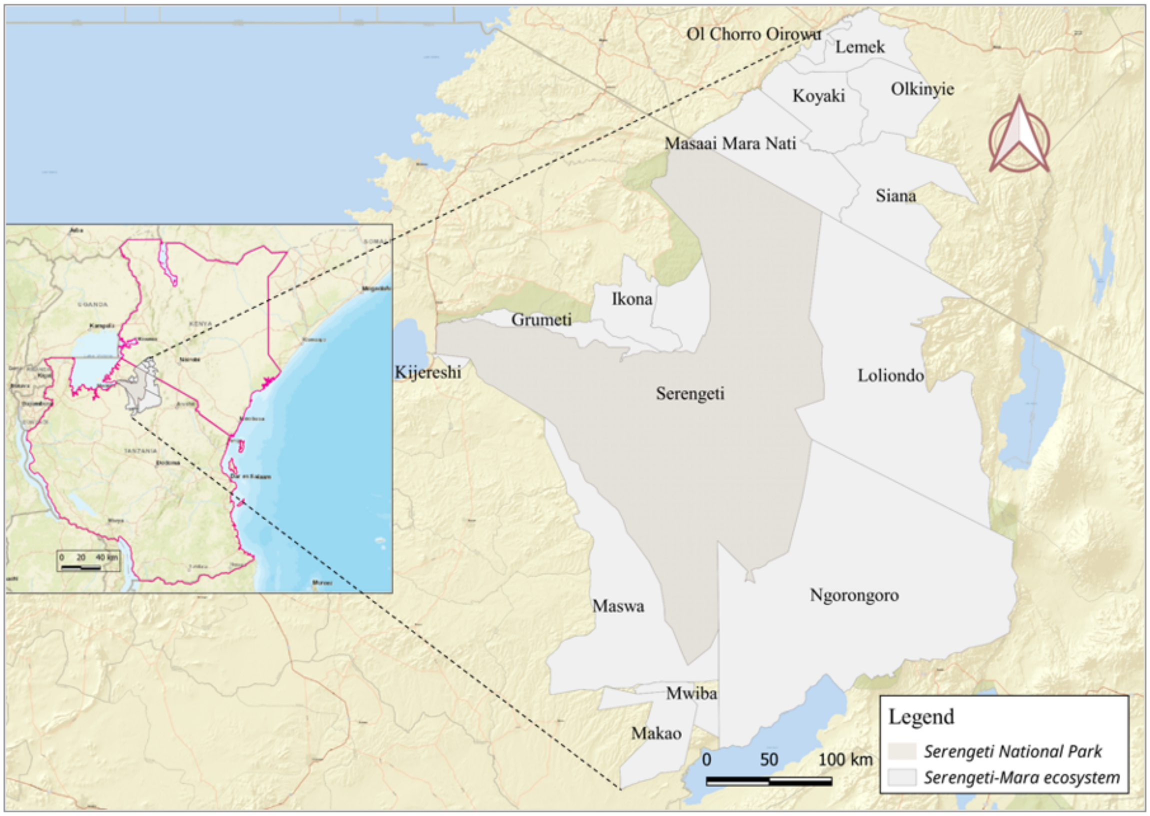

Figure 1.4: The map of Serengeti-Mara ecosystem (*Inset Kenya and Tanzania*), Serengeti National Park which is the core area (*shaded: lightdark grey*) and the surrounding wildlife management areas and reserves.

pact on biodiversity. For instance, a study in Serengeti by Larsen et al. (2020) demonstrated that the demand for infrastructure, such as lodges, is driven by their proximity to wildebeest hotspots, such as areas of high utilisation densities or crossing points. Mass tourism can disrupt migratory animals and potentially alter the timing of their movement. Therefore, if the demand for tourism products and ecological integrity is not managed sustainably, wildebeest spatial distribution and abundance, as well as migration timing, will be negatively affected.

The Serengeti ecosystem is also vulnerable to external threats. Incompatible land use regimes outside protected areas can negatively affect conservation goals. For example, in the western part of the Serengeti ecosystem, the human population increased by 2.4% between 1999 and 2012, leading to increased human activities such as land cover conversion. Crop land cover increased from 34% in 1984 to 54% by 2018 creating a "hard" boundary consequently pushing the migratory wildebeest towards the core area (Estes et al., 2012; Kavwele et al., 2022; Veldhuis et al., 2019). Livestock incursions are prevalent in the western region especially during dry season, leading to a reduction in biomass within the park. The presence of herders, along with their dogs and livestock, leads to the displacement of wildlife, subsequently causing substantial spatial compression of the park (Veldhuis et al., 2019). Despite the prohibition of bushmeat hunting, the proximity of villages inhabited by communities with a culture of hunting for income supplementation, sourcing protein, skill development, or prestige makes it a feasible and accessible activity. For instance, the Wakoma and Wakuria communities traverse 20-40 kilometers into protected area in search of herds or to transport dried meat, collectively constituting approximately 40% of illegal hunting (Knapp, 2012; Loibooki et al., 2002). Such uncontrolled off-takes can decimate the population of ungulates in the long run, hence driving species to local extinction. Availability of surface water is major driver of habitat use and spatial distribution of large herbivores especially during dry seasons (Hopcraft et al., 2012; Owen-Smith, 2015). As such, activities that occur upstream have considerable impacts on the existence of species and other ecological processes downstream. In the context of the Serengeti ecosystem, the volume of flow in the Mara River, which has catchment areas in Kenya, has been declining due to intensive irrigated agriculture involving the extraction of water in large volumes (Kihwele et al., 2021). For instance, the Mara River recession time has decreased from 100 days in 1970s to about 16.4 days in 2021 which is attributable to increased water extraction for commercial agriculture (Kihwele et al., 2021). Hence, the reduction in volume and flashiness of Mara river has the potential to affect several ecological process in the landscape.

In summary, the discussed threats, which can be categorised as either local or non-local impacts largely driven by human activities, such as land conversion for agriculture, illegal hunting, livestock incursions, proposed construction of roads, and unsustainable tourism activities, have the potential to significantly alter processes and functions of the ecosystem. To better manage the species and their habitat, an in-depth of understanding of how species behave and respond to rapid changes in and around the ecosystem requires appropriate tools capable of collecting data on a fine-scale resolution across gradient of disturbance.

## 1.7 Thesis outline

This thesis consists of five chapters. Chapter 1 serves as the general introduction and background, while Chapters 2, 3, and 4 are dedicated to standalone data analysis. Finally, Chapter 5 comprises the general discussion.

In the current chapter I provide a comprehensive overview of ungulate movement in the Anthropocene. I begin by defining the Anthropocene epoch and its major characteristics, followed by an exploration of animal movement patterns during this epoch. Additionally, I discuss the challenges associated with animal tracking and delve into the application of novel technologies and machine learning in wildlife studies. Finally, I present an overview of the key ecological features and threats specific to the expansive Serengeti ecosystem.

In Chapter 2, I delve deeper into the exploration of the spatial distribution of migratory species in Serengeti National Park. Here, I investigate the patterns of occupancy by migratory species in the transition zones between protected areas and human-modified landscapes. Specifically, I compare "hard boundaries" where human-dominated landscapes are directly adjacent to protected areas to "soft boundaries" where human-dominated landscapes are separated from protected areas by a buffer zones. Camera traps are valuable tools that provide data on population-level responses. However, when the focus shifts to individual responses, especially considering the same individual in various situations, the application of camera traps is limited. Therefore, a different approach becomes essential.

In Chapter 3, my primary focus is on fine-scale animal tracking using open-source electronics. The main objective is to develop a tool that automates remote animal tracking, enabling repeated observations of focal individuals and data collection about their nearest neighbours in different seasons, habitats, and in different physiological states. The overarching objective is to develop a tool capable of recording comprehensive data on both movement and collective behaviour. This tool has various applications in animal ecology, including studying patterns of spatial aggregations, leadership roles, alignment, and inter-individual distances across different environments and seasons. The automated tracking tool provides information about individual animals for short time intervals, typically around 20 minutes, limited by the flight time on a single battery charge. Consequently, obtaining detailed behavioural data for longer periods, such as a year or more, is not possible. This limitation necessitates the development of an additional tracking tool.

In Chapter 4, I explore the application of open-source electronics, machine learning, and the Internet of Things (IoT) network to design an animal-borne collar for sensing fine-scale behaviours, such as grazing, lying, standing, and walking. The primary goal is to collect this behaviour data, along with GPS locations, process it, and transmit it to end-users in near-real-time across seasons and in different habitats.

In Chapter 5, I provide an overview of the data chapters in a broad sense, discuss lessons learnt, experiences, trade offs, transferability, flexibility and directions for future as well as the overall conclusion.

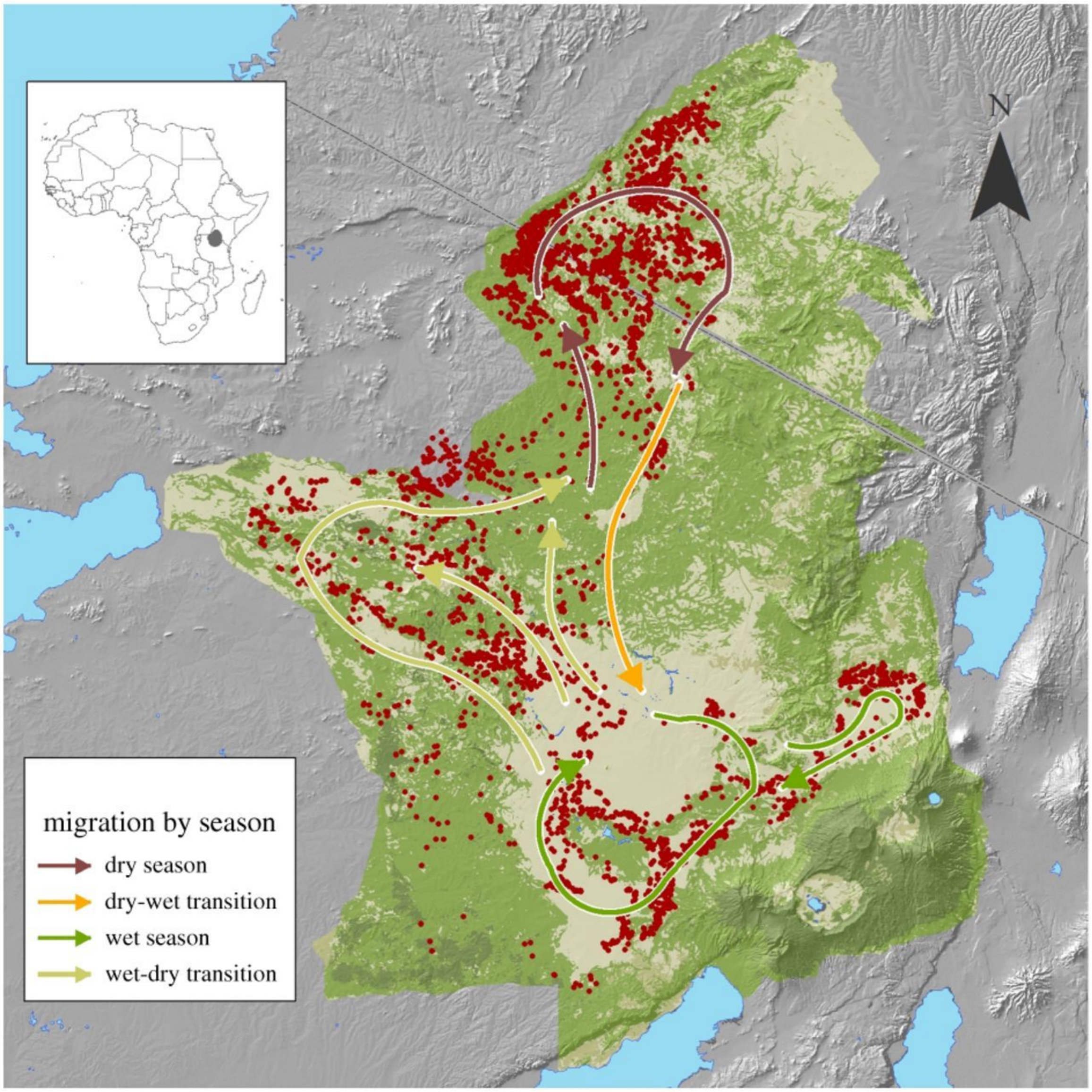

Figure 1.5: Wildebeest annual migration (red dots showing selected data since all the data would cover the entire system) between 1999-2001 in the Serengeti-Mara ecosystem. The dark green colour shows closed canopy forests, green shows open-acacia combretum forests, and light green shows is the open grasslands. The map is adapted from (Torney et al., 2018a).

# Chapter 2

## Non-local effects of human activity on the spatial distribution of migratory wildlife in Serengeti National Park, Tanzania

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## Abstract

Human activities are transforming landscapes and altering the structure and functioning of ecosystems worldwide and often result in sharp contrasts between human-dominated landscapes and adjacent natural habitats that lead to the creation of hard edges and artificial boundaries. The configuration of these boundaries could influence local biotic interactions and animal behaviours.Here, we investigate whether boundaries of different degrees of ‘hardness’ affect space utilization by migratory species in Serengeti National Park, Tanzania. We deployed camera traps along transects perpendicular to the national park boundary at three different locales. The transects were located in areas that consisted of two types of human–wildlife interface: a sudden transition from the national park into agro-pastoral land use (termed a ‘hard’ boundary) and a more gradual transition mediated by a shared usage area (termed a ‘soft’ boundary). Camera traps were placed at 2 km intervals along each 10 km transect from the edge towards the core of the park and were programmed to collect images hourly between dawn and dusk between June 2016 and March 2019. We used a deep neural network to detect the presence of wildlife within images and then used a Bayesian model with diffuse priors to estimate parameters of a generalized linear model with a Bernoulli likelihood. We explored the binomial probability of either wildebeest or zebra presence as a function of distance to the boundary, the rate of grass greening or drying ($d$NDVI) and the concentration of grass protein. There was a strong negative effect of distance to boundary on the probability of detecting wildebeest or zebra; however, this was only observed where the transition from human-dominated landscape to protected areas was sudden. Conversely, soft boundaries had little to no effect on the probability of detecting wildebeest or zebra. The results suggest that boundary type affects migratory species occurrence. The implications of these findings suggest that hard boundaries reduce the effective size of conservation areas; for many species, the area used by wildlife is likely less than the gazetted area under protection. The impacts may be severe especially for narrow protected areas or dispersal corridors.

## 2.1 Introduction

Globally, pristine landscapes are changing at an unprecedented rate due to human demands for resources (Said et al., 2016; Sala et al., 2000). Human-driven landscape change tends to occur more rapidly than naturally driven processes, hence have significantly greater impacts on ecosystems and the spatial distribution of wildlife (Wiens, 1990). At the local scale, habitat fragmentation, habitat loss, and land-use change present a grave threat to the existence of biodiversity. These changes accumulate at the global scale and present a major challenge for conservation (Garrison, 2005; Leblois et al., 2006). For instance, the expansion of agriculture around many ecosystems to meet the demands of growing human populations not only converts natural habitats into cropland, but also displaces wildlife and increases the potential for human-wildlife conflicts (Estes et al., 2012; Olff and Hopcraft, 2008; Wittemyer et al., 2008). Such threats to biodiversity are pervasive and can affect a variety of population and community processes over a range of temporal and spatial scales (Cayuela et al., 2006). The creation of edges, or hard boundaries, that are characterised by an abrupt transition in land use between human dominated landscapes and protected areas are common at the human-ecosystem interface (Laurance and Peres, 2006) and undermine the effectiveness of the conservation efforts. How to best manage the human-ecosystem boundaries presents a serious challenge for conservation managers and raises questions about what techniques work and in what context.

Ecological edges are boundaries or transition zones between two adjacent landscape patches or land cover types (Cadenasso et al., 2003; Murcia, 1995; Porensky and Young, 2013). In human dominated landscapes, the conversion of formerly continuous habitats into small isolated remnant patches through fragmentation is one of the most important contributors to the overall increase in edges (Batary and Baldi, 2004; Laurance and Peres, 2006; Meffe et al., 1995). In general, these transitions can be classed as either being hard and soft. A hard boundary represents a sudden transition between human modified landscapes and natural habitat area over a short distance. Conversely, a soft boundary boundary is characterised by gradual transition between human dominated landscapes and natural landscapes, typically separated by a buffer zone. The prevalence of hard edges is often most evident around protected areas that are surrounded by human activities, or in areas where human activities are progressing into unprotected natural habitats (Veldhuis et al., 2019).

The rate of habitat conversion and the increase of human-ecosystem edges globally are exacerbated by activities such as the construction of road networks, railway lines, gas lines, agriculture, human habitation, cattle grazing, bush fires, firewood collection and hunting among others (Harper et al., 2005; Kiffner et al., 2013). The impacts of edge effects are often driven by various factors such as age of the human-ecosystem edge (Cadenasso et al., 2003; Didham and Lawton, 1999), the synergistic effect of multiple nearby edges (Benitez-Malvido, 1998; Laurance and Peres, 2006), the size and shape of the protected area (Murcia, 1995), the structure of the adjoining vegetation matrix (Cronin, 2003; Pohlman et al., 2007), seasonality (Young and Mitchell, 1994), influxes of animals or plant propagules from surrounding landscapes (Grau, 2004; Nascimento et al., 2006; Ries et al., 2004), or fires and extreme weather events (Cochrane and Laurance, 2002; Laurance et al., 2001). One of the key impacts of edges are changes they impose on the rates of competition and predation (for instance, increased nest predation at the edges of many landscapes (Batary and Baldi, 2004)). Edge effects may also induce changes in herbivore foraging behaviour which leads to changes in seedling recruitment (Asquith and Mejía-Chang, 2005; Wright and Duber, 2001) and potentially alter forest composition (Terborgh, 1992) or facilitate invasion by other plant species.

Several studies have shown that animals change their behaviour in proximity to humans (Ciuti et al., 2012; Gaynor et al., 2018; Hopcraft et al., 2014). These risk-aversion behaviours can result in the redistribution of animals away from the edge and towards the centre of the core protected area (spatial avoidance) (Frid and Dill, 2002; Gaynor et al., 2018). In some instances, this concentration of animals can change the ecological processes related to resilience (such as the rate of green-up after the dry season) resulting in a spatial cascade where the cause at the edge is spatially separated from the effect observed in the core (Veldhuis et al., 2019).

Animal distributions can also be influenced by vegetation dynamics that determine the availability of primary production. Ecologists frequently use the phenological signal through Normalized Difference Vegetation Index (NDVI) to understand how seasonal changes in primary productivity (i.e. green-up and senescence in response to rainfall or snow melt) and animal spatial distribution relate. For instance, migratory Serengeti wildebeest *Connochaetes taurinus*, zebra *Equus quagga burchelli* and Thomson's gazelles *Eudorcas thomsonii* move seasonally between wet and dry season ranges in response to plant phenology (Holdo et al., 2009). However, aside from season, the quality of the grass available to herbivores may also be determined by the species composition and architecture of the vegetation itself. For example, there is a negative relationship between grass height and grass quality (by quality we mean the concentration of grass nitrogen, which is correlated with digestible protein); wet areas encourage tall grass that invest in silica-rich structural support with high carbon to nitrogen ratios, which dilutes the protein concentration and other key elements required by herbivores (i.e. nitrogen, phosphorus, calcium, sodium, magnesium, etc.) (Hopcraft et al., 2010; Olff et al., 2002). As a result, in addition to season, there are often strong landscape level predictors of grass quantity and quality that may account for the distribution of grazers (Hopcraft et al., 2012).

The animal response to the spatial distribution of risks (such as exposure to anthropogenic disturbance) and resources (such as the quantity and quality of forage) may be modified by their proximity to edges. For instance, if the risks associated with the edge outweigh the benefits of the resources, then animals may avoid these areas in which case the "effective" size of a protected area may be less than the true gazetted area. This squeezing effect would further undermine the value of conservation efforts particularly for disturbance-sensitive species, such as black rhinoceros *Diceros bicornis* or cheetah *Acinonyx jubatus* (Tabarelli and Gascon, 2005; Turner, 1996). Therefore, understanding how animals respond to different ways the human-ecosystem interface is managed is an important aspect of conservation management and requires deeper exploration. Migratory species are useful focal organisms in this regard because the same individuals encounter different types of edges during the course of their annual migration; thus, differences in their response to edges are likely due to their perception of the local conditions rather than to habituation, which one would expect from a study of resident animals.

Gathering accurate information of the population level response of animals to the human-ecosystem edge is challenging. Camera traps have become a popular and versatile tool for ecological studies due to their relatively low cost and ability to sample continuously over long periods of time, which allows robust estimation of the distribution and abundance of animals (Henschel and Ray, 2003; Palmer et al., 2018; Pettorelli et al., 2010; Silveira et al., 2003). The increased use of camera traps has resulted in acquisition of millions of images (Swinnen et al., 2014) rendering conventional (expert annotation) image processing protocols infeasible. A tenable approach to this challenge is the application of deep learning algorithms that can process large numbers of images reliably and rapidly (Christin et al., 2019; Torney et al., 2019; Weinstein, 2018). For instance, deep learning has been shown to be an effective tool for processing camera trap images for wildlife classification, enumeration, and detection including within the Serengeti ecosystem (the Snap Shot Serengeti project is a case in point) (Norouzzadeh et al., 2018; Schneider et al., 2018; Villa et al., 2017).

The objective of this study is to explore how the spatial distribution of wildlife is influenced by the management of the human-ecosystem interface. Specifically, we ask if hard edges between human dominated landscapes and wild ecosystems affects the spatial habitat use by migrating ungulates in the Serengeti. Because the sheer abundance of migratory animals is exceptionally large (approximately 1,300,000 wildebeest plus 300,000 zebra) and their movement is somewhat synchronous, it is possible that the safety afforded by large groups of animals moving together outweighs any potential risks that a hard edge may impose. Alternatively, if the management of edge is important then we should observe a difference in the density of duration of migratory ungulates between hard edges and those that are buffered.

## 2.2 Materials and methods

### 2.2.1 Study site

The greater Serengeti-Mara Ecosystem ('SME'; Fig. 2.1) is broadly characterised by two main habitat types: treeless short-grass plains in the southern region of the ecosystem and the tall-grass savannas and woodlands in the north and west of the ecosystem (Holdo et al., 2009). The ecosystem experiences a general gradient in rainfall ranging from 500 in the south east to 1300mm/year in the north west, and a counter-gradient of soil fertility that is lowest in the north west to highest in the south east (Holdo et al., 2009; Morrison et al., 2019). The average temperature is 22°C and fluctuates between 15°C and 30°C as minimum and maximum mean monthly temperature respectively. The landscape is dominated by woody species such as *Acacia tortilis, A. robusta*. Other sub-dominant species include *A. drepanolobium, A. gerardii, A. senegal, Commiphora africana* and *Balanites aegyptiaca* (Rugemalila et al., 2016; Sinclair et al., 2009). Both the rainfall and the soil fertility gradient play a critical role in driving the wildebeest and zebra migration (Holdo et al., 2009). The Serengeti is rich in fauna with 27 species of large and medium sized herbivores and at least 30 species of carnivores ranging in average body size from 0.35kg such as common dwarf mongoose, *Helogale parvula* to 170kg male lion *Panthera leo* (Sinclair et al., 2015), but numerically and ecologically dominated by over 1.3 million wildebeest and approximately 0.3 million plain's zebra (Harris et al., 2009; Hopcraft et al., 2014).

The SME crosses the Tanzania and Kenya border and includes several land-use management authorities (Fig. 2.1). In both Tanzania and in Kenya, the core protected areas (Serengeti National Park in Tanzania and Masai Mara National Reserve in Kenya) are reserved entirely for wildlife and tourism, but are partially surrounded by multiple-use buffer areas that form a soft boundary between the protected area and human dominated landscapes. In Tanzania, each buffer area permits different types of land-use; livestock are permitted in Loliondo Game Controlled Area and Ngorongoro Conservation Area Authority (NCAA) while the remaining areas (Maswa, Ikorongo and Grumeti Game Reserves) are reserved for tourism and trophy hunting with no livestock permitted. In Kenya, the core Masai Mara National Reserve is surrounded by wildlife conservancies which allow mixed use of livestock and wildlife tourism. The social and cultural diversity of the communities living adjacent to the ecosystem are distinctive, but largely dependent on a mixture of livestock, agriculture and subsistence hunting. The western and northern boundary of the SME is occupied largely by Wakuria, Wakoma and Wasukuma communities who practice agropastoralism and engage in mixed cash crops, subsistence hunting and farming with small-herd livestock keeping. The eastern boundary, in contrast, is inhabited largely by the Masai ethnicity who are almost exclusively pastoralists, with livestock herds up to hundreds of animals (Veldhuis et al., 2019). In the absence of buffer zones the core protected areas in both Tanzania and Kenya border a human dominated agricultural landscapes which forms a hard boundary.

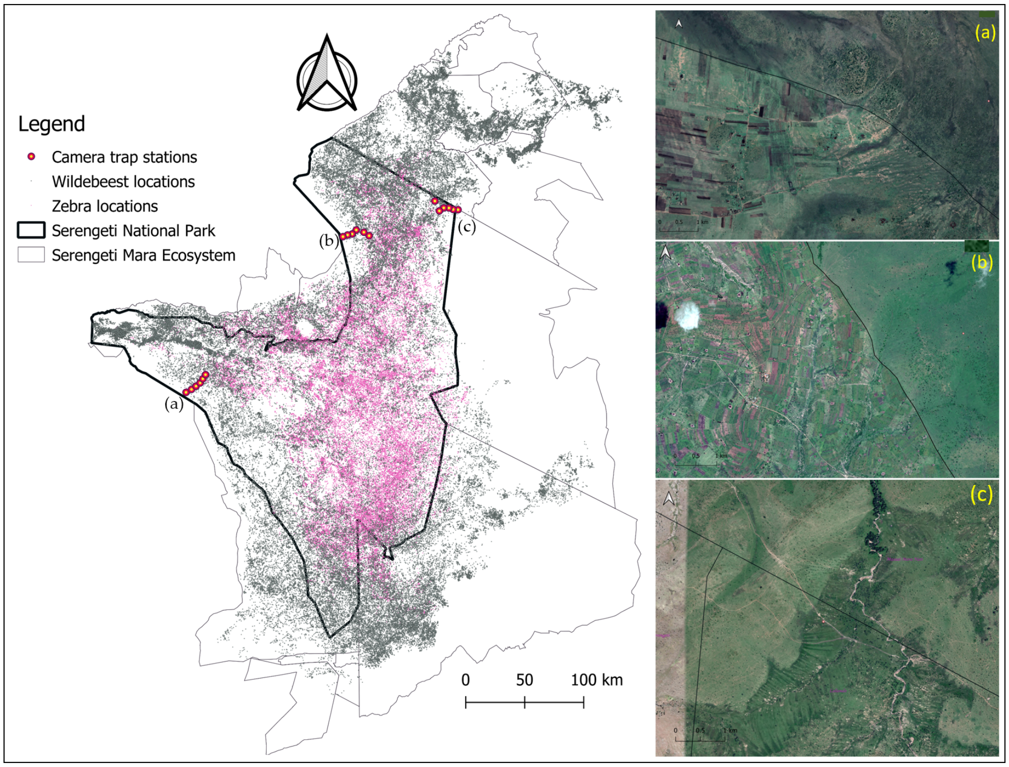

Figure 2.1: Map of the study site on the right. The maps show Serengeti National Park, surrounding conservation areas and general movement of wildebeests (grey dots) and zebras (violet dots) in the ecosystem between June 2016 through March 2019 as well as camera trap locations along the three transects. The satellite maps (zoomed in) on the right side show land-use regimes around areas adjoining the transects (a) Mbalageti ,(b) Tabora and (c) Kuka regions

### 2.2.2 Data collection

We established three camera trap transects inside Serengeti National Park that started at the boundary and radiated perpendicular to the boundary at 2km intervals up to 10km inside the park (thus, 6 cameras per transect) since we were interested in estimating the extent of human footprint into the protected area. The location of each transect was selected based on the adjacent land-use type immediately outside the protected area, and classified as being either a 'hard' or a 'soft' boundary. The Mbalageti transect bordered a hard edge with the Wasukuma agro-pastoral communities (mainly keeping cattle, sheep, goats mixed with subsistence and cash-crop farming). The Tabora transect bordered a hard edge with the Wakuria and Wakoma agricultural lands dominated by subsistence crops with mixed livestock herding. The Kuka transect bordered the Loliondo Game Controlled Area (a soft edge) occupied by Masai pastoralist areas with no cultivated crops (Fig. 2.1). Camera traps *(Bushnell Trophycam and Essential HD cameras)* were mounted on trees at approximately 2.5-3.5m from the ground to ensure a clear view above the tall grass and to deter theft. All camera traps faced North or South to avoid taking photos directly into the sunrise or sunset. We programmed the camera traps to take photos at the top of every hour between 07:00hrs and 18:00hrs. Because of the remoteness of the sites, we downloaded images from camera traps approximately every 8 weeks and replaced batteries and malfunctioning and missing cameras as needed. Data collection lasted from $17^{th}$ June 2016 through $15^{th}$ March 2019 taking a total of 130,157 images across 18 camera traps (Fig. 2.1). A total of 14 species (Fig. S3) were captured ranging from small sized herbivores such as Thomson's gazelles *Eudorcas thomsonii* and Grant's gazelles *Nanger granti*, to large sized species such as buffaloes *Syncerus caffer*, elephants *Loxodonta africana*, and giraffes *Giraffa camelopardalis*. However, the majority of captures involved migrant wildebeest and zebra, which form the focus of this study. The daily image capture per camera trap is illustrated in the supplementary material (Fig. S1).

To estimate the concentration of grass nitrogen at each camera trap (i.e. a metric of forage quality), we used an existing raster layer of grass nitrogen from a previous study (Hopcraft et al., 2012). In summary, grass nitrogen was estimated at 148 vegetation plots (see Fig. S7) across the Serengeti ecosystem taking into account the variation in soil and vegetation types across rainfall gradient. At each plot, a pooled sample of grass was collected, ground to homogeneous size (2mm) and grass nitrogen concentrations measured using near infra-red (NIR) spectrophotometer (NIR). The spatial distribution of grass nitrogen was interpolated by regression krigging the nitrogen concentration at each sampling point with the 19 years mean normalized difference vegetation index (NDVI). To check the accuracy of the krigged grass nitrogen layer, we used leave one out cross-validation (Hastie et al., 2009) whereby, a single observation was excluded and the rest of the $n-1$ (147) observations were used as the training set. The model was then used to predict the grass nitrogen value at the held-out location and the predictions were compared to the true values. The predicted values correlated well with the true values ($r^2 = 0.58$, slope = 0.57, $p < 0.001$) (see Fig. S6 and Fig. S5). The grass nitrogen at each camera trap was then extracted from the interpolated map and their values standardized for each transect with mean 0.

To detect temporal trends in greening or senescence of the ecosystem, we used a dynamic Moderate Resolution Imaging Spectrometer (MODIS) NDVI layers with 250m and 16 days spatiotemporal resolution respectively acquired between April 2016 and April 2019. NDVI is an optical index of vegetation greenness which is used a proxy for productivity measurement of an ecosystem (Rouse Jr et al., 1973). To extract daily NDVI for the dates that fell in between two image acquisition dates (16 day period), we interpolated NDVI values based on the slope between the two data points. We then extracted the daily rate of change of NDVI (i.e. *d*NDVI) for each camera trap for the date image was taken by subtracting the current NDVI value for that particular date from a previous 16 day period NDVI value. *d*NDVI is a metric which describes the change in NDVI such that negative values indicate drying and positive values indicate greening over the 16 day period.

### 2.2.3 Detecting and identifying wildlife in images

To extract data from the collected images we used a semi-automated approach that combined a deep learning object detector with manual annotation and oversight. The process entailed deletion of false positives or addition of false negatives which minimised likelihood of misidentification of objects. For automated object detection we used the YOLO detector

(Redmon and Farhadi, 2018) implemented in TensorFlow (Abadi et al., 2016) and embedded within the Annotation Interface for Data-driven Ecology (AIDE) (Kellenberger et al., 2020) environment for active learning. YOLO, which stands for You Only Look Once (Redmon et al., 2016) is an efficient, single pass multiscale object detector that has been used in several ecological applications (Jalal et al., 2020; Schneider et al., 2018; Torney et al., 2019) and is able to detect and classify multiple objects within images. The output from YOLO is a sequence of bounding boxes and associated object and class probabilities that in our context predict the location and species of wildlife within the images. To train the detector we used transfer learning beginning with a neural network trained on the COCO dataset (Lin et al., 2014), then employed the AIDE interface to create an active training loop; annotators provided training samples for the neural network, the neural network was trained on these samples and then ran predictions over a batch of images, after which, images were then presented to annotators that were most likely to contain wildlife. The object detection model had an accuracy of 97% (Julija, 2021). This process improved the efficiency of training data preparation and dramatically reduced the amount of empty images that were presented to annotators (Kellenberger et al., 2020).

Once sufficient training data were available, we trained the object detector and predicted the location and species classification of wildlife in all images. To control for different fields of view of the camera traps and to exclude wildlife at far distances that were difficult to detect and classify, we defined a minimum object size based on the mean box size of the camera trap with the smallest viewing angle. We then identified images that were predicted to contain wildlife of this size and above for manual verification. These images were manually checked using the AIDE software and all bounding boxes were verified, corrected, or deleted as appropriate.

### 2.2.4 Statistical analysis

We investigated the probability that wildebeest or zebra were present at a camera trap location (see Fig. S4) as a function of distance to the boundary, *d*NDVI (i.e. the rate of greening or drying of the vegetation), and the concentration of grass nitrogen. We excluded days where neither wildebeest nor zebra were observed along the transect to account for the fact that migrants may be selecting areas beyond the range of our camera trap experiment (the migration is constantly moving and may be absent from an area for extended periods of time). Hence, we infer the probability of an observation at a specific camera trap location conditional on there being wildebeest or zebra present along the transect at some point during that day.

We employed a Bayesian model with diffuse priors to estimate parameters of a Generalized Linear Model with a Bernoulli likelihood to estimate the conditional probability of presence/absence of either wildebeest or zebra at a camera trap. The full model is specified as shown in equation 1,

$$\begin{aligned} y_i &\sim \text{Bernoulli}(\lambda_i) \\ \text{logit}(\lambda_i) &= \beta_0 + \beta_1 X_i, \\ \beta_0 &\sim \mathcal{N}(0, 100), \\ \beta_1 &\sim \mathcal{N}(0, 100) \end{aligned} \tag{2.1}$$

where $y_i$ is the presence/absence of either a wildebeest or zebra for image $i$. The probability of a wildebeest or zebra being present is a function of three potential explanatory covariates ($X_i$); where, $X_i$ is either the distance to the boundary for the camera that generated the image, or *d*NDVI value for a particular date and camera for the camera that generated the image, or grass nitrogen content at a particular camera trap site. Firstly, we compared each covariate independently against the intercept-only model to assess whether the covariate changed the overall likelihood of the model. If the covariate did not improve the model, we ignored it. Similarly, if more than one covariate improved the model, we explored the model with two covariates by checking whether the credible interval for the coefficient included zero or not and if the likelihood improved. In our analysis, there were no instances where a more complex model (two or three covariates) was better than a single covariate (distance to the boundary) model. To sample from the posterior distributions for parameters $\beta_0$ and $\beta_1$ we used Markov Chain Monte Carlo (MCMC), specifically using the Hamiltonian Monte Carlo algorithm implemented in TensorFlow Probability (Dillon et al., 2017). We estimated model parameters for each transect independently and assessed convergence of MCMC chains using trace plots and R-hat diagnostics (Gelman et al., 1992) (see Fig. S2). All data manipulation and analysis were performed in Python (Van Rossum and Drake (2009)) and summary maps were prepared in Quantum Geographical Information Systems (QGIS) (QGIS Development Team (2020)).

## 2.3 Results

Summary statistics from the analysis are presented in Table 1. Along the Mbalageti and Tabora transects we observed a significant effect of distance to the boundary on the spatial distribution of migratory wildlife. The 99% highest posterior density interval (HPDI) for both Mbalageti (0.048, 0.176) and Tabora transects (0.023, 0.204) did not contain zero. On the other hand, the 99% HPDI (-0.062, 0.048) for Kuka transect contained zero and therefore there was no detectable effect of the boundary on the spatial distribution of migratory wildlife species. Similarly, *d*NDVI had no detectable effect on the distribution of migratory wildlife across the three transects namely Mbalageti 99% HPDI (-2.864, 2.073), Kuka 99% HPDI (-6.028, 2.267) and Tabora 99% HPDI (-1.806, 4.908). Grass nitrogen concentration had no detectable effect on spatial distribution of migratory wildlife for Kuka 99% HPDI (-0.094,0.284) and Tabora 99% HPDI (-0.163, 0.375) transects unlike Mbalageti transect 99% HPDI (-0.413, -0.021). Generally, the spatial gradient of grass nitrogen content with respect to distance from the boundary for both Mbalageti and Tabora transects was constant. However, for the Kuka transect, nitrogen content decreased with increasing distance from the boundary (Fig. 2.2). Overall, Kuka transect had the highest mean grass nitrogen content (1.01) and Tabora transect had the least (0.64) whilst Mbalageti was intermediate (0.89).

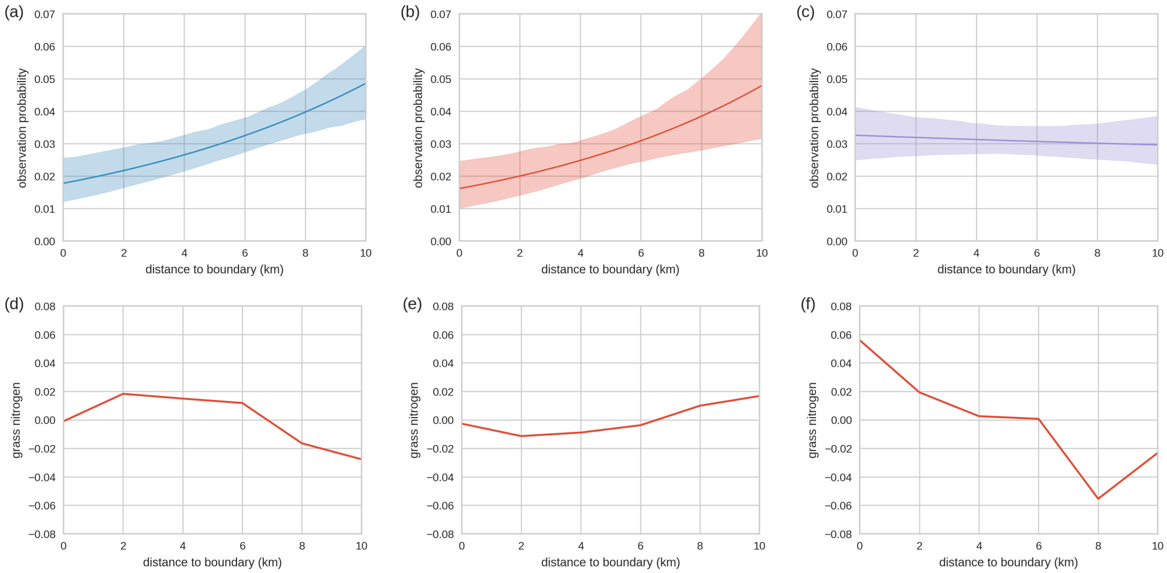

Figure 2.2: The first row shows probability of migratory wildlife presence (either wildebeest or zebra) as a function of distance to the boundary measured in kilometers (Km) for (a) Mbalageti,(b) Tabora and (c) Kuka transects. The second row shows grass nitrogen content against distance to the boundary for (d) Mbalageti, (e) Tabora and (f) Kuka transects to visualise the relationship between grass nitrogen content concentration along the transects. Grass nitrogen plotted values were standardised to mean zero

Table 2.1: Summary statistics of the posterior estimates for several models predicting species observation probability as a function of distance to the boundary (distance), *d*NDVI and grass nitrogen concentration

| **Transect** | **Model** | **Predictors** | **Parameter** | **Mean** | **HDI(0.05%)** | **HDI(99.95%)** | **ΔWAIC** |
|---|---|---|---|---|---|---|---|
| Mbalageti | Model 1 | Intercept | $\beta_0$ | -3.404 | -3.609 | -3.191 | 0 |
| | Model 2 | Intercept | $\beta_0$ | -4.021 | -4.8518 | -3.571 | |
| | | Distance | $\beta_1$ | 0.104 | 0.048 | 0.176 | -25.14 |
| | Model 3 | Intercept | $\beta_0$ | -3.403 | -3.618 | -3.212 | |
| | | *d*NDVI | $\beta_1$ | -0.343 | -2.864 | 2.073 | 1.38 |
| | Model 4 | Intercept | $\beta_0$ | -3.42 | -3.639 | -3.23 | |
| | | Grass nitrogen | $\beta_1$ | -0.233 | -0.413 | -0.021 | -13.58 |
| Kuka | Model 1 | Intercept | $\beta_0$ | -3.442 | -3.637 | -3.261 | 0 |
| | Model 2 | Intercept | $\beta_0$ | -3.391 | -3.719 | -3.065 | |
| | | Distance | $\beta_1$ | -0.01 | -0.062 | 0.048 | 1.26 |
| | Model 3 | Intercept | $\beta_0$ | -3.449 | -3.646 | -3.27 | |
| | | *d*NDVI | $\beta_1$ | -1.694 | -6.028 | 2.267 | -1.04 |
| | Model 4 | Intercept | $\beta_0$ | -3.455 | -3.64 | -3.271 | |
| | | Grass nitrogen | $\beta_1$ | 0.091 | -0.094 | 0.284 | -0.54 |
| Tabora | Model 1 | Intercept | $\beta_0$ | -3.569 | -3.881 | -3.267 | 0 |
| | Model 2 | Intercept | $\beta_0$ | -4.116 | -4.679 | - 3.58 | |
| | | Distance | $\beta_1$ | 0.112 | 0.023 | 0.204 | -14.4 |
| | Model 3 | Intercept | $\beta_0$ | -3.626 | -3.97 | -3.342 | |
| | | *d*NDVI | $\beta_1$ | 1.509 | -1.806 | 4.908 | -0.56 |
| | Model 4 | Intercept | $\beta_0$ | -3.572 | -3.869 | -3.328 | |
| | | Grass nitrogen | $\beta_1$ | 0.098 | -0.163 | 0.375 | 0.2 |

Overall, posterior distributions suggest the probability of wildebeest or zebra occurring in an image increased with distance from the boundaries of Mbalageti and Tabora transects. These transects border agropastoral communities (Fig 2a,b). In contrast, none of the covariates were important in accounting for the probability of detecting wildlife along the Kuka transect boundary, which borders a conservation buffer zone (the Loliondo Game Controlled Area) in which livestock grazing was permitted but cultivated agriculture was not (Fig 2c).

Overall, 129.36km of the Serengeti National Park boundary is directly adjacent to human dominated landscapes, while 612.95km of the boundary is adjacent to a buffer area. This amounts to 17.43% of the perimeter classified as having a hard boundary.

## 2.4 Discussion

The most important finding from our analysis suggests that hard boundaries have strong effects on the spatial distribution of migratory wildebeest and zebra in the Serengeti, indicating that human activity around the edges of a protected area can have large effects on animal distributions extending for several kilometers into the core protected area. Notably, there is a negative relationship between wildlife spatial distribution and boundary "hardness". In particular, there was a reduced probability of wildlife using areas adjacent to the hard boundary such as the Mbalageti and Tabora transects whilst there was no response of wildlife to the soft boundary at the Kuka transect. The aversion of wildlife to hard unprotected boundaries could potentially have knock-on effects for associated ecological processes such as vegetation dynamics, nutrient cycles and trophic interactions.

There are several factors related to the diversity of human activities occurring outside the park boundaries which may contribute to the observed spatial distribution of both zebra and wildebeest in relation to hard versus soft boundaries of the Serengeti National Park. These include the rate of land-use conversion to agriculture, the effects of human disturbance, livestock incursions into the protected area, and bushmeat hunting, as observed in similar ecosystems (Giliba et al., 2022). The extent of these activities are largely determined by national policies that permit certain activities in specific areas (such as trophy hunting in game reserves) and by village land-use policies in the areas beyond the protected areas which focus on subsistence agriculture. Furthermore, the differences in land-use between the east and the west of Serengeti ecosystem largely reflects differences in culture, livelihood strategies and land tenure policy (Walelign et al., 2019). In the east and southeast Masai pastoralists occupy the Loliondo Game controlled Area (LGCA) and Ngorongoro Conservation Area where livestock grazing is permitted. In the west and southwest Maswa, Grumeti and Ikorongo Game Controlled areas are managed for trophy hunting and tourism. There are no physical barriers separating the national park and these buffer areas, which facilitates free movement of animals between the two landscapes (Lyamuya et al., 2016).

### 2.4.1 Land-use conversion

Protected areas are often designed to reduce habit loss as well as stem biodiversity loss across the world (Pimm et al., 2001). Despite their important role in biodiversity conservation, achieving the desired goal is difficult due to incompatible land use regimes on the adjacent landscapes (Castro-Prieto et al., 2017; Giliba et al., 2022; Joppa et al., 2009). It is possible that the associated land-use conversion may account for the patterns we observe in the abundance of wild animals inside the protected area. In Serengeti-Mara ecosystem, the rates of human population growth are markedly different between the eastern and western sides of the Serengeti. For instance, the human population in the west increased by 2.4% per year between 1999-2012, unlike the eastern boundary where the population has remained relatively low (Estes et al., 2012; Veldhuis et al., 2019). As a consequence, the conversion to crop land (both for subsistence and cash crops) in the west has increased from 34% cover in 1984 to 54% cover by 2018 resulting in very little natural vegetation beyond the western boundaries (Estes et al., 2012; Veldhuis et al., 2019). Several authors suggest that the increase in the human population and land-use conversion especially along the western boundary is likely due to a "push effect" rather than a "pull effect". In other words, the last vacant arable land for new agriculturalists to colonize occurs close to the park boundary forcing new farmers into areas directly adjacent to the protected area. Previously published research suggests this "push effect" is more likely than a "pull effect" in which farmers actively select areas close to protected areas over any other areas (Estes et al., 2012; Jiao et al., 2019). On the eastern side conversion to agriculture has been minimal (limited to a few areas close to settlements) resulting in relatively low rates of land conversion and habitat fragmentation (Estes et al., 2012). If land conversion and agricultural expansion is responsible for the pattern of wildebeest and zebra abundance we observed relative to the boundary, then we should expect the abundance of animals in areas with no conversion to have similar values regardless of distance to the boundary (i.e relatively equal probability in the core and the edge of the park boundary), particularly because the quality of the forage does not change (Figure 2b; in some cases the forage quality is better near the boundary). However, the data suggest a much larger negative effect of hard boundaries (extending at least up to 6-8km from the boundary), therefore land-use alone is unlikely to account for the observed pattern.

### 2.4.2 Human disturbance

Given the large human population on western side of the Serengeti ecosystem coupled with the relatively sedentary lifestyle of the agro-pastoralists, it is possible that disturbance such as noise and light pollution emanating from these high-density centers may potentially drive wildebeest and zebra away from the boundaries. The people occupying the western Serengeti-Mara are of mixed ethnic backgrounds including Wakoma, Wakuria and Wasukuma (Kaltenborn et al., 2008), many of whom mix traditional agricultural livelihoods with more diversified economic endeavours associated with market centers and increasing urbanization (Walelign et al., 2019). As a result, access to markets and social amenities such as electricity, schools and medical services attract large concentrations of people in and around these urbanizing hubs. If noise and light pollution associated with the high human density account for the strong negative response of migratory animals to the hard boundaries then we expect to observe a response only when animals are close enough to the source to detect it, but not beyond the sound and view-scapes. Because the effect of the hard boundary is observed for at least 6-8km into the protected area it is somewhat unlikely that wildebeest and zebra are responding just to noise and/or light pollution. However, we cannot rule out that human disturbance does not have an effect on animal presence over short distances.

### 2.4.3 Livestock incursions

Illegal livestock incursions into the protected areas could displace wildlife and may account for the negative effects of the hard edges on wildebeest and zebra presence. Despite a growing consensus that moderate stocking densities of livestock are compatible with the conservation of native savanna biodiversity (Keesing et al., 2018; Reid, 2012; Sitters et al., 2020; Young et al., 2018), at high densities, livestock have deleterious impacts on native biodiversity by consuming large quantities of the most palatable grass species, suppressing savanna fires, and changing the competitive balance between grass, forbs and trees (Sitters et al., 2020; Young et al., 2005) as well as pathogen transmission (Ekwem et al., 2021). Intensive livestock grazing can result in the encroachment of non-palatable woody species and non-native plants (Kimuyu et al., 2017) and these changes in the vegetative composition and structure may affect animal movement by presenting different availability of resources and risks (Hopcraft et al., 2014). Although livestock grazing is illegal in the Serengeti National Park, there are no barriers that physically exclude livestock. Forays into the protected area, particularly in the dry season when grazing opportunities are limited in the adjacent areas, are relatively common on both the east and the west side of the ecosystem (Veldhuis et al., 2019). Such forays into protected areas present a direct pathway through which wildlife species may be displaced; for instance, herders and their dogs may harass wildlife which may subsequently avoid these areas. Both the agro-pastoral communities that live along the western boundary of the ecosystem (adjacent to Mbalageti and Tabora transects) as well as the pastoralist Masai communities in the east (adjacent to the Kuka transect) keep moderate to high-densities of livestock (Ekwem et al., 2021; Ogutu et al., 2009). Therefore if livestock incursions were responsible for displacing wildebeest and zebra then we should observe similar patterns on both the east and west sides, and these effects should be seasonal (i.e. only when the communal grazing outside the protected area is limited). The evidence from the camera traps does not support this hypothesis (Figure 2a), therefore livestock alone are unlikely to account for the patterns we observe.

### 2.4.4 Illegal hunting for bushmeat

Unregulated hunting of wildlife is a major conservation issue affecting wildlife populations across Africa. In most situations, hunting can be a way for local people to off-set protein shortages by supplementing their diet with bushmeat, or a business opportunity (i.e organized cartels harvesting and retailing wildlife products such as bushmeat, skins and ivory for profit) (Bitanyi et al., 2012; Mfunda et al., 2010). For many people, hunting wildlife is part of their culture and is often associated with prestige and skill development (Forsyth and Marckese, 1993; Knapp, 2012). For instance, in the Serengeti, the Wakoma and Wakuria communities along the western boundary are responsible for 40% of illegal hunting in the ecosystem (Bitanyi et al., 2012; Holmern et al., 2004). Conversely, in the Masai communities on the eastern boundary bushmeat consumption is uncommon due to their cultural norms (Ceppi and Nielsen, 2014; Kaltenborn et al., 2005) (although Masai consume bushmeat occasionally, the quantity is much less than other ethnic groups (Kiffner et al., 2015)). The annual off-take of wildlife in Serengeti varies each year depending on the rainfall; poaching tends to be highest during droughts when crops fail. Past research estimates up to 70,000-129,000 wildebeest are illegally harvested per year using wire snares (Mduma et al., 1999; Rentsch and Packer, 2012) (these estimates do not include the other species illegally hunted such as zebra, impala (*Aepyceros melampus*),and Thomson's gazelles). Evidence suggests that areas closest to villages have the highest rate of offtake and that hunting parties will move 20 to 30km into the protected area in search of herds and transport dried meat back (Loibooki et al., 2002). The proximity of villages with a culture of bushmeat consumption living next to the hard edge of a protected area with no buffer area makes illegal harvesting of wildlife easy and viable. Hunters generally check their snares every day or two, therefore it is possible that the combination of distressed animals struggling in snare and the routine checking of snare lines by people repels animals, which may account for the pattern we observe on the western boundary of the Serengeti particularly.

### 2.4.5 Ecological consequences of hard boundaries

The presence of hard boundaries displaces wildlife from adjacent areas and this could have deleterious impacts on biodiversity and diminish the ecological integrity of the ecosystem. For instance, estimates suggest that migratory wildebeest and zebra consume more than 4,500 tons of grass per day and deposit equivalent amounts of dung and urine (Hopcraft et al., 2015). The ecological effects of the migration fundamentally changes the energy flow between all trophic levels in the Serengeti; if the migration avoids an area, this alters the diversity of vegetation, insects, birds, and mammals (Sinclair et al., 2015). Furthermore, once animals are displaced from an area the expansion of human activities such as farming becomes less inhibited and this can speed the rate of landuse conversion as seen by the decadal shrinking of the Maswa and Ikorongo boundaries (Sinclair et al., 2015). The ecological consequences of hard boundaries underscores the increasing complexity in the trade-off between human land uses and long term conservation goals (DeFries et al., 2007). While our work focused on migratory herbivores, other guilds may respond to hard boundaries differently hence future work could focus on understanding which guilds thrive and which are intolerant to hard boundaries.

### 2.4.6 Future steps and limitations

We have shown that the type of boundary, which we define based on the land use activities in the landscape adjacent to the protected area, may influence space utilisation by migratory wildlife. Additionally, other environmental metrics tested such as forage quality and vegetation phenology did not have influence on space utilization by migratory species in the ecosystem. Although our findings are significant and pertinent to biodiversity conservation, there is a possibility that there are other factors which may account for the observed patterns but cannot be tested using our empirical data. With our data, we may conclude that distance to boundary is a predictor of migratory species presence in two of the three transects we studied. The two transects where distance is a significant predictor are associated with a ‘hard’ boundary whereas the transect where distance is not significant is associated with a ‘soft’ boundary. This finding aligns with our *a priori* hypothesis that both distance to boundary and the nature of the boundary will influence the spatial distribution of wildlife, however there may well be other factors specific to the locations under investigation that contributed to this finding. Further exploration of factors such as the depth of buffer zones, the density of people along the boundaries, prolonged rainfall seasons like El Niño, changes in land use as well as increased resource protection should be considered along with more transects per treatment in order to solidify our understanding of the effects of boundary characteristics on space-use by wildlife.

### 2.4.7 Management implications and potential mitigation measures

Managing the boundary of a protected area requires addressing different threats than those experienced in the core. Our results suggest that migratory animals consistently avoid areas within 5km from the edge of a hard boundary, suggesting the effective area being conserved is much less than the true area gazetted for protection. In the case of the Serengeti National Park, 129.3km (~17.4%) of the boundary is classified as hard suggesting that over 1000km$^2$ may be legally protected but rarely used by the migration because of their aversion to attributes associated with hard boundaries. In these situations, increasing the number and frequency of ranger patrols along hard boundaries could reduce illegal hunting of wildlife species as well as reduce livestock incursions or other forms of natural resource extraction and potentially allow wildlife to return to these areas. The effects of hard boundaries are likely to be most severe for small, narrow protected areas or wildlife dispersal corridors where animals may be particularly exposed. Furthermore, the effects of hard boundaries may be most acute in areas with fertile soils and good rainfall where the surrounding land is susceptible to rapid conversion to agriculture. The results highlight the value of surrounding core protected areas with buffer zones to mitigate the potential negative effects of human activity on wildlife conservation. This ecologically informed approach to managing the cascading effects of hard boundaries is central to the protection of wildlife and their habitats, and could considerably slow the rate of biodiversity loss.

### 2.4.8 Conclusion

In conclusion, we demonstrate that hard boundaries characterised by a sudden transition in land cover configuration between human dominated landscapes and protected areas present a perceived risk to herbivores and hence they are used infrequently. On the other hand, soft boundaries characterised by buffer zones have an insignificant effect on spatial distribution of wildlife. The observed patterns of wildlife space utilisation as a function of hard unprotected boundaries suggests the effective area actually used by wildlife is likely much less than the area gazetted for conservation. This notion requires consideration as it suggests the management of the protected area boundary can have large consequences on the system's ecological viability.

# Chapter 3

## Automated and repeated aerial observations of GPS-collared animals using UAVs and open-source electronics

**Note:** This chapter has been submitted as a manuscript to the journal *Ecosphere*.

## Abstract

Telemetry technology has enabled ecologists to link animal movement trajectories and environmental features at a fine spatio-temporal resolution, however the effects of social interactions on individual choice within large mobile groups remains largely unknown. Estimating the effect of social interaction in the wild remains challenging because existing long-term tracking tools such as GPS collars focus on the movements of a single individual and cannot observe the behavior of other individuals within the group. The progression of socially-informed movement models requires measuring simultaneous trajectories of many individuals at once, as well as the instantaneous social cues to which individuals may be responding. The availability of low-flying unmanned aerial vehicles (UAVs) and low-cost open-source electronics presents a promising opportunity to collect fine-scale data on social interactions in order to advance our understanding of collective behavior. Here, we present a tracking system that enables the repeated localization and observation of a collared individual and its near neighbors using nadir video footage collected from a commercial UAV. We make use of open-source electronics combined with the UAV's in-built functionality that allows it to follow a stream of GPS locations to create an automated system that can follow a specific individual without user control. We demonstrate the tracking systems' performance by studying the group movements of a herd of Exmoor ponies (*Equus ferus caballus*) and as a proof of concept we examine the position of the focal individual (collared animal) in relation to the center of the video frame. We also collect information about the focal individual's nearest neighbors. The automated animal observation tool is effective at consistently keeping the focal individual close to the center of the video frame, offering a new dimension to existing remote telemetry tools. For instance, the repeated observation of the same individual in different physiological states, seasons, and demographic groups, potentially opens new avenues in collective movement ecology research. By making our design, software, and firmware freely available, we aim to encourage continuous improvements to collective behavior research and to facilitate replicable approaches across other species and ecosystems.

## 3.1 Introduction

In the last several decades, technological innovation has advanced rapidly in the field of movement ecology. This powerful synergy between science and technology has transformed the way we study ecology and has resulted in many exciting discoveries (Cagnacci et al., 2010). In the context of remote telemetry, technological developments have focused on GPS device miniaturisation, increased temporal resolution, greater spatial accuracy, and longer battery life (Kays et al., 2015). As a result, vast amounts of high-accuracy animal location data for a variety of species can be collected (Bridge et al., 2011). Sensors, such as accelerometers, magnetometers, temperature sensors, and acoustic recorders, further enhance data collection by augmenting location data with information on physiological variables and energy expenditure (Boyers et al., 2019; Hooten et al., 2019; Martin Lopez et al., 2015; Qasem et al., 2012; Wilson et al., 2006). When combined with environmental data collected from remote sensing, aerial surveys, or transect sampling, animal movement patterns can be linked with physiological and environmental factors, providing an integrated view of the animal and its environment (Kays et al., 2015).

Although modern telemetry tools can provide high resolution data on the movement and behavior of animals, they are limited in that they only allow for the tracking of a single individual and do not provide information on the instantaneous social cues and signals an individual animal may be observing. Many species move collectively and social interactions play a significant role in decisions relating to when and where to move (Westley et al., 2018). Collective behaviors therefore drive many fundamental ecological processes (DeLellis et al., 2014; Sumpter, 2010), for instance, herds of ungulates find safety in numbers (Scheel, 1993), schools of fish display synchronized escape responses under predatory attack (Beauchamp, 2012; Herbert-Read et al., 2015), avian species such as penguins huddle for social thermoregulation (Ancel et al., 2015; Gilbert et al., 2010), and foraging routes are copied in species such as sparrows (Lima and Zollner, 1996).

Despite the ecological importance of collective movement (Hughey et al., 2018), we currently lack effective tools for studying social interactions in animals in the wild. In small, highly cohesive groups it may be possible to equip every individual with a GPS collar (Strandburg-Peshkin et al., 2015). However in many species it is either not feasible to tag multiple individuals within a group, or the fission-fusion dynamics of group formation mean that individuals quickly separate (Couzin, 2006). Several studies have employed unmanned aerial vehicles (UAVs) (or drones) to study collective movement in situ (Hui et al., 2021; Iwamoto et al., 2022; Torney et al., 2018b; Van Andel et al., 2015), however, there are many important ecological questions that can't be addressed through short term studies of this type. Tools that allow repeated observation of the same individual at multiple time points and in different environmental conditions while simultaneously observing other individuals within the group are required to investigate questions relating to leadership dynamics (Krause et al., 2000; Pettit et al., 2015), spatial aggregation of individuals within the group (Couzin et al., 2003; Hansen et al., 2016), information sharing and cultural transfer within the group (Simons, 2004; Stewart and Harcourt, 1994; Ward et al., 2008), and individual personality (Sasaki et al., 2018). A promising approach to address these open questions in ecology is the use of customizable open-source electronics that are available from manufacturers such as Arduino, Raspberry pi and Adafruit. There is a growing use of these devices in ecology for monitoring and tracking wildlife (Alarcón-Nieto et al., 2018; Foley and Sillero-Zubiri, 2020; Greenville and Emery, 2016; Wild et al., 2022) as they offer a low cost, highly flexible alternative to traditional commercial telemetry devices.

In this work we propose an open-source low cost system designed to enable repeated observations of GPS collared individuals using UAVs. We combine a custom-built GPS collar and LoRa radio transmitter with a commercial UAV and take advantage of the inbuilt capacity of the UAV to follow a stream of GPS locations. We first describe our system and then demonstrate the efficacy of the method by applying it to an example case study on the social dynamics of a small group of Exmoor ponies.

## 3.2 Materials and methods

An overview of our proposed system can be found in Figure 3.1 which illustrates the roles of the different components we employ and the manner in which they communicate with one another. In summary, we use an off-the-shelf commercial drone that automatically follows a stream of GPS locations that are transmitted from a collared animal via a base station and controller tablet. The GPS collar broadcasts high frequency GPS fixes (1Hz rate) to a base station using a long range (LoRa) radio transmitter. The base station receives GPS fixes and forwards them to the tablet via Bluetooth, which then controls the drone. A custom Android app installed on the tablet spoofs the tablet's GPS location by replacing its own location with the GPS coordinates from the collar. By implementing the drone's 'follow-me' mode, the drone is instructed to follow the collared animal rather than the tablet controlling the drone. As a result, the drone tracks and records nadir footage of a specific collared individual which is on-average located at the center of the video frame. Detailed specifications and descriptions of components and the protocol of assembling both the base station and GPS collar are outlined in Table 6.1 and Table 6.2.

### 3.2.1 Hardware

Following the approach of Foley and Sillero-Zubiri (2020), we used a variety of microcontrollers and breakout modules developed by Adafruit Industries (`www.adafruit.com`), which manufactures a wide range of components for DIY electronics projects. All components employed were part of the Feather family, a range of microcontroller main boards (termed Feathers) and extension boards (termed FeatherWings) developed by Adafruit that provides a modular framework for creating bespoke devices by combining different microcontrollers, communication boards, and functional extensions, such as GPS modules. We created two custom devices for the system, a GPS tracker collar for transmitting locations, and a base station for receiving locations and forwarding to the controller tablet.

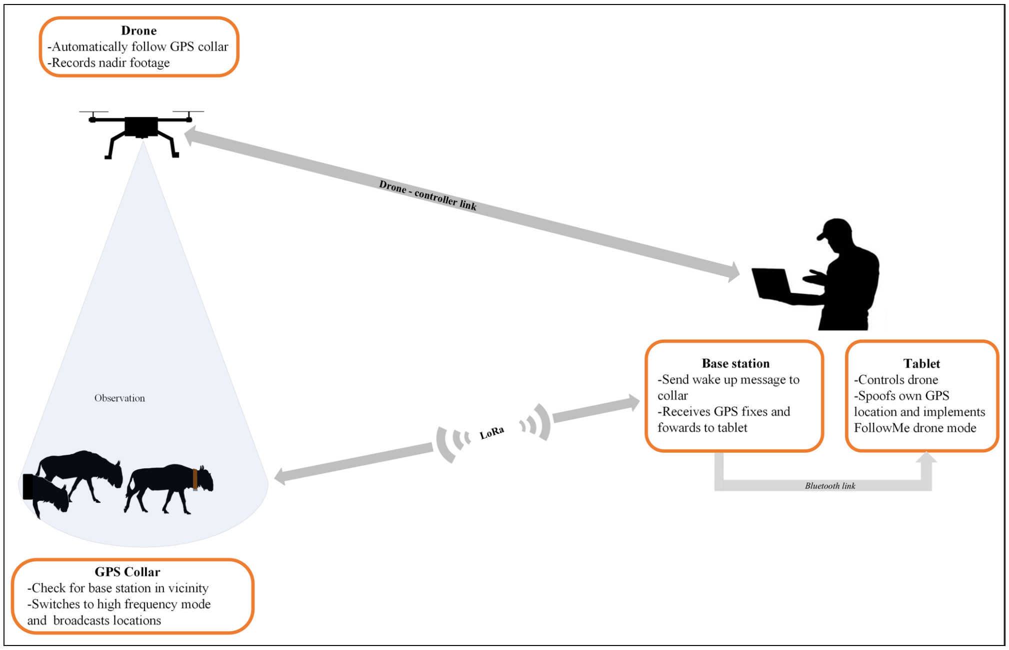

Figure 3.1: A schematic showing the key components of the automated tracking system set up including the GPS collared animal, the operator, a base station, the tablet and a drone as well as description of each component's role and how they are linked via various communication networks

.

### Custom GPS collar

To construct our custom GPS collar, we used an Adafruit Ultimate GPS FeatherWing (a low power module for GPS location acquisition) and an Adafruit Feather M0 with RFM95 long range (LoRa) radio transceiver for wireless communication. Male and female stacking headers were used for connecting boards together, a uFL to RP-SMA antenna adapter cable connected the board and antenna which was then connected to a dipole swivel antenna (Fig. S9). We soldered the female stacking header onto the Adafruit Ultimate GPS FeatherWing while the male stacking header and the uFL connector was soldered onto the Adafruit Feather M0. Then, we connected the uFL to RP-SMA antenna adapter cable and the antenna. The GPs collar was powered by a 3.7V, 2000 mAh rechargeable lithium ion battery pack. To protect the assembled unit, we placed it in a 3D printed plastic casing custom designed in FreeCAD, an open source 3D parametric modeler. The custom GPS collar, including the casing, electronics, and the halter, weighed 150g.

### Base station

The components used to construct the base station include; (a) FeatherWing Tripler Mini Kit that connects several featherwings boards together, (b) Adafruit FeatherWing monochrome organic light-emitting diode (OLED) for display purposes, (c) Adafruit long range (LoRa) radio FeatherWing transceiver for wireless communication, (d) Adafruit Feather nRF52840 Express for bluetooth communication, (e) RP-SMA tilt Swivel 1/2 wave whip omnidirectional antenna 2.4GHz, (f) edge-launch SMA connector for connecting to whip antenna, and (g) male and female feather stacking headers for stacking boards together (Fig. S8). Soldered onto the FeatherWing Tripler Mini Kit were female feather stacking headers, while the male feather stacking headers were soldered onto the other components; the Adafruit FeatherWing monochrome OLED, the Adafruit (LoRa) radio FeatherWing, and the Adafruit Feather nRF52840 express. Then the SMA connector was soldered onto the Adafruit LoRa radio FeatherWing and the whip antenna attached. Lastly, components were stacked together to make a single base station unit and powered by a power bank using a USB cable. To protect the base station, we placed it in a 3d-printed plastic housing that was again designed using FreeCAD as shown in Fig. 3.2B. The design files for both the custom GPS collar and the base station are available here `https://github.com/ctorney/collar-follower`, however for long term field deployment they will require modification to be made watertight and shockproof.

### Unmanned aerial vehicle (UAV)

We used the DJI Mavic 2 Pro drone (`www.dji.com`). The drone (shown in Fig. 3.2C) is a quadcopter that can be controlled at a maximum distance of 6km, has a maximum flight time of 27-31 minutes, and maximum speed of 20m/s (no wind). The drone is equipped with a 20 megapixel Hasselblad camera which has 1"-type CMOS sensor and 4K resolution (3840 x 2160 pixel) recording at 30fps. The camera is mounted on a stabilizing gimbal with control range pitch -90 to +30 (tilt). The drone is powered by a lithium ion polymer intelligent flight battery with a capacity of 3850mAh. Key specifications of the drone are as highlighted in

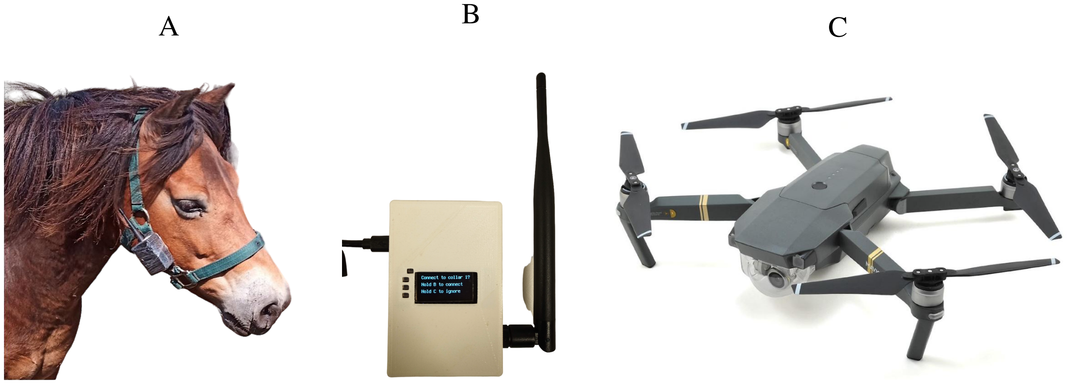

Figure 3.2: Panel A custom GPS colar attached to an adult Exmoor pony using harness, panel B is a fully assembled base station housed in a 3d-printed case and panel C is the DJI Mavic 2 Pro drone used for video recording. Photos by Cyrus Kavwele.

supplementary material Table. 6.3. To control the UAV, we used the third party autonomous flight app Litchi (`https://flylitchi.com/`) as it has an in-built 'follow-me' mode.

### 3.2.2 Software

All software used for the microcontrollers and the custom android app is open source, released under the MIT license, and available here `https://github.com/ctorney/collar-follower`.

The software for the GPS collar was designed so that it remains in a low-power state until the base station is in proximity, then when instructed to do so it enters a high fix rate 'GPS tracker mode' that sends a continuous stream of GPS locations to the base station via a peer-to-peer LoRa connection (see Algorithm 1).

From the perspective of the operator the system works as follows. Once the operator expects to be within range of a collared individual they turn on the base station, and it begins broadcasting a *wake-up* message to any custom GPS collar attached to an animal that is within range. The base station broadcasts the message, waits 10 seconds for a response then if no response is received repeats the message (see Algorithm 2). If a GPS collar is within range and is in its listening mode, the collar will send an acknowledgement to the base station that includes a unique identifier for the custom GPS collar. The base station then prompts the operator to either ignore the GPS collar connection (which if selected, sends the base station back to broadcasting mode) or to connect to the GPS collar which involves sending a message that is addressed to the specific GPS collar instructing it to enter standby mode. During standby mode, both base station and GPS collar switch from a long-range communication mode to a short-range mode and the GPS collar enters a high-fix rate GPS mode (1Hz). Once the GPS collar has confirmed it has entered the short-range communication, high-fix rate mode, the base station prompts the operator to either disconnect and send the GPS collar back to sleep or to initiate its GPS tracker mode.

If the operator selects the GPS tracker mode, the base station starts receiving the high fix rate locations from the GPS collar on the animal and forwards them to the tablet via a Bluetooth link. At this stage the custom app on the tablet begins to spoof the tablet's GPS location, making it appear as if the tablet is located with the GPS collared animal when it is actually held by the operator. The operator then launches the drone and once it is launched they activate the in-built 'follow-me' mode in the Litchi drone controller with a pre-specified altitude. This causes the drone to start tracking the focal individual (collared animal) and record nadir footage of the focal individual and its near neighbors within the herd. The initiation and termination of the recording are controlled by the operator. While the base station is receiving GPS locations, the operator has the choice to either keep the base station receiving and listening for location messages or send a sleep command to the GPS collar which disconnects the communication channel and sends the GPS collar back to its low-power state. Typically, the operator will take control of the drone at this point, however in the absence of user control or GPS locations being received, the 'follow-me' mode will automatically deactivate and the drone will remain airborne at the last GPS location received.

## 3.3 Case study

### 3.3.1 Study species and location

We conducted a field test of our framework at the University of Glasgow's Cochno Farm and Research Center ($4^{o}24.467^{'}$E, $55^{0}56.237^{'}$N), which covers approximately 66 hectares is about a 25-minute drive to the north of the university. The facility is home to an Exmoor

**Algorithm 1** Pseudocode for custom GPS collar

```
Setup GPS & Radio
loop
1.0Enter listening mode
    while time listening $<$ 10 min do
        Listen for wake-up msg
        if wake-up msg received then
3Enter standby mode
            while time in standby $<$ 10 min do
                Listen for start tracking msg
                if start tracking msg received then
5Enter tracker mode
                    Set GPS to high frequency
                    Set LoRa to short range
                    while time since last msg $<$ 5 min do
                        Send GPS location
                        Listen for confirmation
                    end while
5Re-enter standby mode
                end if
            end while
        end if
    end while
    Sleep 30 minutes
end loop
```

**Algorithm 2** Pseudocode for base station

```
Initialize Bluetooth, Display & Radio
0.0Initialize tablet connection
while tablet not connected via bluetooth do
    attempt connect to tablet
end while
0.0Begin collar communication
loop
1.0Enter broadcast mode
    Broadcast wake-up msg to all collars
    Listen for 10 seconds
    if reponse received then
        User input: connect or ignore?
        if connect then
3.0Enter standby mode
            Send standby msg to collar
            User input: start or disconnect?
            if start then
4Enter tracker mode
                Send start tracking msg to collar
                while no user interrupt: do
                    Receive GPS coordinates
                    Send acknowledgment
                    Forward coordinates to tablet
                end while
            end if
3Disconnect from collar
            Send sleep msg to collar
        end if
    end if
end loop
```

pony (*Equus ferus caballus*) herd that was introduced in November 2020 and consisted of four mares, one with a foal, and a stallion at the time of introduction. The herd is part of a breed conservation initiative and currently supports research into Exmoor pony conservation and rewilding. Ponies are true grazers that form small herds with a preference for open habitats (Vermeulen, 2015), and they influence ecological succession by preventing shrub and tree overgrowth, which in turn hinders forest succession (Hagstrup et al., 2020). At the time of data collection, more ponies had been introduced, bringing the total to 11 individuals, which included 7 mares, 1 stallion, 1 sub-adult, and 2 foals.

### 3.3.2 Data collection

We collected data between 9th April 2022 and 2nd October 2022, on 5 separate days. The GPS collar was deployed and collected at the start and end of each field test and no chemical immobilization was required due to the ponies' familiarity with their handler and fondness for carrots. The GPS collar was attached to the side of a horse halter, strapped on to an adult mare, and adjusted to avoid discomfort.

Once the GPS collar was deployed, we relocated to a location approximately 100m away from the herd and prepared a take-off and landing zone. This distance was selected to minimize any potential disturbance to the herd caused during the setup and launch of the drone. We activated the base station by connecting a power source and once connected to the tablet via bluetooth, it began to periodically broadcast the *wake-up* message to any GPS collar within range. The base station continued to broadcast the *wake-up* message until the deployed GPS collar entered its listening mode (see Algorithm 1) at which point we were able to initiate the connection between the base station and GPS collar, and we then placed the GPS collar in standby mode awaiting the instruction to enter the full GPS tracker mode.

After successfully placing the GPS collar in standby mode, we launched the drone and climbed away from the herd at a 45° angle up to 80m above ground level to ensure that the ponies' natural behavior was not disrupted. Climbing at an angle enhances stability and control, counters the airflow around the drone that affects stability, and is energy-efficient since the drone uses forward thrust to gain altitude. We considered 80m above ground level to be the optimal height for the drone as it resulted in high-resolution imagery and the ponies did not respond to the noise of the drone at this altitude. Once the drone was airborne at the target altitude, we initiated the GPS tracker mode of the GPS collar and activated the ‘follow-me’ mode on the drone controller application. The final stage of tracking was to begin GPS spoofing on the tablet, after which the drone automatically flew towards the collared individual, positioned itself directly above and began to track the collared animal and record nadir footage. Recording bouts lasted for about 15-20 minutes depending on weather conditions, and repeated flights were undertaken with breaks in between to change battery. A raw sample of the footage recorded using automated systems is available here `https://figshare.com/articles/media/A_raw_footage_recorded_using_the_automated_tracking_system_mp4/25249906?file=44609950`.

### 3.3.3 Data processing and analysis

To locate animals within video frames we used established computer vision techniques, specifically employing the *you only look once* (YOLO) (Redmon et al., 2016) single shot object detector. YOLO object detectors are a family of deep convolutional neural networks that predict bounding boxes and class probabilities in a single pass through the network and have been applied in several ecological computer vision tasks (Kavwele et al., 2022; Roy et al., 2023; Torney et al., 2019).

For our application, we employed an implementation of YOLOv3 (Torney et al., 2019) that had been pre-trained on drone images collected from a study of wild horses in Portugal (Inoue et al., 2020) in combination with a detection linking algorithm to create tracks (Wojke et al., 2017). Due to the similarity in the study animals, the YOLOv3 object detector differentiated objects from the background satisfactorily; hence, no further fine-tuning was required. We used this method to detect every individual within a frame of the video, create tracks for individuals, and then employed a manual process of track inspection to link broken tracks and to determine the collared individual. The procedure involved inspection of video footage at points where a track ended and manually linking any subsequent new track that was associated with the same individual. The track ID of the individual wearing the GPS collar was noted based on its position to the center of the frame and its coloration. We took the xy-pixel location of the center of the bounding box associated with an individual as its location, and used this value to calculate nearest-neighbour distances and the Euclidean distance to the center of the video frame.

### 3.3.4 Performance of the aerial observation system

We firstly evaluated the performance of our automated tracking system by examining the average position of the focal individual (collared animal) relative to the center of the video frame. The results revealed that the distance of the focal individual to the center of the video frame is on average approximately twice the focal individual's body length, as shown in Figure 3.3A. Furthermore, as indicated by the dotted line in Figure 3.3A, the average distance of all other individuals within the frame to the center of the video frame are nine times the body length. This is illustrated in Figure 3.3C, which is a cropped version of the original, where the blue dot indicates the center of the frame while the focal individual is outlined with a red bounding box. The fact that the focal individual is typically located at the center of the frame provides a straightforward way to identify this individual when analysing the herd's trajectories. Once all individual's are tracked, the collared individual will be associated with the trajectory that has the shortest average distance to the center of the frame.

We also provide an example of a behavioral metric that can be extracted from data collected with the automated tracking system. In Figure 3.3B, we show density plots of the near neighbor distances for the first, second, and third nearest neighbour. This analysis shows that the nearest neighbour typically found within a distance equivalent to one body length of the focal individual, while the second and third nearest neighbors are within a distance of approximately 2.5 times the body length. While investigating near neighbor distances represents a very simple example of the type of analysis that may be performed using repeated observations of a single collared individual, it provides insight into the spatial structure of the herd and if repeated for multiple individuals may reveal different levels of sociality between individuals or within a single individual at different points in time.

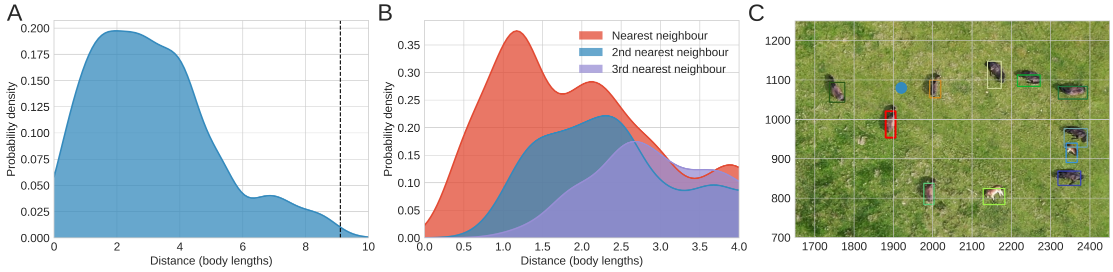

Figure 3.3: Panel A depicts the distribution of the collared individual's distance to the center of the frame. For comparison, the dotted line shows the average distance from the center of the video frame to all other individuals within the frame. Panel B depicts the distribution of the collared individual's nearest neighbour distances, as an example of behavior analysed from data collected using a custom-built tracker. Body length was calculated based on the maximum length of the bounding box surrounding the focal individual in each video. Panel C is a cropped still frame showing the collared individual bounded by a red box with the center of the frame indicated by a blue dot. Photo by Cyrus M. Kavwele.

## 3.4 Discussion

We introduce an innovative approach for developing a tracking system utilizing low-flying drones and affordable programmable open-source electronics (Cressey, 2017). By utilizing data obtained from Exmoor ponies, we assessed the effectiveness of our tracking system by analyzing the position of the collared individual relative to the center of the video frame. Moreover, we demonstrated the system's capability to gather individual-level data within the social context of a group, expanding the range of potential questions that such data can address. This automated tracking system is novel in its ability to allow users to observe collared individuals across multiple time points, in different seasons and habitats while collecting data on the individual's near neighbors.

The continuous advancement and refinement of telemetry technology, increased computational power, and robust mathematical models have enabled researchers to delve into the intricacies of movement ecology and behaviors (Hooten et al., 2017; Joo et al., 2020; Mennill et al., 2012; Nathan et al., 2022; Northrup et al., 2022), unlocking new avenues for exploration. Despite significant progress in movement ecology, the study of localized social interactions within collectively moving species in the wild has not progressed at the same pace.

This discrepancy arises from the limited capabilities of existing tracking tools, which fail to provide simultaneous fine-scale trajectories for each individual in a group over extended periods. However, with the development of our automated tracking system, it becomes feasible to acquire fine scale data on the social behavior of a collared animal in the wild. The ability to repeatedly observe an individual within its social context presents a unique opportunity to investigate complex behavioral questions, such as decision-making, personality, leadership roles, and the role of social cues in movement decisions under varying physiological and environmental conditions. Additionally, obtaining simultaneous trajectories of non-focal individuals within a group will enable researchers to explore other social interactions. For example, it allows for investigating how individuals respond to social cues such as the influence of nearest neighbors or group average heading (Dalziel et al., 2016), potentially unveiling stereotyped individual responses to collective attributes of the group. This tracking system could also be employed to study social behavior in the context of post-reintroduction monitoring. As an example, (Mertes et al., 2019) utilized GPS location data to monitor the post-release movement of reintroduced scimitar-horned oryx (*Oryx dammah*). Therefore, adopting our automated tracking system could enhance data collection by providing insights into the cultural transmission of information (Berdahl et al., 2018) and the leadership roles of naive individuals introduced into experienced populations. In the realm of social interactions and dynamics, investigations can be conducted into aspects such as the formation of "leader-follower" relationships, consensus building as clusters explore new habitats, and the influence of nearest neighbors, among other factors. However, acquiring trajectories of non-focal individuals within a herd depends on factors such as the spatial extent of the herd, the flight altitude, and the camera field of view. Thus, a comprehensive understanding of the study system and the behavior of the target species is crucial when designing behavioral studies involving non-focal animals.

Along with the new ecological questions that can be addressed through repeated observations of the same individual, the use of GPS collars to control and position a drone will potentially also facilitate existing approaches to studying collective behaviour in the field. The communication system has an expected range of 15km in the long range mode and 2km in the short range mode depending on the terrain and the height of the base station. Further, the GPS coordinates of the collar are transmitted to the base station and can be displayed on the tablet. Beyond the tracking capacity the system will therefore make finding animals more straightforward in the field, and once located will facilitate staying with the herd. Strategies for constant observation of a herd, such as the relay system of drones described in (Koger et al., 2023), could in principle also be automated with multiple controller tablets receiving locations from the base station.

Our automated tracking system presents a valuable tool for facilitating the acquisition of collective behavior data in the wild if its full potential is realized. However, when considering drone usage, there are several limitations and challenges that need to be overcome. The legal framework governing the use of unmanned aerial vehicles (UAVs) may acts as a barrier to fully harnessing their potential in ecological studies (Witczuk et al., 2018). For instance, long-distance flights become impossible due to the requirement to maintain visual line of sight with the drone. This necessitates frequent relocation of UAV operators, which can be time-consuming. Furthermore, legal regulations vary across countries, resulting in inconsistencies in drone operations. The flight time of a UAV depends on its model, payload, and battery size and is greatly reduced by high wind speeds and/or low temperatures (Beaver et al., 2020; Torney et al., 2018b). In addition to regulations and battery life, UAVs are also affected by prevailing weather conditions and poor visibility during precipitation, fog, or haze restricts operations.

The tracking system is highly customizable, allowing for the incorporation of user-defined requirements and the integration of additional components to enhance performance, thus expanding its applicability across various biomes and species. The flexibility and potential for future modifications are discussed further below. To begin with, the use of programmable microcontrollers enables researchers to modify the software to suit their specific research needs. For example, they can adjust the frequency of GPS fix rates, determine the type of data to store, and set the frequency of low-power states, among other user-specific settings. Changing the drone camera sensors is also a possibility. UAV-based platforms can leverage a wide range of sensors available on the market, such as RGB cameras, hyperspectral, thermal, LI-

DAR, and multispectral sensors (Sun et al., 2021). Employing different sensors can enhance the data collected, such as evaluating plant health and assessing the influence of stress on ungulate collective behavior using multispectral sensors (Wang et al., 2019). Another example is the utilization of thermal infrared sensors, which can discriminate endotherms from their surroundings (Beaver et al., 2020; Burke et al., 2019) and enable the detection of animals in low-light conditions, such as herds in dense woodlands. Drones have become a versatile tool for ecological studies and have been employed in studies of species distribution and abundance (Corcoran et al., 2021), human-wildlife conflict mitigation (Gorkin III et al., 2020), and habitat structure and its influence on collective decision-making (Strandburg-Peshkin et al., 2017). Our proposed methodology has the potential to broaden the scope of ecological questions that can be addressed in this context since the system has the ability to collect data on the surrounding physical and biotic environment (as discussed in (Koger et al., 2023)) alongside capturing footage of both focal and non-focal individuals and their interactions. For instance, the drone footage can be analyzed to extract information on landscape features, human disturbance, habitat structure, and resource availability, and as such, the extracted data would allow ecologists to infer group navigation and decision-making processes, and investigate dynamic, individual-level responses to environmental features. Such empirical data on fine-scale movement can yield valuable insights into an animal's memory of the landscape, particularly when encountering linear structures/features like rivers, roads, or resource patches, among others.

The 3D housing cases can be customized to fit various ungulate species, ranging in size from medium to mega-herbivores found in different biomes. The objective is to ensure a perfect fit, watertightness, and robustness to withstand any shock or disturbance caused by the collared animal. We emphasise, however, that our 3D cases were not tested for robustness since we attached and detached them at the end of every filming event, therefore modifications would be necessary before field deployment. Additionally, future modifications could explore ways to harness green energy by using a mini solar panel that charges the battery or the use of vibration energy harvesters, which convert the kinetic energy of the collared animal into electrical energy (Zhang et al., 2021). Such changes would eliminate the need to recover the

GPS tracker for charging or replacement, significantly increasing its lifespan from several months to years and resulting in more extensive data, spanning multiple seasons. Without additional charging, we estimate a 2000mAh lithium ion battery will provide approximately 20 hours of high-frequency observation and would last approximately 6 months if entering listening mode once per day.

In conclusion, our low-cost, automated tracking system has been tested and demonstrated functionality for repeatedly observing collared animals, enabling the collection of fine-scale behavioral data on species that live in groups. This system represents a significant advance, allowing for the transition from individual tracking to the simultaneous tracking of all individuals in cohesive groups with the focal individual at the center of the frame. Consequently, this bespoke tool empowers researchers to explore ecological questions with unprecedented levels of detail and complexity, yielding fresh insights into the movement ecology and collective behavior of group-navigating species in the wild.

## 3.5 Ethical statement

Handling of the Exmoor pony (*Equus ferus caballus*) was approved by the Research Ethics Committee in the School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, under the approval number EA45/19.

# Chapter 4

## Near real-time classification of Serengeti wildebeest behaviour with edge machine learning and a long-range IoT network

**Note:** This chapter has been prepared as a manuscript which I aim to submit to the journal *Methods in Ecology and Evolution*.

## Abstract

Anthropogenic activities and global warming are driving irreversible transformation of natural ecosystems thereby imperilling the persistence of biodiversity. For instance, habitat loss and fragmentation affect migratory ungulates and disrupt various ecological processes. Given the rate with which these transformations are taking place, our knowledge about how species behave and respond to disturbances on a finer scale is limited. This is partly due to the lack of appropriate tools capable of collecting data *in situ* across disturbance gradients spanning multiple seasons. To address this gap, we present a custom designed low-cost solar-powered GPS collar with edge-processing that classifies accelerometry data to provide near real time behaviour monitoring over a Long Range Wide Area Network (LoRaWAN) that is suitable for collecting scale appropriate data in the wild. It incorporates the use of open-source electronics, edge machine learning, internet of things (IoT) network, and a firmware that manages the periodic switch between low and high power modes with each mode lasting for 30minutes. The LoRa collar records 6 axis inertial measurement unit sensor data at 5Hz, preprocesses and sends to the on-board preprocessor where a pretrained convolutional neural network examines the accelerometry data over a 10 second period and classifies the period as one of the four behaviours (grazing, lying, standing, and walking). Each 10-second window is classified as one behaviour which translates to 180 behaviours in a period of 30 minutes. The predicted behaviour classes, GPS location and timestamp as header are transmitted to the server via LoRaWAN. If the collared individual is outside LoRaWAN network data are stored on-board and transmitted when next in range. Finally the LoRa collar switches to low-power mode to preserve battery and the cycle is repeated. We field tested the LoRa collar on Serengeti wildebeest to demonstrate its effectiveness by recording both positional and behavioural data and successfully transmitting it to server via the LoRa network. Moreover, the analysis of both positional and behavioural data provides clear evidence of the LoRa collar's effectiveness as a fine-scale tracking tool, capable of accurately recording daily animal activity patterns in its natural environment. The performance evaluation serves as a proof of concept, showcasing the ability of the LoRa collar to transmit data to end users in near real-time. Our approach offers an alternative to commercial telemetry devices, as it comes at a relatively lower cost,

and with free guides and a large user group to assist in customising the programme. Overall, the use of open-source electronics allows other researchers and innovators to improve on our approach, as well as opening a wide range of questions that can be investigated in wildlife conservation using these novel technologies.

## 4.1 Introduction

One of the most significant environmental challenges of our era lies in understanding the cumulative effects of the numerous stressors on biodiversity and ecosystems (Parry, 2007; Peñuelas and Filella, 2001). The compounding impact of global warming and habitat loss predominantly driven by human activities continues to jeopardise the existence of flora and fauna globally. Climate change-induced alterations to temperature and precipitation patterns is leading to changes in geographical range shifts (Parmesan and Yohe, 2003), community interactions (Both et al., 2009), phenology (Parmesan, 2007), genetic shifts (Bradshaw and Holzapfel, 2001), and species extinctions (Sinervo et al., 2010). Consequently, species survival is dependent on a range of responses such as dispersal capacity, reproductive strategies, genetic diversity, population growth rates, and phenotypic plasticity. However, human-induced fragmentation of landscapes is occurring at faster rates than those produced by natural events such as the affect of volcanic activity on albedo (Wiens, 1990). As a result, there is a mismatch between the time needed for organisms to develop coping mechanisms and rate of occurrence of human induced disturbances, which undermines survival and population resilience (Salmón and Burraco, 2022).

Wildlife species may respond to increasing human activity in various ways. For example, to minimize encounters with humans, wildlife species may infrequently use habitats that gradually or suddenly transition into human-dominated landscapes (Kavwele et al., 2022; Veldhuis et al., 2019). Another behavioral response to changes in landscapes perceived as high risk may involve increased walking or vigilance at the expense of other activities, such as resting or grazing. To address persistence of biodiversity in the face of future ecological disturbances, development of sound management policies will greatly benefit from a thorough understanding of how animal behaviour responds to human-driven alterations in the landscape.

Continuous remote monitoring of animals is essential for comprehending their behavior and their responses to ecosystem changes. Since the advent of telemetry which originally involved ecologists tracking animals on-foot and therefore potentially disturbing them (Cagnacci et al., 2010; Hebblewhite and Haydon, 2010), the technology allowing ecologists to relate an animal to its environment has progressively advanced. For example, using high precision global positioning system (GPS) in collars it is possible to identify key habitats selected or avoided by wildlife, map corridors such as African elephants (*Loxodonta africana*) (Graham et al., 2009), or identify the kill sites of large predators (Knopff et al., 2009) amongst others. Furthermore, GPS data have been used to identify behavioural states of individuals such as encamped versus exploratory state using measurements of step lengths and turn angles (Morales et al., 2004; Roever et al., 2010). Step lengths and turn angles metrics have been used to explore animal movement patterns function of resources or risks (Hopcraft et al., 2014). While the ability to identify behaviours based on position data and time is a valuable approach, it also has several drawbacks in terms of interpretation. For instance, a high tortuous movement trajectory characterised by short steps and high turn angles could be interpreted as a behaviour of an animal that is searching for resources or avoiding obstacles. Alternatively, the same trajectory path could be interpreted as a behaviour associated with fear and uncertainty about the next move. Different interpretations of an animal movement trajectory arise due to the absence of additional information about behaviours such as resting, vigilance, walking, and grazing. Therefore, it is evident that location and time data alone cannot provide detailed insights into animal behaviour and responses to human-induced disturbances. To advance our understanding of an animal behaviour along its movement trajectory, the integration of fine-grained complementary data from other animal-borne sensors becomes paramount, such as accelerometer devices.

Advances in telemetry technology, machine learning and miniaturisation of processors have made it possible to deploy GPS collars with animal-borne sensors such as accelerometers for quantitative measurements of the movement behaviour and activity of free-roaming animals in situations where direct observation is impractical or logistically unfeasible (Brown et al., 2013; Tatler et al., 2018). Many of these high resolution biologging devices collect large amounts of data within a short period of time (often recording at 40Hz and reaching several million records) (Ropert-Coudert and Wilson, 2005; Wilson et al., 2008). Simultaneously, machine learning techniques have proven valuable in addressing the challenges posed by intricate and vast high-dimensional data given their ability to recognize patterns such as the extraction of behaviour classes from accelerometry data (Tatler et al., 2018; Valletta et al., 2017). This has been matched by the miniaturization of computer processors that can operate at very low-power and have become more robust. While technological advances have ushered the study of animal behaviour and movement ecology into the realm of big data (Kays et al., 2015), there are new challenges associated with handling, transmitting, and processing the large volumes of accelerometry data required for precise behaviour classification (Le Roux et al., 2017). For example, transmission of large raw sensor data through a network such as VHF/UHF, mobile or satellite network is still slow and energy demanding (Nuijten et al., 2020), which can severely limit the deployment period. As such, there is a need for a continuous remote tracking system with some form of data shrinkage that would allow researchers to gain access to accelerometry data and the insights into the behaviour of hard to observe species, especially in response to ecological disturbances in near real-time basis.

The annual migration of wildebeest (*Connochaetes taurinus*) in the Serengeti ecosystem represents a unique opportunity to understand movement and behaviour of animals over a diverse landscape. The annual migration influences multiple ecological interactions partially because of the abundance of animals (1.36 million according to Tanzania wildlife research institute internal report) and partially because of the extent of their migratory range; on average individuals will travel about 2800km (Thirgood et al., 2004) each year. The wildebeest consume virtually all the grass in a given area on a given day, and are forced to move to find fresh grazing which supports a natural rotational grazing that in turn promotes compensatory growth in the grasses (McNaughton et al., 1997). The movement of the grazers transports nutrients to other parts of the ecosystem (Subalusky et al., 2017). As such, wildebeest are constantly making decisions about grazing locations, departure times from patches, resting spots, and crossing points of features such as river channels or thick vegetation that conceals ambush predators. In addition, wildebeest encounter humans and infrastructure such as tourism pressure (Larsen et al., 2020) or land cover conversion (Kavwele et al., 2022; Veldhuis et al., 2019) particularly around the edges of the ecosystem. In light of these threats, little is known about the behaviour and response of migratory wildebeest to anthropogenic pressure in the Serengeti ecosystem at a fine scale. For example, there is evidence that animals avoid or infrequently use habitats that gradually transition into human-modified landscapes (Kavwele et al., 2022). However, the specific behaviours exhibited by animals in response to disturbances, such as the amount of time spent grazing versus being vigilant or walking vs resting at a fine-scale level, remain unknown.

In this paper, we address this methodological gap by developing a near real-time behaviour classifier using edge machine learning to better understand the fine scale behaviour of migratory wildebeest. We employ a custom-designed low-cost telemetry device and a low-power long range wide-area network (LoRaWAN) for connectivity. The device is solar-powered and incorporates two modules: an inertial measurement unit (IMU) and a GPS tag for recording accelerometry and positional data, respectively. Additionally, it has a micro-controller board with the capacity to run machine learning models or store data on-board, and it offers connectivity via LoRaWAN. We refer to this device as the 'LoRa collar.' It utilizes a pretrained convolutional neural network (CNN) to classify IMU sensor data into behavioural classes. The predicted behavioural classes are then transmitted to the server or stored on-board in the absence of a LoRaWAN network within range. To achieve near real time transmission of data, we use Tanzania National Park's (TANAPA) LoRa network with gateway towers strategically placed throughout the Serengeti ecosystem. In the following section we describe the development and training of the behavioural classifier. We next present a more detailed description of the design of the LoRa collar. Finally, we present results from a pilot study whereby the collars were deployed on migratory wildebeest in Serengeti National Park in April 2023.

## 4.2 Behavioural classifier

To train the CNN model used in the LoRa collar real-time classifier, we mirrored the collar but replaced the LoRaWAN with a Wi-Fi modem (hereafter referred to as the Wi-Fi collar) that recorded and transmitted 6-axis IMU raw data to a hand-held data receiver as described below. The purpose of this separate design was to enable the collection of large volumes of data that would not be possible to transmit via a LoRa network.

### 4.2.1 Wi-Fi collar design

The Wi-Fi collar was designed specifically for collecting training data and was able to transmit high-frequency IMU data over a range of up to 1km. We used an Arduino MKR Wi-Fi 1010 microcontroller board, an Adafruit ICM-20649 sensor, which incorporates a 3-axis accelerometer and a 3-axis gyroscope that measures acceleration force and angular velocity respectively, an Adafruit Mini GPS PA1010D module that provides time and positional data, and a custom designed solar charge controller. The PCB incorporating the charge controller was manufactured by European circuits (`https://european-circuits.co.uk/`), and the MKR Wi-Fi 1010 board, IMU sensor, and the GPS were surface mounted to the PCB. A 3D casing was custom designed in FreeCAD (`https://www.freecad.org/`) which is an open source parametric modeler and printed by Additive-X using Formlab's Tough 2000 Resin. We mounted a solar panel on the upper side of the case then connected the PCB solar charge controller to the panel and to a rechargeable 2000mAh LiPo battery. Finally, we sealed the joint between the top and bottom cases using a silicon O-ring cord to ensure that the unit was dust and waterproof.

Software for the collar was developed using the Arduino IDE and is freely available here `https://www.github.com/ctorney/active-tracker`. The software was designed to periodically create a Wi-Fi network and then wait 5 minutes to see if any devices connected to the network. The collar launched the network three times in a day at 07:00hrs, 12:00hrs, and 16:00hrs local time and at other times remained in a low-power dormant state. If no device connected to the network within 5 minutes, the Wi-Fi network was terminated, and the collar switched to its low-power mode until the next scheduled high-power state. However, if a device connected, the collar would switch to a broadcast state and the Wi-Fi collar began to broadcast timestamped IMU data at 5Hz. IMU data were preprocessed by the microcontroller using a complementary filter (Kim et al., 2009) and the acceleration in an absolute frame of reference along with the pitch and roll angle of the collar were transmitted. The IMU data was transmitted to the connected device using the telnet protocol, and the device (typically a laptop) logged the data to a text file. In the event that the Wi-Fi connection was lost for more than 5 minutes during data transmission, the collar went back to its low-power state until its next scheduled high-power mode.

### 4.2.2 Data collection

To collect behavioral data for training our machine learning model, we immobilized and collared six mature wildebeest at Kilimanjaro Golf and Wildlife Estate in Arusha, Tanzania. This facility manages a captive wildebeest population, among other species. We approached the ideal candidates for collaring slowly in a vehicle and immobilized them using a combination of three drugs: Etorphine (3mg-5mg, depending on the animal's body size), Azaperone (50mg), and Medetomidine (3mg). The drugs are administered using a Dan-inject projectile system, which has a 3ml volume and 1-inch-sized dart needle. Within a time frame of 3 to 8 minutes, the darted animal was fully immobilized, approached cautiously and a Wi-Fi collar attached. To reverse the immobilization effect, Diprenorphine (24mg) was used to reverse both Etorphine and Atipamezole, while Atipamezole (10mg) was used to reverse Medetomidine. The immobilization exercise was led by a veterinary officer approved by the Tanzania Wildlife Research Institute (TAWIRI).

Once on site for data collection, we turned on the handheld data receiver's Wi-Fi and waited for it to establish a connection with the Wi-Fi collar. Once a successful connection was established, we tracked the collared individual by a vehicle or on foot while receiving 6-axis IMU sensor data recorded at 5Hz, translating to 5 samples per second. At the same time, we utilized a handheld data logger synchronized with the GPS time of the Wi-Fi collar to record the initiation time of each of the four mutually exclusive behaviors: grazing, lying, standing, and walking. This allowed us to precisely match the switch points of each recorded behaviour. In addition to the accelerometry and behavior transition data, we also filmed the focal individual for potential later behavior verification purposes. Data collection took place from 25th November 2022 to 8th December 2022 totalling to 40 hours of observational data, which resulted in 662,000 labelled observations from 5 individuals (one collar failed to transmit data).

### 4.2.3 Neural network behaviour classifier

Before developing a CNN ((LeCun et al., 1995)) which is a deep feed-forward artificial neural network, we performed pre-processing steps to enhance the quality of the data. To begin with, we inspected whether each unique window had 50 samples and retained windows with 40 samples or more. Missing samples occurred as a result of communication disruptions between the Wi-Fi collar and the handheld receiver, particularly when the collared individual moved a significant distance away from the receiver. To ensure all windows had equal number of samples ($n=50$), we filled the missing values using mean imputation method. The 50 window size was a product of 10 frames per second and a frame size of 5 and the model returned the dominant behaviour for each 10frames per second window. To train our classification model, we employed a deep learning CNN architecture shown in figure 4.1A. The CNN model comprised of a series of layers beginning with a convolutional layer, followed by max-pooling layers for down sampling and a flatten layer. We used a rectified linear unit (ReLU) activation function to introduce non-linearity. The final layers were fully connected and followed by softmax activation function to obtain class predictions. We trained the CNN model using a batch size of 256, a learning rate of 0.01 and trained for 300 epochs with assigned class weights to prevent over sampling of the most frequency class. To evaluate the performance of the trained CNN model, we split our dataset into training and testing sets with a ratio of 90:10. We assessed model performance accuracy by plotting train loss and test accuracy curves presented in figure 4.1B.

The classification results of the four wildebeest behaviour classes are as presented below. Standing behaviour class had the least accuracy of 79.93%, with approximately 15% and 8%

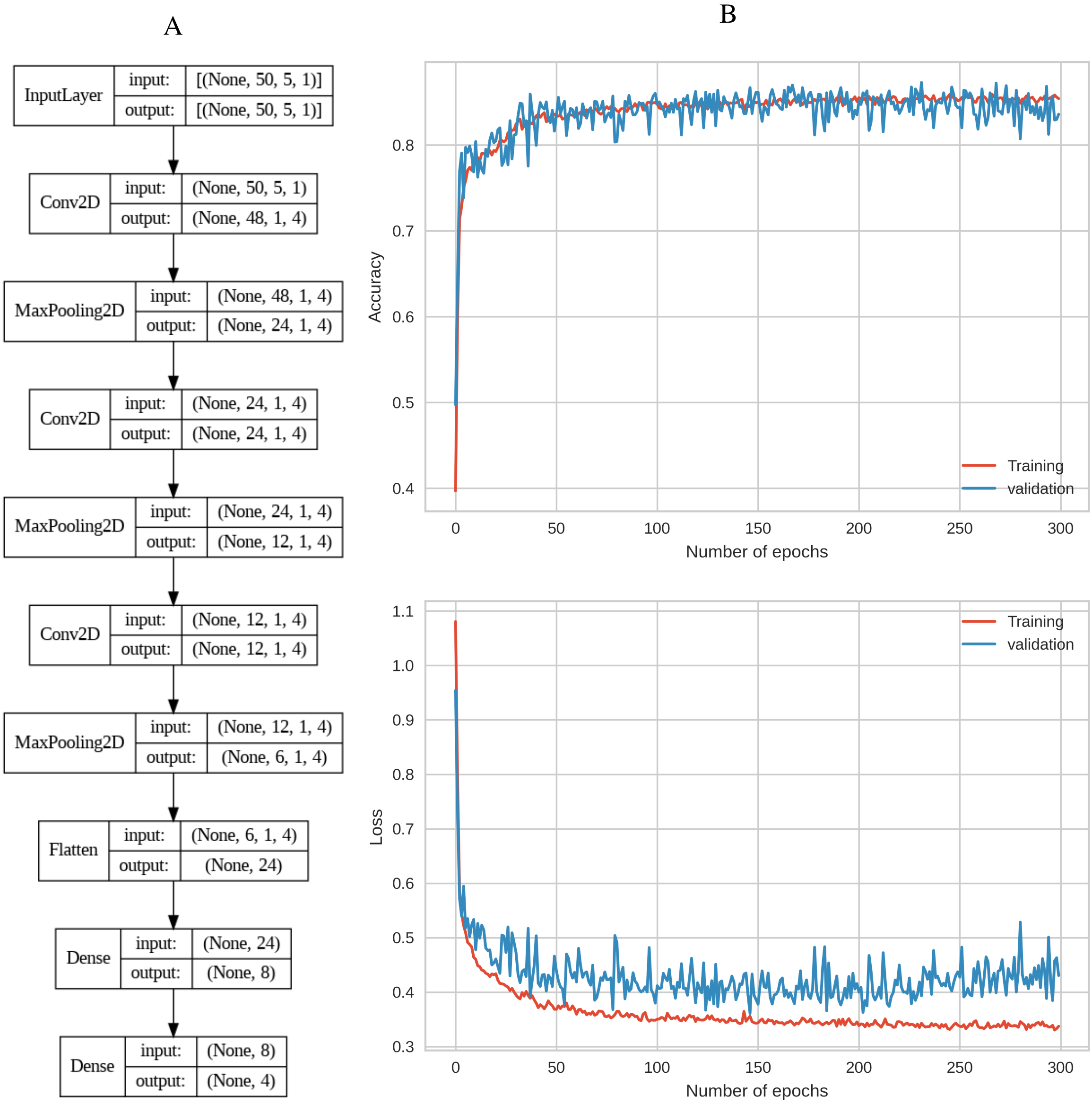

Figure 4.1: Panel A is the architecture of CNN used to train the model, panel B is the train loss and test curves for visualising model performance.

misclassified as lying and walking, respectively. Walking behaviour class had an accuracy of 82.86% with approximately 6% and 9% misclassified as grazing and standing respectively. Lying class had 89.22% with about 9% misclassified as standing while grazing achieved the highest classification accuracy of 94.08%, with about 5% misclassified as walking behavior class. The confusion matrix for the four behavior classes, displaying true positive and false positive classifications, is presented in figure 4.2. Overall, the CNN model achieved an accuracy of 84%.

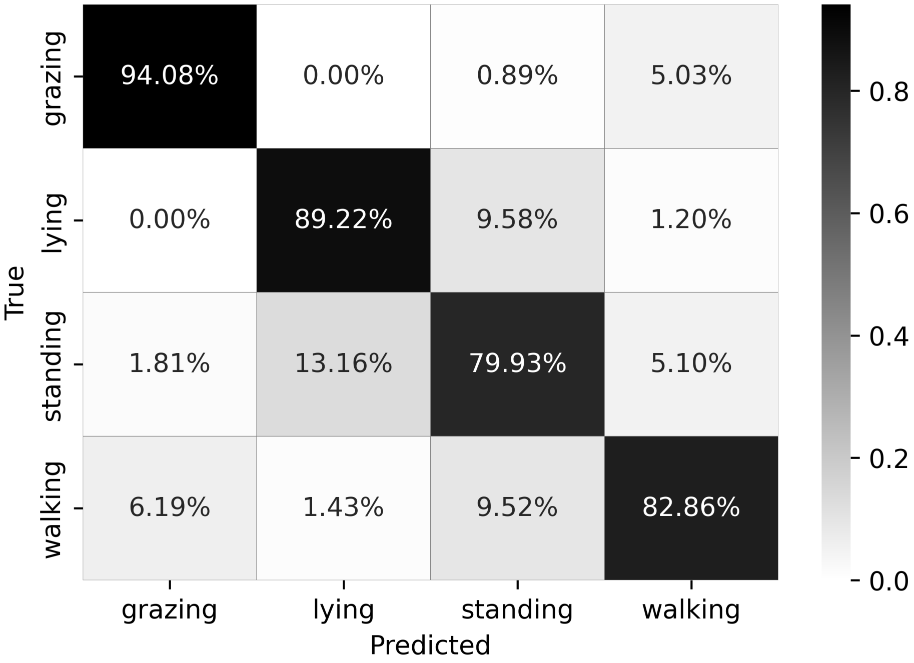

Figure 4.2: Confusion matrix plot of wildebeest behaviour classification showing true and predicted behaviour categories.

## 4.3 Deployment and field test

### 4.3.1 LoRa collar

We designed a LoRa collar to collect IMU sensor data, prepossess it, predict behaviour class and transmit the prediction output to the end-users. The LoRa collar components include an Arduino MKR WAN 1310 microcontroller board, designed for low-power wide area network (LPWAN) connectivity using the long-range wide area network (LoRaWAN) protocol. The board is ideal for long-range wireless communication and has the capacity to run machine learning models on board. The Adafruit ICM-20649 wide-range IMU, a 6-axis IMU sensor, which incorporates a 3-axis accelerometer and a 3-axis gyroscope that measures acceleration force and angular velocity respectively, an Adafruit mini GPS PA 1010D that provides position data, a custom designed solar charge controller board from European circuits `https://european-circuits.co.uk/`, a flexible antenna 868/915MHz to transmit and receive signal, a 2000mAh LiPo rechargeable battery to provide power, Seeed studio 0.5W solar panel to recharge LiPo battery, and, a Silicone sealing cord to seal joints. The Arduino MKR WAN 1310, which had the connection for the flexible antenna, the IMU sensor and the mini GPS were surface mounted on the PCB by Eurpean circuits. A 3D casing, consisting of a bottom and top case, was custom designed in FreeCAD (`https://www.freecad.org/`), an open-source parametric modeler, and then printed by Additive-X using Formlab's Tough 2000 Resin. We mounted a solar panel on the upper side of the case then connected the PCB solar charge controller to the panel and to a rechargeable LiPo battery. Finally, we sealed the joint between the top and bottom cases using a silicon O-ring cord to ensure that the unit was dust and waterproof. The final design is as shown in figure 4.3B.

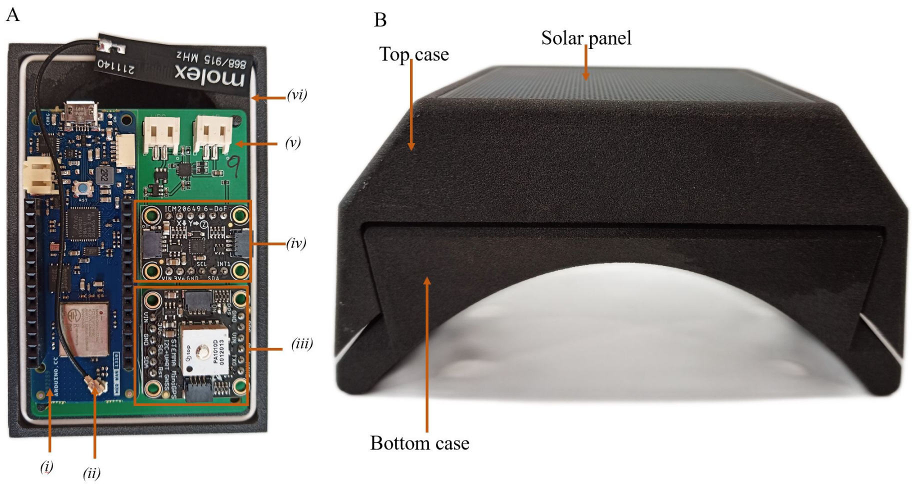

Figure 4.3: Panel A shows various components used to assemble LoRa collar (i) Arduino MKR WAN 1310, (ii) flexible antenna ISM 868/915MHz, (iii) Adafruit Mini GPS, (iv) IMU (located in the same position as in the Wi-Fi collar), (v) solar power controller board and (vi) silicone sealant cord while Panel B show solar panel, top and bottom case of the fully assembled On-board LoRa collar unit (without the Biothane harness for attaching to the animal).

Software for the LoRa collar was developed using the Arduino IDE and is freely available here `https://www.github.com/ctorney/active-tracker`. The software was designed to manage both low and high power states, each lasting for a duration of 30 minutes and another 20 minutes for data transmission.

Once the LoRa collar switched to the high-power state, it initiated the GPS and began recording 6-axis IMU data, which were then preprocessed by the microcontroller using a complementary filter to calculate acceleration in an absolute frame of reference. Subsequently, for every 10-second burst of preprocessed accelerometry data alongside pitch and roll angle of the collar data, the pretrained models predicted one of four mutually-exclusive behaviours: grazing, lying, standing, or walking. If the collared animal was within the coverage of the LoRa network, the predicted behaviour class was transmitted to the server through a LoRa gateway which occurred after the 30 minutes of behavioural data recording and processing. However, if the animal was outside of network coverage, the model's prediction output was stored onboard and transmitted once it was back within range.

For transmission purposes, data corresponding to each behaviour was encoded as a binary digit. For instance, each behaviour was encoded in binary as follows: grazing: *00*, lying: *01*, standing: *10*, and walking: *11*. Therefore, in 10 seconds of sampling, the equivalent of 1 behaviour was 2 bits; hence, 4 sequential behaviours were 8 bits or 1 byte, while in 30 minutes, there were 180 behaviours amounting to 360 bits of data, totaling 45 bytes. The 45 bytes of data, including a header with the timestamp in Unixtime format, were less than the 51-byte maximum packet size in categories datarate DR0, DR1, DR2. The final processing occurred on the server, where data was received and decoded to provide a stream of behaviours.

### 4.3.2 LoRa collar deployment process

The LoRa collars were deployed in Serengeti National Park, which is an expansive protected area that adjoins Masai Mara National reserve to the north in Kenya, forming the greater Serengeti-Mara ecosystem as shown in figure 4.4. The southern region of Serengeti NP is dominated by treeless short grassland plains while tall grass and woodlands are dominant in the north and west of the ecosystem respectively (Holdo et al., 2009). Rainfall gradient ranges between 500mm/year in the southern east and gradually increases to 1300mm/year in the northern west regions. The temperature ranges between 15$^{o}$C and 30$^{o}$C and the average temperature is 22$^{o}$C while soil fertility is highest in the southern regions and lowest in the northern west (Holdo et al., 2009). These climatic variables play a crucial role in influencing vital ecological processes, most notably the migration patterns of wildebeest and zebras as they track phenological green-up waves throughout the year. The ecosystem is rich in faunal diversity; however, it is numerically dominated by approximately 1.3 million wildebeest and 0.3 million plains zebras (Hopcraft et al., 2014).

To deploy LoRa collars on wildebeest, we conducted opportunistic searches in areas likely to be frequented by herds during that time of the year. Upon sighting a herd, we approached it slowly by a vehicle at a speed of 5 km/h or less to minimise any potential disturbance. Ideal candidates for collaring were identified and immobilised using a combination of three drugs: Etorphine (3mg-5mg, depending on the animal's body size), Azaperone (50mg), and Medetomidine (3mg). These drugs are administered using a Dan-inject projectile system, with a 3ml by 1-inch-sized dart needle. Within 3-8 minutes, the animals were fully immobilised. At this point, we approached them slowly and attached the LoRa collars around their necks. To initiate recovery, Diprenorphine (24mg) was used to reverse both Etorphine and Atipamezole, while Atipamezole (10mg) was used to reverse Medetomidine. The animals typically recovered and rejoined the herd within an average of 7 minutes. Subsequently, we closely monitored the collared individuals to ensure they resumed normal activities. In total, we successfully collared 8 mature wildebeest in an exercise led by a veterinary officer approved by TAWIRI.

### 4.3.3 Real-time behaviour classification data analysis

To evaluate the performance of the LoRa collar GPS, we extracted longitude and latitude spatial points and visually examined them by overlaying them on the map of the Serengeti ecosystem. We also calculated the distance walked between every two successive spatial points, representing the distance moved by a collared animal in 1 hour. We used a generalised linear model (GLM) with a binomial distribution to predict the probability of each activity (1 activity presence or 0 activity absence) as a function of the predictor variable distance walked in one hour. We also used generalized additive model (GAM) (Hastie, 2017) (*gam* function in *mgvc* R package (Wood, 2001)) with cyclic cubic regression spline ideal for cyclic or periodic data to smooth the non-linear relationship between activity and time of the day. The response variables had binary distribution (1 activity presence or 0 activity absence) modeled as a function explanatory variable as time of the day along 24hr period. All the analysis were carried out in Python version 3.9.12 (`https://www.python.org/downloads/release/python-3912/`) and R version 4.0.2 (R Core Team, 2020) (`https://www.r-project.org/`).

### 4.3.4 Real-time behaviour classification results

The distance walked by a collared individual within one hour ranged from 0.49m (min) to 4225.99m (max), with an average of 337.32 ± 1.67m. Visually, the distance walked between points is as shown in figure 4.4, representing the trail walked over the sampling period in the Serengeti ecosystem. As the distance between two spatial points increased, the probabilities of grazing, lying, and standing decreased, while the probability of walking increased as presented in table 4.1 and figure 4.5. The results demonstrate that when there is a very large displacement between two GPS points (indicative of walking activity), the CNN model has a high probability of classifying the behaviour as 'walking' based on the accelerometer data. Conversely, it assigns low probabilities to other behaviour classes, namely: grazing, lying, and standing, which is biologically meaningful. Importantly, this finding confirms that the two different data streams (GPS and accelerometer) corroborate each other, indicating that the device is effective.

Generally, the activity patterns fluctuated with peaks and valleys occurring at different times of the day. Overall, during the night, the probability of both lying and standing was high, while grazing and walking were less likely. During the day, the probability of grazing was high, especially in the early morning and late afternoon. The probability of walking was high during the day, while lying and standing had the lowest probabilities, with slight peaks around mid-day as shown in Figure 4.6.

As such, the probability of a given activity is strongly influenced by the time of day. The observed patterns have biological significance; for instance, increased immobility during the night may represent a strategy to minimize encounters with predators. This activity budget extracted from the data is intended to demonstrate how animals allocate their time to various activities in typical scenarios, along with other influencing factors. It also serves as a key performance indicator for assessing the effectiveness of the LoRa collar as a tool for fine-scale animal tracking.

Table 4.1: Binomial GLM summary describing the probability of an activity with respect to distance moved by a collared wildebeest in one hour

| **Model** | **Variables** | **Coefficient** | **SE** | **Z value** | **P value** |
|---|---|---|---|---|---|
| Grazing model | Intercept | -0.8472 | 0.007 | -125.41 | $< 0.00$ |
| | Distance | -0.0002 | 1.08e-05 | -21.737 | $< 0.00$ |
| Lying model | Intercept | -0.5256 | 0.007 | -74.015 | $< 0.00$ |
| | Distance | -0.0018 | 2.5e-05 | -71.747 | $< 0.00$ |
| Standing model | Intercept | -1.1742 | 0.008 | -154.222 | $< 0.00$ |
| | Distance | -0.0007 | 1.72e-05 | -41.529 | $< 0.00$ |
| Walking model | Intercept | -1.8344 | 0.009 | -213.677 | $< 0.00$ |
| | Distance | 0.0015 | 1.27e-05 | 118.391 | $< 0.00$ |

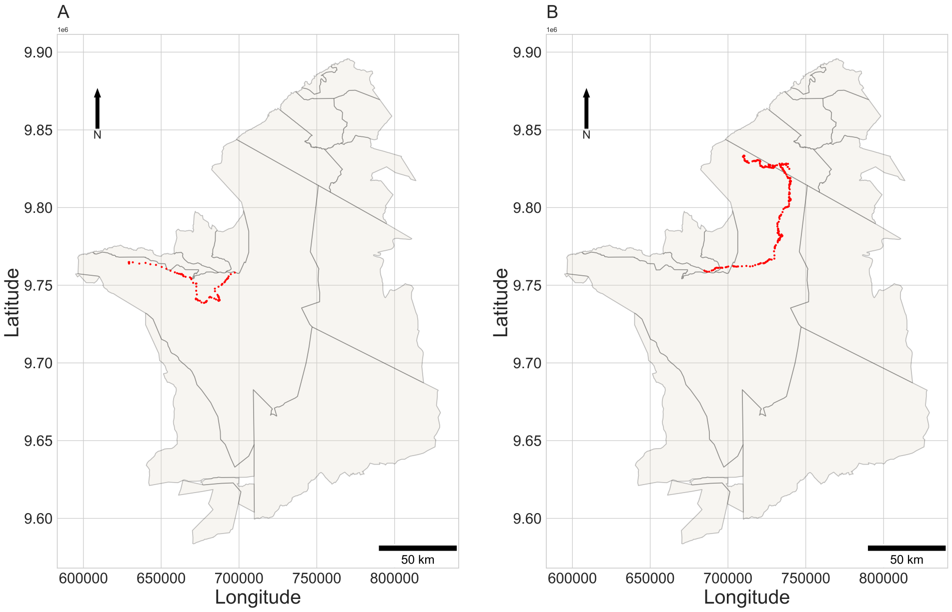

Figure 4.4: GPS points location map of LoRa collared wildebeest in Serengeti ecosystem showing their movement trajectories.

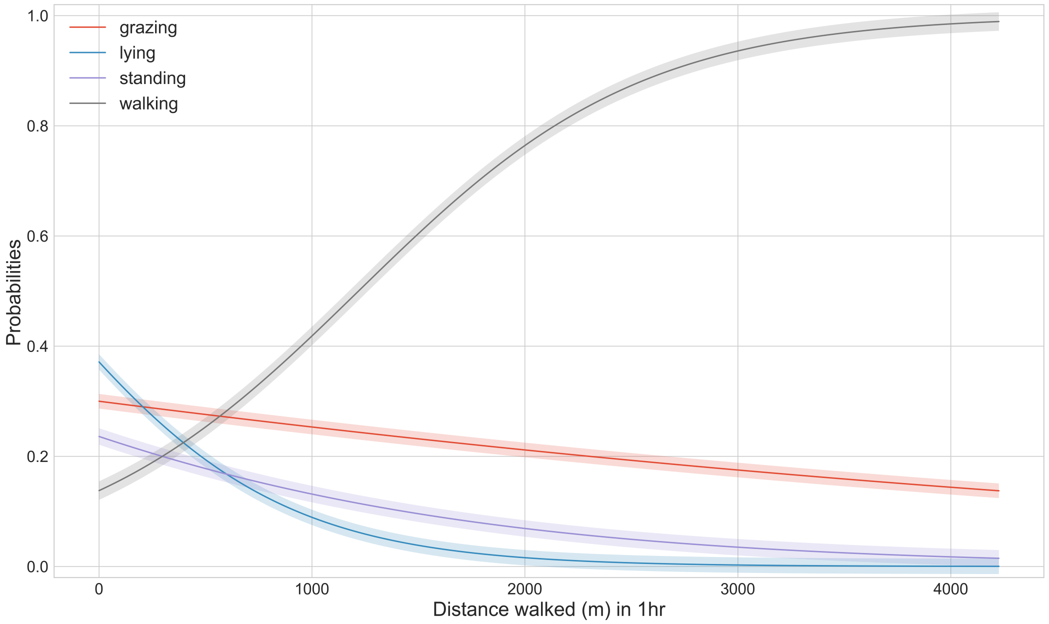

Figure 4.5: Predicted probabilities of grazing, lying, standing and walking in relation to the distance moved by a collared wildebeest within one hour in Serengeti ecosystem.

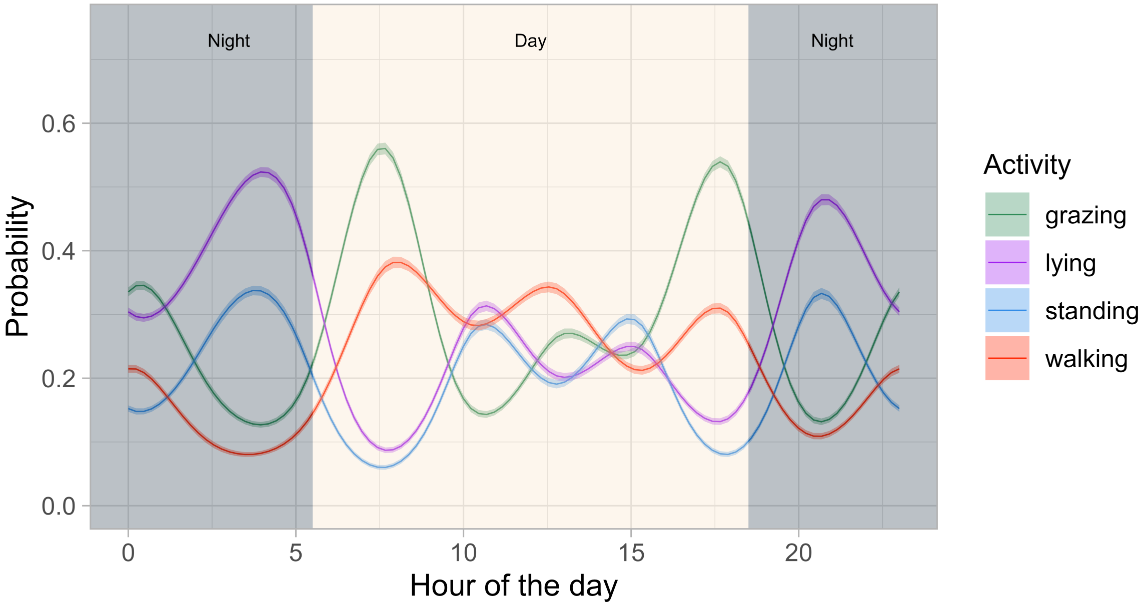

Figure 4.6: Probabilities of wildebeest activities namely: grazing, lying, standing and walking over 24hr time frame. The light brown background represents daylight time while the light grey background represents night time.

## 4.4 Discussion

This study demonstrates a method for developing a low-cost animal tracking system capable of near real-time behaviour classification using open-source electronics, an edge machine learning, and an IoT network. The model used is robust and consistently demonstrates the ability to reliably distinguish behaviour classes with a high degree of accuracy on validation data. Furthermore, field tests conducted on Serengeti wildebeest have confirmed that the LoRa collar can successfully record, preprocess IMU sensor data, predict behaviour classes, and transmit this information, along with auxiliary data such as positional and date-time data, to a server via a LoRa network. This data can then be easily accessed by end-users for download in near real-time. These key performance indicators illustrate the strengths of the LoRa collar as a tool suitable for remote tracking of animals as they navigate heterogeneous habitats and encounter varying levels of threats. Consequently, this tool holds significant value and will assist researchers in gaining new insights into how animals perceive their environment in relation to anthropogenic disturbance gradients.

Globally, human-driven landscape modifications continue to jeopardise the persistence of biodiversity (Dobson et al., 1997) in many ecosystems worldwide. These deleterious ecological changes result in direct mortality due to a lack of adequate behavioural flexibility or induce costly shifts in behaviour among affected species (D'Ammando and Bro-Jørgensen, 2023; Greenberg and Holekamp, 2017). To quantify fine-scale animal responses to ecosystem changes, technological innovations that broaden our knowledge of animal behaviour are required. The development of the LoRa collar system to collect scale-scale data in diverse habitats and spanning seasons and ensure rapid transmission holds the potential to usher in new possibilities for comprehending fine-scale animal responses to disturbances as well as applications in other research areas, as explored below.

In the context of animal fitness, survival, and performance, constant decision making and complex trade-offs of activities in relation to the immediate surroundings such as perceived predation are crucial. Here, LoRa collar tracking systems can be used to track and monitor activity budget patterns of migratory ungulates to gain insights into their perception of the environment. For example, in areas where an animal rests frequently, it may be perceived as "safe zones," whereas in areas where an animal moves quickly, it may be perceived as extremely risky or lacking in resources. As such, the LoRa collar tool is exceptionally well-suited for investigating the manifestation of fine-scale animal behaviours and responses in near real-time scenarios, owing to its remarkable ability to transmit data rapidly.

Understanding the behavior of species or wild populations in relation to daylight length, meteorological patterns, and seasonal variations such as winter versus summer activities in the context of a changing environment is crucial. The LoRa collar tool provides a valuable opportunity to investigate how rapid weather changes, including phenomena like snowfall, precipitation, temperature, humidity, among others, impact the activity time budget of rare or endangered species and the mapping of their critical habitats. Its exceptional ability for rapid data transmission is particularly advantageous for gaining long-term insights into the seasonal and meteorological influences.Broadly, the tool is relevant in studying and predicting how climate change will affect species in the future.

Elsewhere, encamped or exploratory states (Hopcraft et al., 2014; Michelot et al., 2016) based on directional persistence or step lengths (Klappstein et al., 2023) have been used to link animal behaviour and its movement trajectory. For instance, this approach has been used to describe movement patterns of Neotropical forest deer (Grotta-Neto and Duarte, 2019), crop consumption in elephants (Vogel et al., 2020) among other species. However, relying solely on hourly GPS fixes can lead to a generalized interpretation of the behaviour of a collared animal. Consequently, this approach has serious limitations in the sense that the coarse scale overlooks other crucial behaviours. For instance, instances where short step lengths are interpreted as resting may actually encompass various behaviours such as brief bursts of walking, grazing, vigilance, and standing. Therefore, to advance our understanding and obtain an integrated view of an animal's perception of its immediate environment and behaviour along its movement trajectory, the adoption of tools that collect scale-appropriate data such as LoRa collars and transmit data on the fly is imperative. This approach also solves the issues of data retrieval, the risk of losing data if the collar goes missing is minimal as well as uncertainty as to whether the device is working.

Hunting and other forms of animal persecution reduce restorative behaviours like grazing and resting (Ciuti et al., 2012; D'Ammando and Bro-Jørgensen, 2023). Similarly, ungulate proximity to tourism facilities may generate "shielding effect" due to eradication or deterrence of large predators, which may affect prey species ability to assess predation cues in core areas devoid of human presence (Berger, 2007; Berger et al., 2020). As such, some species tend to respond to threats in a way that corresponds to the degree, magnitude, and temporal scale of the threat (Chittka et al., 2009; Helfman, 1989). For instance, plains zebras are more vigilant when in dense bushes than open habits (Chen et al., 2021), while elephants cover more distance at night than during the day when in patches that have higher poaching levels (Ihwagi et al., 2018). In the context of behavioural plasticity monitoring, integrating positional and behavioural data over time and analysing it, researchers can establish baseline behaviours for different species and consequently generate a comprehensive view of ecosystem dynamics. For instance, if an animal's behaviour deviates from norm at a given time, in a given habitat and season can act as a real-time indicator of ecological disturbance or intrusion by poachers especially if an entire ecosystem has LoRa network coverage (de Knegt et al., 2021). As such, application of LoRa collars on animals can be used as an early warning monitoring tool circumventing challenges such as surveillance, benefiting wildlife conservation or testing theories in relation to the landscape of fear (Laundré et al., 2001).

This concept of spatial-temporal niche partitioning in relation to the Human Footprint Index is common in species that are sensitive to disturbances (Carter et al., 2015; Wevers et al., 2020), as well as in sympatric species that aim to minimise interspecific competition (Sogbohossou et al., 2018). Given that ongoing human-induced environmental changes exceed the evolutionary response rate of many species or populations, an in-depth understanding of their responses to such changes has become a topical question (Sih et al., 2011; Snell-Rood, 2013). In these circumstances, the LoRa collar can be a highly valuable tool for collecting data at a scale commensurate with the rate of occurrence of ecological disturbances, offering profound insights into how species adjust their nocturnal or diurnal activities as a coexistence mechanism, as well as overall behavioural plasticity in response to human-induced disturbances.

Here, it is critical to get real-time information rather than waiting until a collar is retrieved; hence, the LoRa network coverage needs to scale geographically. Rewilding or reintroducing wide-ranging species in areas where they have been exterminated is challenging due to limited information about their habitat requirements and movement ecology (Mertes et al., 2019; Parlato and Armstrong, 2013); hence, post-release monitoring is imperative to document their response to a new environment. For instance, GPS data with fix acquisition ranging between 1 to 12 hours have been used for post-release monitoring to investigate aspects such as exploratory movements, home range establishment, overlap, and interactions (Mertes et al., 2019; Sarmento et al., 2019). However, activity pattern monitoring is often missed due to limitations imposed by the use of GPS collars. Therefore, incorporating other auxiliary devices, as exemplified by the LoRa collar with rapid data transmission, is key to generating more detailed insights into animal responses to new environments and can serve as an early warning system, especially when animal behaviour deviates from the norm. For example, prolonged periods of lying or resting could signal the possibility of a sick or dead animal, prompting a timely response from park managers.

The LoRa collar real-time behaviour classification tool exhibits flexibility and versatility through the utilisation of programmable open-source electronics, among other features. This feature implies that the user has the option of changing the programme or incorporating additional modules to collect more data, as elaborated upon below. For example, the programme can be modified to sample more during diurnal, nocturnal, or crepuscular hours for species known to exhibit such behaviour. In terms of shape and size, the 3D housing cases can be modified to fit a range of species, particularly medium to large ones, as long as watertightness and robustness aspects to withstand shock are maintained. Furthermore, additional biologging sensors, including temperature and humidity sensors, can be integrated to enhance both the quality and quantity of collected data. Although the tool has the potential to open up new research avenues, there are a number of obstacles to fully utilising it. For example, using it to study animal species that spend a significant amount of time in low-light conditions may severely limit its deployment's longevity. Likewise, the transmission of voluminous raw sensor data where mandatory, necessitates increased power consumption, potentially compromising the longevity of LoRa collar deployments, which typically span from a few weeks to several months. As a result, users are faced with the need to balance between the amount of data collected and transmitted via the LoRa network. Additionally, setting up and maintaining a LoRa network in protected areas is logistically involving, and the associated budget may be out of reach for many organisations. To overcome some of these challenges, users may consider collaboration, especially in cases where a LoRa network is required. Future development of the tool could explore possibilities of harvesting green energy by using vibration energy harvesters that convert the kinetic energy of the collared animal into electrical energy (Zhang et al., 2021).

This study has successfully demonstrated the feasibility of a near real-time behavior classification tool applicable in the wild by combining open-source electronics, edge machine learning techniques, and an IoT network. The proposed LoRa collar tool has successfully collected behavioral data alongside auxiliary information from collared wildebeests in various locations within the ecosystem and transmitted it to the server. Future work could consider using training data gathered from wild populations, which are subject to natural environmental pressures and interactions with predators. This approach could lead to more precise behaviour classification compared to data collected from captive populations, which reside in facilities devoid of predators. For example, accuracy in walking and standing behaviours is likely to improve, making them more distinguishable, whereas, due to similarities between vigilance and lying distinguishing them may present a challenge for wild populations (typically the head is slightly raised in both cases). Additionally, running behaviour, which we were unable to collect data on in captive populations, is biologically important and should be considered in future research. In the face of rapid human-driven changes that outpace evolutionary response rates, the quick process of transmitting data to end users after acquisition is crucial. This approach, which enhances our integrated understanding of animals and their environments at a fine scale, has the potential to significantly improve conservation strategies, particularly in cases requiring adaptive management policies. Additionally, it will enable researchers to overcome restrictions imposed by accessibility issues and observer influence, as well as eliminate the need to recapture animals for data downloading. The use of open-source components also paves the way for other innovators to enhance the design or customize it to address specific needs. As such, this approach underscores the potential for fine-scale, long-term species monitoring, leading to unprecedented insights into animal behavior and responses to short- and long-term ecological disturbances.

# Chapter 5

## General discussion

## 5.1 Achievements, challenges, and trade-offs

The thesis focused on ungulate movement in the Anthropocene taking an interdisciplinary approach that encompasses ecology, mathematics, computer science, and engineering. The study focused on remote animal tracking, starting with an evaluation of the existing tools, their limitations, and possible alternatives with the application of machine learning and open-source electronics. The existing animal tracking tools, primarily off-the-shelf devices, are relatively costly and offer limited flexibility, often resulting in additional costs. Processing voluminous data, such as camera trap data, is sometimes done manually, hence, time-consuming. Transmission and storage of data present additional challenges. Furthermore, extracting relevant information for analysis from data collected by current tracking tools, such as images and footage, often requires sophisticated models. In this study, I demonstrate novel approaches to developing bespoke animal tracking tools that will drive forward the boundaries of ecological understanding into new frontiers: for instance, how to combine two data streams, such as positional and observational data, to understand the role of social interaction in collectively navigating species. Additionally, I demonstrate approaches for fine-scale monitoring of animals in the wild, whilst addressing issues of data transmission, storage, and processing using machine learning models. Overall, this has been made possible by the availability of open-source electronics that scientists can use to develop low-cost bespoke tracking tools that can be customised to answer specific questions.

The study involved a critical evaluation of animal tracking tools, providing an opportunity to gain an in-depth understanding of their strengths and limitations. For example, camera traps are valuable tools for data collection relevant to species occupancy/presence analysis as well as monitoring cryptic mammals. When set up in an array, camera traps can cover vast areas beyond what can be achieved by direct observation. This makes them logistically sound and suitable for long-term monitoring. Customisation features, such as the ability to change the trigger rate, are crucial, as they allow researchers to address specific questions. The data collected in the form of still images or videos is voluminous, which implies that manual annotations are Laborious and time-consuming. However, using techniques such as deep learning to automate the processing of still images or videos makes the use of camera traps for short and long-term monitoring appealing because it is faster and feasible even with large data sets.

Unmanned aerial vehicles (drones) are ideal for tracking focal animals and collecting information about their nearest neighbours, which is relevant in collective behaviour studies. Similar to camera traps, the recorded footage is often extensive, depending on the study's objectives. However, the raw data are challenging to analyse and requires preprocessing. To extract pertinent information, artificial algorithms, such as computer vision which is capable of interpreting visual information, are necessary for tracking individuals frame by frame and subsequently reconstructing their movement trajectories. Additionally, data extracted from the footage are complex and do not conform to assumptions of parametric tests such as, homoscedasticity, normality, among others. Therefore, given the characteristics of the data any analysis requires a hypothesis-free approach, making machine learning appropriate (Valletta et al., 2017).

In instances where the application of off-the-shelf devices is unable to meet the requirements of a given study, bespoke tools could provide a solution. From a pilot's perspective, manual tracking of a focal animal using a drone, especially when they move collectively in large numbers, can be challenging. For instance, controlling a drone while keeping pace with the abrupt changes in direction of the focal animal is difficult and can introduce noise in the data. Low-cost and open-source electronics play a central role in the development of custom-built tracking tools and the automation of such operations. Therefore, the use of open-source electronics to develop bespoke tools offers advantages over commercial devices since they can be customized to meet the specific needs of a study. This is exemplified by their application in automating animal tracking in Chapter 3 of the thesis.

In this study certain aspects proved successful, while others presented challenges. For instance, some of the camera traps were tampered with or damaged by individuals who suspected covert surveillance within the protected park. Differentiating between species, such as cows and wild animals, presented a challenge due to the variety of coat colours and the limited detection of cows. Consequently, we focused exclusively on migratory species. Additionally, the field of view posed another challenge, with the detection model struggling to accurately identify species at a far distance.

Issuance of a permit to import and use drone in the Serengeti National Park took a long process. The legal frame governing use of UAVs vary from country to country which might hinder progress as well as come at a cost. For example, in some jurisdictions, drone pilots are required to be accompanied by a supervisory team from the Ministry of Defence. This requirement not only leads to significant expenditures but may also pose challenges if these costs were not budgeted. Additionally, on-site filming operations might be susceptible to unforeseen disturbances and threats to equipment, such as drones being targeted by raptors. While co-pilots, observers, and operational manuals play a crucial role in such situations, temporary halts in operations are frequent, disrupting what is expected to be a smooth flow of activities necessitating extra field day.

Developing bespoke tools is a challenging task, contingent upon the specific goals of the study. Bespoke tools intended for deployment in the wild must undergo thorough testing to ensure they will serve their intended purposes. However, testing, especially when one is located away from the actual field site, involves simulating the target species' behaviour. While this approach might be more budget-friendly, tests using simulated animal manoeuvres may not yield conclusive results. For instance, when developing a release mechanism for animal-borne collars, there is a risk of underestimating the target species' aggressiveness, which can lead to premature activation of the collar's drop-off feature. The robustness of the 3D casing is a significant consideration that must be preceded by the creation of prototypes. Therefore, before final production of the 3D housing casing, rigorous testing to ensure water-tightness and shock resistance is essential. However, the lack of 3D modeling printers for early prototypes poses a risk of compromising the quality standards that guarantee the safe use of the device in the wild.

Despite the enormous potential of bespoke tracking tools to open new avenues of ecological research, the trade-off between using custom-built gadgets and off-the-shelf devices involves several factors. To begin with, custom-built tools allow for greater customization to meet specific requirements or preferences, unlike commercial ones. An example of this is the integration of various components such as accelerometers, gyroscopes, and magnetometers, alongside other sensors like temperature and humidity sensors. For many companies, manufacturing such integrated components may seem unappealing due to market uncertainties and the absence of a known customer base, making such investments financially infeasible. However, if scientists explore the possibility of developing bespoke tools tailored to specific needs, there is a greater likelihood of generating valuable insights and advancements in understanding complex biological phenomena. Cost-wise, bespoke tools are relatively cheaper than pre-built devices; however, they require some level of technical expertise to program and assemble different components. Off-the-shelf devices often come with support and warranty, unlike custom-built tools. However, developers can utilize guidelines available from various companies involved in the production of open-source electronics, as well as fostering collaborations across disciplines, which is a viable way to address the expertise issue and is highly encouraged. Lastly, bespoke tools require time and effort, especially when technical challenges arise, necessitating iteration of design, unlike off-the-shelf devices that offer convenience and immediate availability. However, sharing codes, 3D designs, printed circuit board layout designs, information on sourcing parts, commenting on all codes, and making them available in repository platforms like GitHub, could facilitate faster modification or replication of designs. This approach will reduce time and effort required to develop bespoke tools and encourage wide use by non-specialists, thereby fostering the adoption of the technology. As such, prior planning when working with open-source electronics is necessary to allow for prototype development, testing, and eventual production of the final product especially where the commercial options are unavailable.

## 5.2 Transferability, flexibility and directions for future

The remote tracking tools developed in this study have a broad range of potential applications and can be used effectively in various settings to study animal movement and behaviour. The core concept is robust, but users will need to make minor adjustments to tailor it to their specific needs. This is due to the inherent flexibility of the tools. For instance, when developing a near-real-time classifier for other species, the machine learning model has to be retrained with behavioural data from the target species. This is a vital consideration because species vary in morphology and behaviour. Where drone operations are necessary, visible light cameras can be replaced with thermal sensors for tracking animals that inhabit low-light habitats. For instance, when tracking arboreal species that move, feed and find shelter in forest canopies. 3D housing cases can be modified to fit species of different body size. Additionally, the use of open-source programmable electronics provides an opportunity to alter firmware to address study-specific objectives or enhance innovation.

Future modifications of the tracking tools could involve the incorporation of additional sensors, such as temperature sensors, humidity sensors, and heart rate sensors, which will enhance the quality of data and broaden our understanding of species and their environments. The longevity of animal-borne collar deployment depends on the availability of sufficient power to run the device. Therefore, exploring various methods of recharging batteries while still attached on the animal is essential. For instance, incorporating solar panels, which have proved successful, should be considered going forward. Similarly, kinetic energy harvesters are also a viable solution that should be integrated.

## 5.3 Conclusions

In this thesis, I have explored the application of machine learning and open-source electronics to gain a deeper understanding of ungulate movement in the Anthropocene. Firstly, I highlight the significance of existing animal tracking tools and their contribution to our comprehension of animal spatial ecology on a course scale. However, in the context of rapid occurrence of ecological disturbances that threaten biodiversity, there is a compelling need for a paradigm shift in our data collection methods. Any data-driven solutions will necessitate fine-scale data that aligns with the pace of ecological disturbances although such tools are lacking. I have further demonstrated the application of novel tools capable of collecting multi-dimensional data that can be processed using machine learning algorithms. The proof-of-concept results showcase the effectiveness of custom-built tracking tools developed using low-cost open-source technology and their suitability for application in the wild. The application of such tools holds significant potential, enabling researchers to focus on more nuanced ecological research at unprecedented levels. These tools also offer an alternative approach to commercial devices, allowing for greater end-user customisation and the potential to catalyse further innovation in the application of novel tools, thereby enriching our understanding of animal ecology.

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# Chapter 6

# Appendix

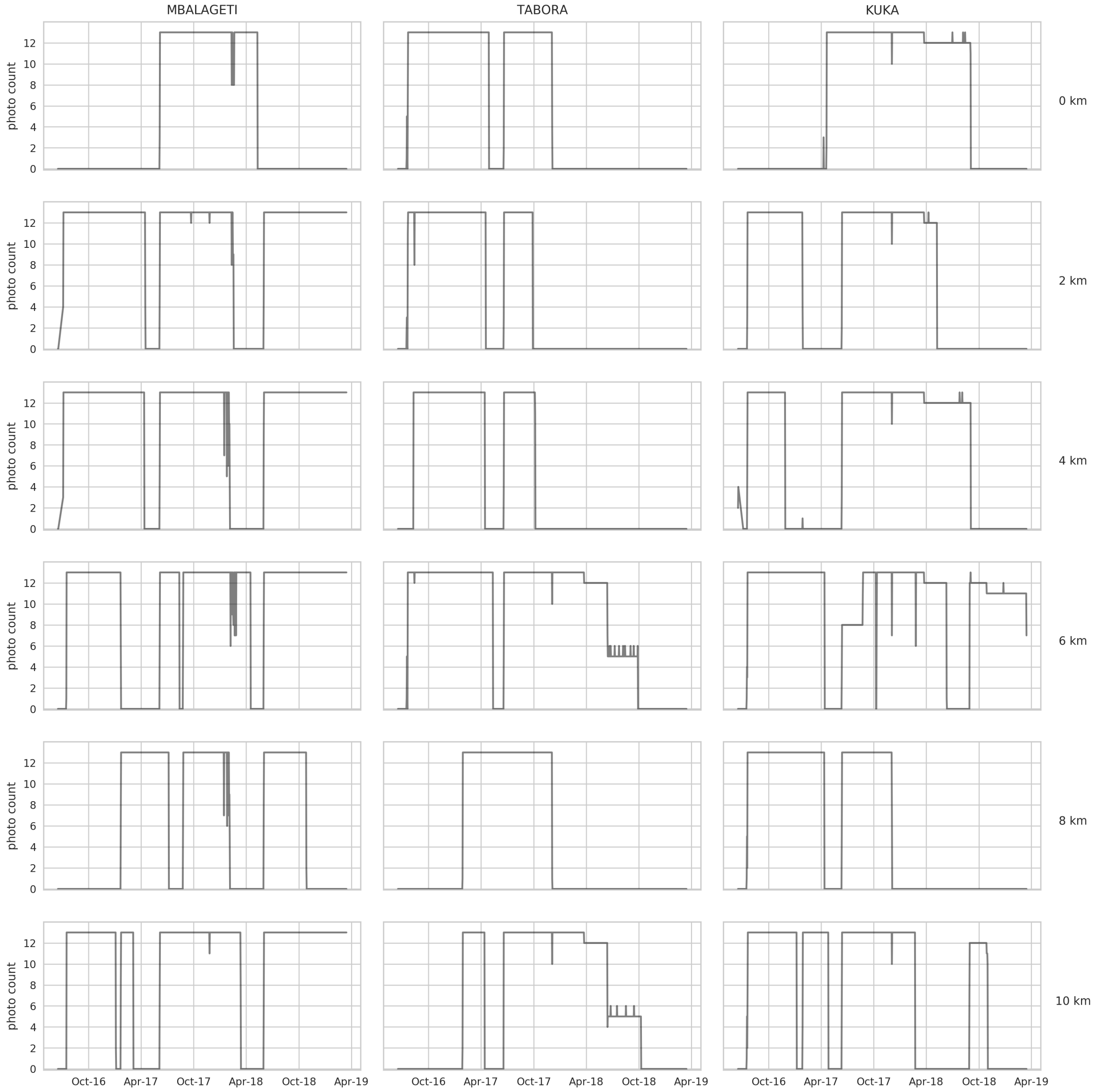

Figure S1: Time series graphical representation of daily image captures across all the camera traps along the three transects between June 2016 and March 2019

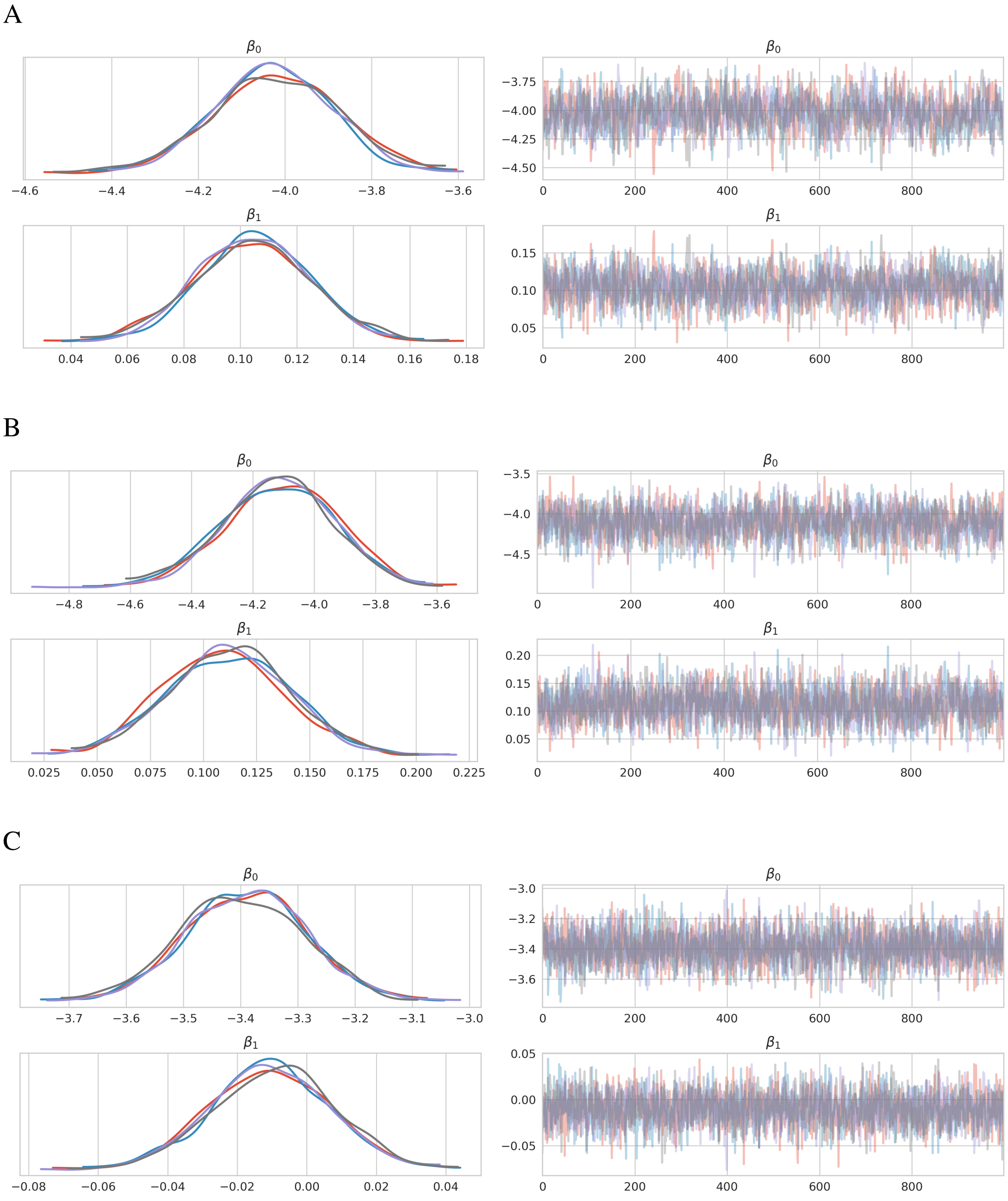

Figure S2: Samples from 4 independent MCMC chains fit to (A) Mbalageti transect, (B) Tabora transect, (C) Kuka transect. Left: Kernel density estimation intercept ($\beta_0$) and slope ($\beta_1$) of GLM. Right: Trace plots for 4 chains. Convergence and mixing was assessed by calculating $\widehat{R}$ statistics (Mbalageti: $\beta_0 = 1.003$, $\beta_1 = 1.001$; Tabora: $\beta_0 = 1.001$, $\beta_1 = 1.001$; Kuka: $\beta_0 = 1.001$, $\beta_1 = 1.001$) and effective sample sizes (Mbalageti: $\beta_0 = 969$, $\beta_1 = 1173$; Tabora: $\beta_0 = 1659$, $\beta_1 = 2019$; Kuka: $\beta_0 = 2554$, $\beta_1 = 2907$)

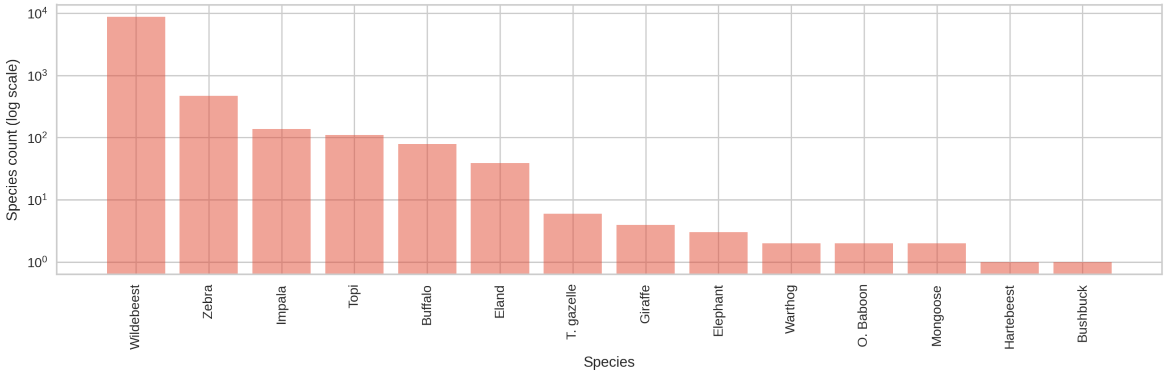

Figure S3: Total count of species captured by the camera traps for a period between June 2016 through March 2019

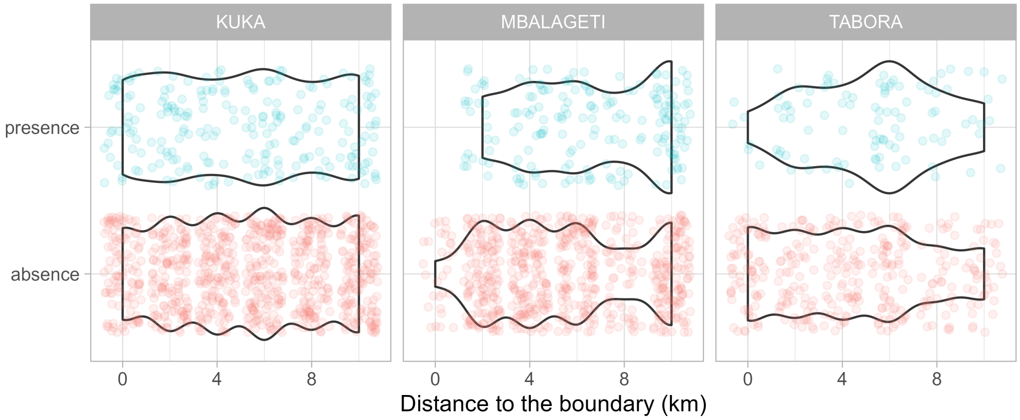

Figure S4: Shows the presence or absence of migratory species along the 10km long transects at 2km interval for each of the three transects namely: Kuka, Mbalageti and Tabora

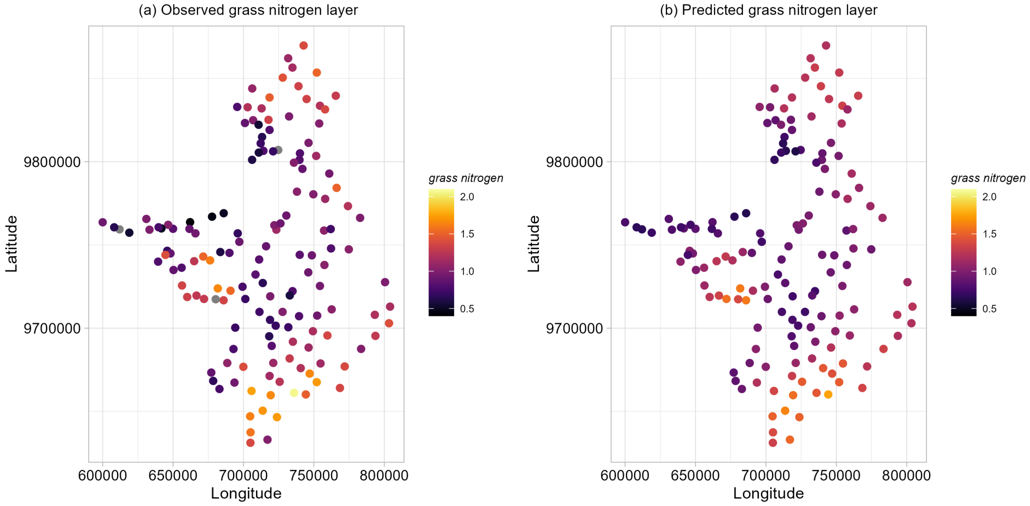

Figure S5: Grass nitrogen layers showing (a) observed grass nitrogen layer and (b) predicted grass nitrogen layer for the 148 sampling sites

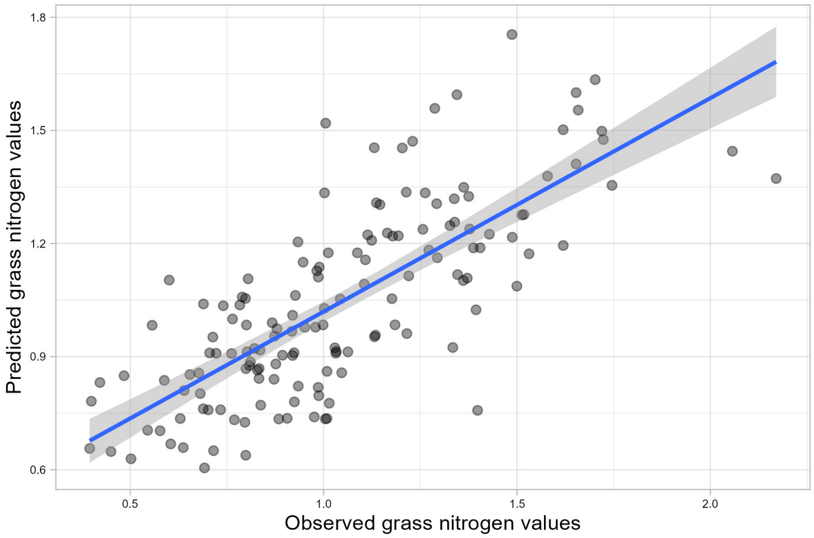

Figure S6: Regression krige plot to evaluate the accuracy of the kriged grass nitrogen layer across the 148 sampling sites

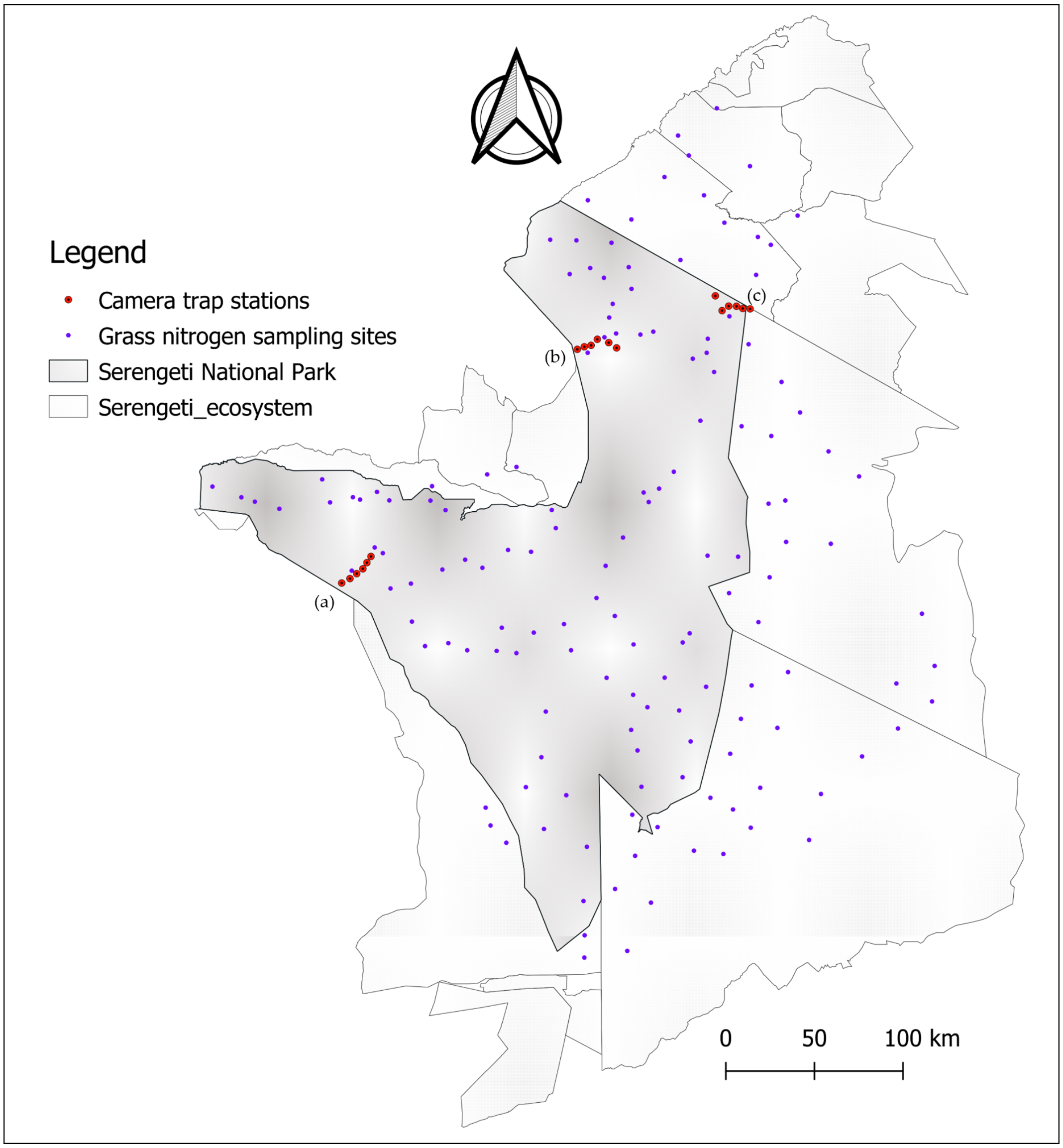

Figure S7: Shows the transects (a) Mbalageti, (b)Tabora (c) Kuka and the 148 vegetation plots where grass were collected to measure grass nitrogen content across the entire Serengeti Mara Ecosystem

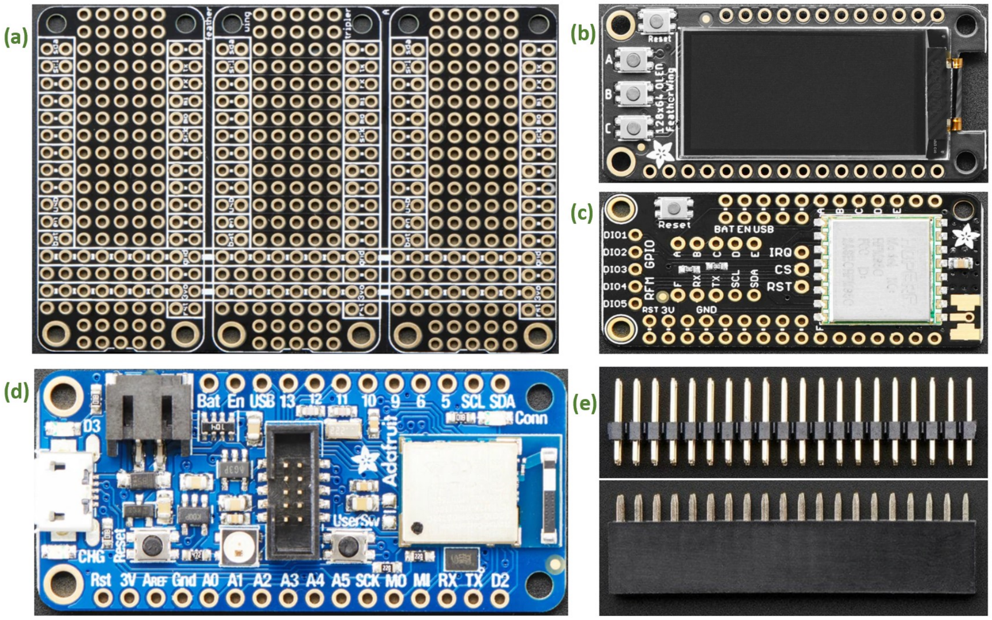

Figure S8: Several printed circuit boards (PCB) components used to assemble a hand- held base station (a) Featherwing tripler mini kit (b) Adafruit Featherwing 128x64 monochrome OLED, (c) Adafruit LoRa Radio featherwing (d) Adafruit feather nRF52840 express and (e) Male and female feather stacking header. Photos by Cyrus Kavwele.

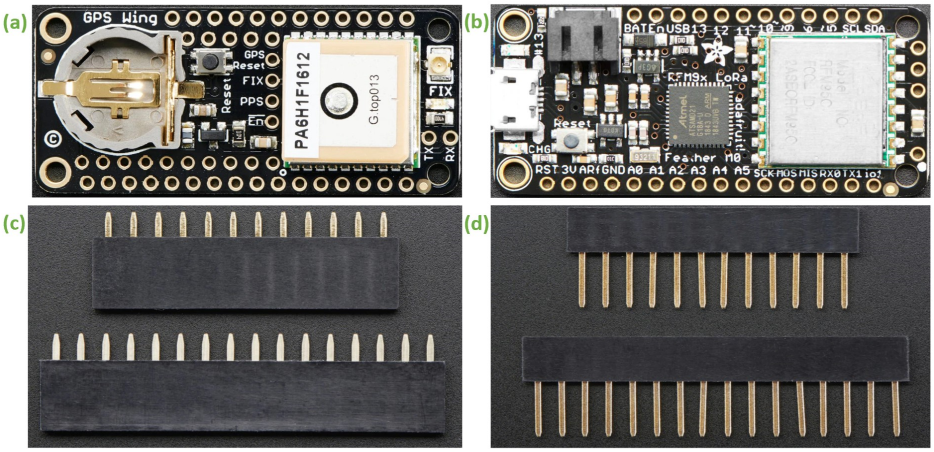

Figure S9: Several PCB components used to assemble a GPS collar; (a) Adafruit Ultimate GPS featherwing, (b) Adafruit Feather M0 with RFM95 Long Range (LoRa) Radio, (c) Male feather stacking header and (d) Female feather stacking header. Photos by Cyrus Kavwele.

Table 6.1: Key features of the PCBs, cost per unit and quantity required to assemble base station.

| **Item** | **Features** | **Cost per unit(£)** | **Quantity** |
|---|---|---|---|
| Featherwing tripler | Assembled dimensions 2.8"x2"x0.46"<br>Assembled weight 18.2g | 7.40 | 1 |
| Adafruit featherwing OLED | PCB dimensions 0.9"x2"<br>Display area 1.0" | 13 | 1 |
| Adafruit LoRa Radio featherwing | Dimensions 2.0"x0.9"x0.1"<br>weight 4.6g | 17.40 | 1 |
| Adafruit feather nRF52840 express | Dimensions 2"x0.9"x0.28"<br>Bluetooth low energy compatible 2.4GHZ<br>Up to +dBm output power<br>Weight 6g | 21.70 | 1 |
| Female stacking header | 12 and 16 pins | 1.10 | 3 |
| Male stacking header | 12 and 16 pins | 0.80 | 3 |
| Dipole swivel whip antenna | 2.4-2.5GHz receiver/transmitter<br>length 8" | 7.80 | 1 |
| Edge-launch SMA connector | Impedance 50ohm<br>Length 1.6" and diameter 0.24"<br>Weight 2g | 2.20 | 1 |

Table 6.2: Key features of the PCBs, cost per unit and quantity required to assemble one GPS collar.

| Item | Features | Cost per unit(£) | Quantity |
|---|---|---|---|
| Adafruit Ultimate GPS featherwing | Satellites: 22 tracking,66 searching<br>Position accuracy <3m<br>Velocity accuracy 0.1m/s<br>Warm/cold start 34 seconds<br>Maximum velocity 515m/s<br>Jammer detection and reduction<br>Weight 8.8g (excluding coin cell)<br>Dimensions 0.90"x2.02"x0.26" | 21.70 | 1 |
| Adafruit feather M0 RFM95 LoRa Radio | ATSAMS21G18 with 3.3V<br>USB native support<br>8xPWM pins, 10x analog inputs, 1x analog output<br>Reset button, power/enable pin | 30.40 | 1 |
| Female stacking header | 12 and 16 pins | 1.10 | 1 |
| Male stacking header | 12 and 16 pins | 0.80 | 1 |
| Dipole swivel whip antenna | 2.4-2.5GHz receiver/transmitter | 7.80 | 1 |
|  | uFL to RP-SMA antenna adapter cable | 3.40 | 1 |
|  | Lithiumion Polymer Battery<br>Output: 2500mAh at 3.7v<br>2-pin jST-PH connector<br>Dimesions 1.3"x1.4"x0.3", weight 5.7g | 12.00 | 1 |

Table 6.3: Key features of the DJI Mavic 2 Pro drone used

| **Item** | **Features** |
|---|---|
| Performance | Sport mode 65 km/h (no wind)<br>Flight time; up to 27 minutes (no wind at a consistent 15.5 mph / 25 km/h)<br>Hover time Up to 24 minutes (no wind)<br>Flight distance 13km (no wind) |
| Flight control system | GPS Mode (*GPS and GLONASS*) |
| Radio controller | Frequency 2.4 to 2.483 GHz<br>Communication distance 7 km (line-of-sight)<br>Transmit power Up to 26 dBm<br>Battery lithium-ion polymer (LiPo) capacity: 2970 mAh |
|  | Photo resolution up to 4000 x 3000 (12 MP)<br>Video resolution UHD 4K (3840 x 2160): 24/25/30p |
| Gimbal | Number of axes 3-axis (pitch, roll, yaw)<br>Control Range Pitch: $-90^0$ to $+30^0$ |
| General | Operating temperature 32 to 104 F / 0 to 40 C<br>Weight 743 g (including gimbal cover) |