ADVANCING REMOTE SENSING METHODS TO MONITOR WILDLIFE

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Declaration

I declare that this thesis was composed by myself and that the work contained herein is my own except where explicitly stated in the text. The work has not been submitted for any degree or professional qualification except as specified.

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"Vladimir: That passed the time"

"Estragon: It would have passed in any case"

"Vladimir: Yes, but not so rapidly"

Samuel Beckett

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Abstract

Historically, natural history museums have collected and preserved specimens to provide data on the occurrence and distribution of wildlife populations. Zoologists still track animals by recording footprints, collecting dung and spoor and observing, recording and quantifying behaviour from the ground. However, these traditional observational techniques allow only a few populations to be monitored at once at limited spatial scales and disturbance from the ground can disrupt observation of natural behaviour. We are now in a golden age of technological advances and are able to remotely monitor and track wildlife via a variety of electronic sensors. Significant questions remain about how best to methodologically apply these new technologies for the purposes of wildlife monitoring. In this thesis, I consider challenges of using Earth observation satellites and unmanned aerial vehicles (UAVs) to track wildlife and understand movement in relation to the expanding human footprint and anthropogenic risk. Specifically: (i) I collate and analyse spatially explicit data on the distribution of illegal hunting incidences via a systematic map. I show that hunting increases in proximity to roads, water bodies, and human settlement areas and there is a considerable lack of systematically collected quantitative data. (ii) I investigate acoustic disturbance to understand anthrophony from the species perspective. I create a mitigation method applied in the case of UAV noise using species weighted audiograms (iii) I test whether very high-resolution satellite imagery and machine learning can be used to automate the detection of African elephants in vast heterogeneous landscapes. This is achieved presenting a new method to monitor elephants (iv) I record the spatial relationship of African elephants in relation to the human footprint using GPS tracking data and satellite imagery. I show elephants readily adapt their foraging habits and itineraries, spatially and temporally in relation to human settlement. Accurate and up-to-date data is vital for effective wildlife conservation planning. Remote sensing technologies offer enhanced capabilities to understand the spatial relationship between wildlife and the increasing human footprint. As a whole, this body of work contributes to the global wildlife conservation effort by devising methods that can enable more reliable data collection at larger spatial scales.

Abbreviations

AGL	Above ground level
AI	Artificial Intelligence
AWL	Above water level
CNN	Convolutional Neural Network
CNP	Carbon, Nitrogen, Phosphorous
dB	Decibels
ESA	European Space Agency
GPS	Global Positioning System
IUCN	International Union for Conservation of Nature
NASA	North American Space Agency
SMART	Spatial Monitoring and Reporting Tool
UAV	Unmanned Aerial Vehicle

PART I: INTRODUCTION

WILDLIFE MONITORING

The broader context in which this research is situated is outlined before detailing the specific technologies and applications of interest. The Earth is experiencing a sixth mass extinction event comparable in magnitude to previous geologically recorded mass extinctions [1-3]. Globally, extinction rates during the past five centuries have increased up to one thousand times the historical extinction rate, as shown by the fossil record [4]. Between 1970 and 2016 an average 68% decrease in the population of wild vertebrates was recorded [5] and it is predicated that the rate of extinction is likely to grow by another order of magnitude in the near future [6]. The eminence of human life is driving this extinction - ‘Anthropocene’ is proposed for the current geological period in which human activity is the major determinant of evolution on Earth [7]. Estimates of 50 to 70% of the Earth’s land surface is modified by human activity, much of it for the husbandry of domesticated livestock [8, 9]. Availability of natural resources and space is reduced and natural habitats are polluted [10] which has led to increased interspecific competition and conflict between humans and wildlife [11, 12]. Illegal wildlife hunting is at unsustainable levels comprising the fourth largest global illicit market [13] and large numbers of animals are killed accidentally via human activities e.g., by-catch, road-kill [14-16].

To address the sixth mass extinction several multilateral treaties have been ratified. These outline broad-based action plans to stabilise biodiversity loss and recover natural ecosystems i.e., Convention on Biological Diversity (CBD) and the United Nations Sustainable Development Goals. To track these agreements and provide a point of reference on progress a set of metrics are used [17]. These metrics provide a means to monitor longitudinal trends and fluctuations in wildlife abundance (Living Planet Index [5]), extinction risk (IUCN Red List Index [18]), composition (The Mean Species Abundance Index and Biodiversity Intactness Index [19]) and distribution (Species Habitat Index [20]). However, definitions of biodiversity loss change over time, which complicates longitudinal monitoring. For example, the Food and Agriculture Organisation of the United Nations changed the definition of forest from 10% of canopy cover in 1990 to include a minimum height of 5m in 2005 complicating the tracking of deforestation [21].

Reliable information on species numbers and movement relies on effective wildlife monitoring. This can be challenging to collect in difficult to reach locations. Improving monitoring will bolster conservation efforts. Stable definitions and metrics are needed to understand longitudinal trends and effectively track loss and recovery. There is currently no single metric to track illegal hunting incidences [22] or to monitor spatial patterns in hunting incidences, beyond the site level. One of the other biggest threats to wildlife is the expanding human population and associated competition from livestock, which is difficult to assess at the required temporal and spatial scale to make data meaningful. The development of remote sensing technologies offers enhanced capabilities to track wildlife and habitat use and to monitor the increasing human footprint. This is the focus of this thesis.

REMOTE SENSING

We are now in a golden age of technological advance to remotely monitor and track wildlife electronically via a variety of sensors [23-26]. Historically, natural history museums have collected and preserved specimens that provide data on the occurrence and distribution of wildlife populations. The Smithsonian Institution, (USA) houses the world's largest physical collection; with just under 600,000 georeferenced records of wild mammals spanning 180 years. However, these are no longer regularly updated. Zoologists still track animals by recording footprints, collecting dung and spoor and observing, recording and quantifying behaviour from the ground [27, 28]. These traditional observational techniques are limited by human tracking competency allowing only a few populations to be monitored at once. Increased accessibility and decreased cost of hardware and software is expanding what was previously possible [24, 29]. Contemporary tools include GPS tags, unmanned aerial vehicles (UAVs) and earth-observation satellites. Development of these monitoring devices has largely been the domain of the military enterprise with the goal to monitor human beings. The advantage these technologies offer, over traditional wildlife observation methods, is that they allow large datasets to be collected in short periods and over vast areas. They minimise disturbance as human presence is reduced, in the case of UAVs, or removed entirely, in the case of satellites and GPS tracking. Additionally, provoked movement is avoided so wildlife can be observed in a natural state. Storing and reviewing raw data is possible as an electronic record (image, video, GPS fix) is automatically recorded. This means multiple observers can review data, minimising error and increasing objectivity and reliability of observations [30]. It is important that research into methods of application keep pace with technological development. The technologies focused on in this study include unmanned aerial vehicles, very high-resolution satellites and GPS tracking. Below how each technology is used in wildlife monitoring applications is briefly outlined.

UNMANNED AERIAL VEHICLES

Zoologists have long used aerial platforms to obtain imagery of wildlife including from manned aircraft, kites, and balloons [31]. Unmanned aerial vehicles (UAVs), commonly referred to as drones, are a recent addition to the zoologists' toolbox. Originally developed for military applications [32] UAVs can also be used for a range of applications. Recent examples include applications for gathering biological samples (e.g., blow samples from whales) [33-35], monitoring morphometric attributes [36], collecting behavioural data [37, 38] conducting census surveys [39-41], mapping wildlife habitat use and distribution [42-45], tracking radio-tagged animals [46], assessing body mass and condition [47, 48] or for analysing gait kinematics (i.e., recording running giraffes) [49].

UAVs offer several advantages over traditional methods – models that are small, lightweight and agile can provide access to hard-to-reach locations that are impractical or unsafe to visit on foot (e.g., volcanoes, rocky cliffs and remote aquatic environments). UAVs can provide a privileged aerial view of fine-scale movement, undetectable from the ground. UAVs can also complement satellite monitoring to provide in-situ ground truthing of detections [50]. As manned aircraft crashes are one of the leading causes of death amongst wildlife biologists, the increased use of UAVs reduces risk of mortality [51]. UAVs enable faster and more accurate monitoring compared to human observers [52, 53]. Bias introduced by the fallibility of human observers i.e., low visual acuity, attention and concentration [54] are mitigated. Improvement in image post-processing software further increase speed and accuracy. For example, "off-the shelf" machine learning applications for non-specialists enable automatic object detection in resulting imagery [55-57].

Aerial counts of animals from manned aircraft have been carried out in Africa since the mid-1950s [58]. However, over the last decade UAVs have become competitive in terms of both cost and coverage. Most wildlife applications can use consumer-grade drones (commonly used for photography and filming). However, custom-builds or adaption of existing models (e.g., addition of suction cups or radio receivers) is often made for specific data collection requirements [35, 59, 60]. For census work or habitat mapping, long-range fixed wing UAVs are preferred, because they cover more ground in less time and have longer flight time. For most other applications, multi-rotor UAVs (commonly quadcopters) are suitable and unlike fixed-wing models, multi-copters can make observations from a fixed aerial position. As camera resolution and battery life improves, enabling longer flight times they will likely replace the use of manned aircraft for zoological research.

Whilst the applications of UAVs are vast and continue to grow, they also constitute a new source of acoustic disturbance in natural environments. The operation of UAVs is banned or highly restricted in many countries and protected areas due to concerns over disturbance [61, 62] . This anthrophony (man-made sound) obscures auditory communication, which can displace time and energy from primary survival functions (e.g., feeding, mating and breeding). The research presented in Chapter 2 of this thesis addresses the issue of acoustic disturbance with the intention to support extended use of this monitoring tool for Zoological research and conservation.

VERY HIGH-RESOLUTION SATELLITE IMAGERY

Advances in the spatial resolution and accessibility of space-borne sensors parallel that of UAVs which have been used, over the last four decades, to monitor wildlife in a number of ways [31, 63]. There are multiple benefits to remotely detecting animals using satellite imagery. Large areas are captured in just one pass (milliseconds), so double counting and miscounts are largely avoided. As the revisit time of a satellite is only 24 hours, repeat surveys and reassessments are possible at short intervals. Thus, an accurate picture of animal movement can be built even if some records are absent or impaired due to bad weather or concealing vegetation. As many animals migrate freely across international borders, this approach is particularly applicable for wildlife in frontier areas without requiring multiple permissions from national civil aviation authorities. Satellite monitoring is non-invasive requiring no human presence, eliminating the risk of disturbing wildlife and concern for human safety. Disadvantages include the cost for high-resolution imagery that is outside the budget of many conservation agencies, compute capacity needed to process the imagery and the technical expertise required to perform analysis.

Two of the data chapters of this thesis (Chapter 3 & 4) use very high-resolution satellites (Worldview 2, 3 & 4) to monitor wildlife and movement in relation to the human footprint. These satellites belong to Maxar Technologies who were the first providers of <1 metre resolution imagery (since IKONOS launched in 2000) and continue to provide the world's highest resolution optical satellite imagery (Worldview-3) at 31cm resolution. High-resolution imagery is only available from commercial satellite providers and is costly to acquire. The higher spatial resolution comes at the cost of temporal resolution as these commercial operators have narrower coverage of the earth surface compared to freely available imagery from state-run space programmes (e.g., the Landsat series from NASA available since 1975 and the European Space Agency available since 1990). This free long-term medium-resolution imagery is at >5metre resolution. This imagery cannot monitor species directly but presence can be identified via land cover change. For example, changes in vegetation have been used to infer presence of African elephants (*L. Africana)* [64, 65] or mound and burrow identification to infer presence of marmots (*Marmota flaviventris*) [66] and wombats (*Lasiorhinus latifrons)* [67]. To date there is only one study that used satellite imagery for a global species census, in the case of emperor penguins (*Aptenodytes forsteri*) [68]. This study discovered four new colonies and confirmed presence of three more, demonstrating the capability of satellite imaging as a global wildlife census technique. One recent advance in earth observation satellites comes from the advent of nanosats (<10kg) and low earth orbit (U-class) spacecraft - CubeSats, developed in 1999. This advance has increased the number of earth-observation spacecraft in orbit [69]. However, these systems do not yet provide the spatial image resolution (<1m) of larger satellite systems and have not been used for satellite monitoring. Nanosats are cheaper and easier to build and launch. Advances in the temporal and spatial resolution of these systems and future provision by state-run programmes (e.g., NASA & ESA) will likely enable freely available imagery to be used for individual wildlife detection.

Detecting animals from satellite imagery is impacted by body size, background complexity and contrast between body and surrounding habitat. Groups of animals are more visible than individuals and have been detected successfully in the case of flocks of flamingos (*Phoenicopterus roseus* and *Phoniconias minoir*) [70], herds of Weddell seals (*Leptonychotes weddellii*) [71], muskoxen (*Ovibos moschatus*) [72] and waddles of penguins (*Aptenodytes forsteri* and *Pygoscelis adeliae)* [73, 74]. Monitoring solitary species requires very-high spatial resolution imagery. This has only been achieved for polar bears (*Ursus maritimus*) [75] using the shadow of the bear against the ice and for the world's largest marine mammal – baleen whales [76-78].

Manual identification of wildlife in large satellite images is highly time and labour intensive and counts tend to be error-prone [79]. Automating detection using a deep learning algorithm means a process that would have formally taken months can be completed in a matter of hours. While observer errors in human-labelled data are inconsistent, false negatives and false positives in deep learning algorithms have consistent characteristics and can be rectified by systematically improving models. Automating detection helps process data faster, more accurately and increases analytical insight [80-82]. Machine learning has successfully been used to automate the detection of wildlife from imagery from manned aircraft imagery [83-85] camera trap survey data [86-88] and UAVs [56, 57, 89]. Automated detection of species in satellite imagery has only been tried in the case of pack-ice seals, baleen whales and albatross [78, 83, 90] and African elephants in this study (Chapter 3).

GPS SATELLITE TRACKING

Given the increasing extent of human presence worldwide there is great interest in understanding and predicting how wildlife populations are affected by human activities. Species need to move to survive, different movement strategies are adopted depending on availability of forage and water, mating opportunities, water, predation risk, and competition for resources [91, 92]. Movement is critical to enable species to fulfil critical ecological functions that affect human activities (e.g., seed dispersal, pollination, etc.). Changes in movement have cascading impacts on ecological communities and functional ecological dynamics. This is the case for elephants, who are key ecological engineers in the landscape redistributing organic matter and nutrients through forage dynamics and dung deposition [93-96].

The increasing human footprint has a demonstrable impact on animal movement largely constituting a contraction in space use [97, 98]. This reduction in movement can be due to species retreating to smaller areas of habitat further from human activity, experiencing physical barriers to movement (e.g., fences), changes in the distribution of required resources (e.g., water or forage) and expanding and shifting anthropogenic activity (e.g., farming practices). Changes in species movement are both context and taxa specific, driven by sensitivity to human activity and the cost-benefit of sharing space and resources with humans.

Better observational capabilities from satellite and advances in biotelemetry enable us to monitor large-scale landscape changes and wildlife movement. Biotelemetry has advanced rapidly over the last decade. Miniaturisation of GPS tags with the addition of on-board sensors allow collection of data on animals' physiological state, activities and responses to environmental change. Contemporary tags can measure changes in heart rate, body and ambient temperature and position & orientation. This allows changes in fine-scale movement to be understood and correlated with physiology and energy expenditure. GPS tracking data can provide a detailed picture of ecological interactions when used in combination with satellite imagery. Combining these data sources provides rich information to assess landscape resistance and habitat suitability for wildlife in light of increasing anthropogenic pressure [99-105]. In chapter four of this thesis GPS tracking data is combined with high resolution satellite imagery to better understand elephant movement in relation to the expanding human footprint.

GEOGRAPHIC AND SPECIES FOCUS

Three of the four data chapters in this thesis focus on Sub-Saharan Africa while chapter two is purely methodological.

Africa is the continent with the highest number of wildlife species listed by the IUCN as vulnerable, endangered and critically endangered [18] and has the steepest rate of average proportional change in wildlife abundance [17]. Datasets on the distribution of wildlife are not collected equally geographically. The tropics are largely underrepresented, particularly Sub-Saharan Africa [106] even though terrestrial biodiversity is highest near the equator [107]. This lack of data highlights the need for reliable monitoring using automated detection techniques to speed up data collection and processing. As the continent on Earth with the lowest GDP per capita and highest human population growth rate [108], resources for wildlife monitoring are limited. Using remote sensing technology to improve provision of data on wildlife presence, movement and distribution in the vast areas of the continent can strengthen and support conservation action.

Chapter 3 & 4 focus on the African Elephant (*Loxodonta africana*) which is an evolutionarily distinct genus classified as Evolutionarily Distinct and Globally Endangered (EDGE). The EDGE metric measures the relative contribution of phylogenetic diversity of a species combined with a measurement of its endangerment and is thus an extremely valuable metric for guiding decisions on which wildlife species should be regarded as conservation priorities [109-111]. African elephants were once a widespread clade, of which many species became extinct during the Pleistocene. The remaining species are relics of an ancient clade for which extinction would represent a greater loss to the fauna than more recently evolved species whose close relatives are still extant [6]. Population numbers have significantly declined over the last century due to legal hunting, poaching (mainly for ivory), habitat fragmentation and increased killing in retaliation for crop raiding [112, 113]. As proximity of human settlement to elephants increases and conflict rises, it is important to have reliable and objective data on elephant movement and the human footprint. As African elephants are the world's largest terrestrial mammal, they provide a suitable species to test the remote sensing methods trialled in this thesis. The adults are visible from satellites under favourable conditions of daylight, weather and vegetation cover and a rich dataset of GPS tracking of their movement was available to use in combination.

RESEARCH OBJECTIVES AND OUTLINE OF THESIS

The research objectives of this thesis are:

- To analyse the spatial relationship between the human footprint and wildlife
- To investigate methods of monitoring wildlife using remote sensing technologies

The specific research objectives of each chapter are as follows:

- **Chapter 1:** Provide an overview of illegal hunting incident data in Sub-Saharan Africa and assess the spatial distribution of such data in relation to proximity to roads, water bodies, and human settlement areas.
- **Chapter 2:** Investigate acoustic disturbance and develop a mitigation method to enable increased use of UAVs in wildlife research.
- **Chapter 3:** Investigate whether very high-resolution satellite imagery and machine learning can be used to monitor African Savannah Elephants in vast heterogeneous landscapes.
- **Chapter 4:** Record the spatial relationship between African Elephants and the human footprint using GPS tracking data and high-resolution satellite imagery.

The research aims to contribute to the global wildlife conservation effort by providing new methodological approaches to use remote sensing technology to gather data on wildlife. I focus on the application of UAVs for monitoring and very-high resolution satellite imagery combined with deep learning and GPS tracking data. This is done to better understand the relationship between the increasing human footprint and wildlife in the hope that richer, more accurate and reliable data collected using these tools can support conservation action.

PART II: DATA CHAPTERS

I

The spatial distribution of illegal hunting of terrestrial mammals in sub-Saharan Africa: a systematic map

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Environmental Evidence

SYSTEMATIC MAP

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The spatial distribution of illegal hunting of terrestrial mammals in Sub-Saharan Africa: a systematic map

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Abstract

Background: There is a rich body of literature addressing the topic of illegal hunting of wild terrestrial mammals. Studies on this topic have risen over the last decade as species are under increasing risk from anthropogenic threats. Sub-Saharan Africa contains the highest number of terrestrial mammals listed as vulnerable, endangered or critically endangered. However, the spatial distribution of illegal hunting incidences is not well documented. To address this knowledge gap, the systematic map presented here aims to answer three research questions: (1) What data are available on the spatial distribution of illegal hunting of terrestrial mammals in Sub-Saharan Africa in relation to environmental and anthropogenic correlates i.e. proximity to roads, water bodies, human settlement areas, different land tenure arrangements and anti-poaching ranger patrol bases? (2) Which research methodologies have primarily been used to collect quantitative data and how comparable are these data? (3) Is there a bias in the research body toward particular taxa and geographical areas?

Methods: Systematic searches were carried out across eight bibliographic databases; articles were screened against pre-defined criteria. Only wild terrestrial mammals listed as vulnerable, endangered or critically endangered by the International Union for Conservation of Nature (IUCN) whose geographical range falls in Sub-Saharan Africa and whose threat assessment includes hunting and trapping were included. To meet our criteria, studies were required to include quantitative, spatially explicit data. In total 14,325 articles were screened at the level of title and abstract and 206 articles were screened at full text. Forty-seven of these articles met the pre-defined inclusion criteria.

Results: Spatially explicit data on illegal hunting are available for 29 species in 19 of the 46 countries that constitute Sub-Saharan Africa. Data collection methods include GPS and radio tracking, bushmeat household and market surveys, data from anti-poaching patrols, hunting follows and first-hand monitoring of poaching signs via line transects, audio and aerial surveys. Most studies have been conducted in a single protected area exploring spatial patterns in illegal hunting with respect to the surrounding land. Several spatial biases were detected.

Conclusions: There is a considerable lack of systematically collected quantitative data showing the distribution of illegal hunting incidences and few comparative studies between different tenure areas. The majority of studies have been conducted in a single protected area looking at hunting on a gradient to surrounding village land. From the studies included in the map it is evident there are spatial patterns regarding environmental and anthropogenic correlates. For example, hunting increases in proximity to transport networks (roads and railway lines), to water sources, to

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the border of protected areas and to village land. The influence of these spatial features could be further investigated through meta-analysis. There is a diverse range of methods in use to collect data on illicit hunting mainly drawing on pre-existing law enforcement data or researcher led surveys detecting signs of poaching. There are few longitudinal studies with most studies representing just one season of data collection and there is a geographical research bias toward Tanzania and a lack of studies in Central Africa.

Keywords: Poaching, Snaring, Bushmeat, Wildmeat, Wildlife, Trapping, Conservation, Biodiversity, Anthropocene

Background

We are now in the geological epoch of the Anthropocene, where human activity is the dominant force of change on earth and the planet is undergoing a sixth mass extinction [1]. Rising human populations and industrialisation is causing habitat fragmentation reducing habitat connectivity for many species [2, 3]. Restricted home ranges mean species have greater contact with human settlements resulting in increased retaliatory killing. This is particularly noticeable in the case of elephants who have less foraging space and resort to crop-raiding [4–6] and carnivores who predate on livestock and, occasionally, humans [7–9]. In addition to habitat fragmentation, one of the primary drivers of species decline is an increase in illegal hunting used as a source of subsistence and income driven largely by poverty and limited employment opportunities [10]. Due to these converging pressures, an increasing number of terrestrial mammals have been uplisted into the endangered categories by the International Union of Conservation for Nature (IUCN)—the leading international authority on species population monitoring [8]. Sub-Saharan Africa is the region that contains the highest number of terrestrial mammals listed as vulnerable, endangered or critically endangered by the IUCN, and is the focus region of this study.

The landscape of anthropogenic risk is shifting as land tenure and land ownership arrangements change. While tenure arrangements (i.e. who holds ownership rights) are different to how land is managed and administered, ownership has a significant impact on the potential land uses of an area. Domestic speculation and erosion of tribal controls and mores are significantly altering local land ownership arrangements [11, 12]. Globally, increasing liberalisation of land markets is leading to the rising privatisation of land. This trend is particularly noticeable in Sub-Saharan Africa, where 60% of the world's uncultivated arable land is found—acquiring this land is highly attractive to foreign agribusiness investors, particularly as large tracts of land are meeting less than 25% of potential yield [13]. In Sub-Saharan Africa, over 80% of land outside of protected areas is under a customary land tenure arrangement. While there is a rich literature on the impact foreign land acquisition has on local communities, there are few studies on the way the shifting land ownership mosaic is affecting wildlife [14–16]. Generating a better understanding of the spatial distribution of illegal hunting incidences can guide conservation practitioners to identify locations that would be most beneficial to position wildlife ranger posts and concentrate anti-poaching activities.

Analysing spatial variation in poaching incidences is of increasing relevance as an increasing number of tools using Artificial Intelligence (AI) and Machine Learning are developed to predict where illegal hunting incidents will take place [17]. Analysing patrol data is complex because of biases in the way data are collected i.e. rangers more frequently patrol around posts and locations where carcasses were previously detected. Improved analytical insight is now possible due to improved modelling capabilities, which work to account for collection bias [18], however, outputs will always be highly dependent on the quality of the input data. One model using data from the Serengeti, Tanzania assessed the cost and benefit of different poaching hotspots in the landscape. The model made high accuracy predictions when compared with areas where animals were subsequently snared [19]. Another predictive spatiotemporal model applied in Uganda evaluated against 5 months of field data was able to successfully predict poaching locations [18].

Generating an overview of the spatial distribution of illegal hunting incidences in Sub-Saharan Africa can guide conservation efforts. The map outlines the research methodologies that have been used to collect illegal poaching data.

The questions this systematic map responds to were identified as a knowledge gap during several meetings at the Wildlife Conservation Research Unit, University of Oxford. It has been requested that the findings from this map be presented at the Fourteenth United Nations Congress on Crime Prevention and Criminal Justice in Kyoto, Japan at an event considering "Rethinking the 'boundary-arrangement' for an evidence-based approach in addressing wildlife and forest crime".

The objective of the review

The objective is to collate the spatially explicit evidence on the illegal hunting of wild terrestrial mammals of conservation concern in Sub-Saharan Africa. The map answers three research questions:

(1) What data are available on the spatial distribution of illegal hunting of terrestrial mammals in Sub-Saharan Africa in relation to environmental and anthropogenic correlates i.e. proximity to roads, water bodies, human settlement areas, different land tenure arrangements and anti-poaching ranger patrol bases? (2) Which research methodologies have primarily been used to collect quantitative data and how comparable are these data? (3) Is there a bias in the research body toward particular taxa and geographical areas?

The map analyses comparable static geographical information across various locations. It is recognised that there are important sociological drivers of illegal hunting i.e. education level, wildmeat value chains and alternative sources of protein, among others, however, these are not the focus of the study.

To understand the spatial distribution of illegal hunting of terrestrial mammals in Sub-Saharan Africa, the main components of the question are as follows:

- Population: Wild terrestrial mammals listed as vulnerable, endangered or critically endangered by the IUCN for whom the threat assessment includes hunting and trapping and whose geographical range falls in Sub-Saharan Africa (listed in Additional file 1).
- Exposure: Location of illegal hunt
- Comparator: Contrasting proximity of illegal hunt to the following geographical variables—water bodies, transport networks, anti-poaching range patrol bases, human settlement areas.
- Outcomes: Spatial data on the geographic distribution of illegal hunting.

Methods

The protocol of this review was published in November 2018 [20]. The protocol largely focuses on how tenure influences illegal hunting, however, once the review was underway the focus shifted toward the spatial distribution of illegal hunting in relation to numerous geographic variables e.g. proximity to water, transport networks, ranger patrol posts. This shift was necessary because it became apparent that the majority of studies analyse illegal hunting in one protected area looking at distribution in relation to surrounding village land. Many articles that analyse illegal hunting do not go into detail on what constitutes illegality, cross-border trafficking chains complicate legality as legal status changes across borders. It was decided that if the study referred to hunting as illegal it would be included.

Search for articles

We searched the eight academic databases outlined in the protocol; the review team validated the search terms across databases testing alternative search strings. The terms were tested against four known articles; these articles were selected as the benchmark articles as they reflect a selection of methodological approaches relevant to the systematic map (Additional file 2). The search strings were developed in the Web of Science Core Collection. The search string was designed with assistance from information specialists at both the Oxford Bodleian Library and the University of Exeter to ensure that variations of relevant terms were included, and the Boolean logic applied was consistent across databases. All searches were conducted between December 2018 and January 2019.

All results were exported into EndNote X8 and the searches from Web of Science Core Collection and SCOPUS were used as the reference set for de-duplication. The search terms and results per database are recorded in Additional file 2. Access to all databases was provided by the University of Oxford Bodleian Library Institutional License. The search was restricted to studies conducted in the last three decades, since 1990; this cut off was chosen so the results have contemporary relevance. Only articles published in English were screened and the search string was applied under Topic subject covering Title, Abstract, and Keywords.

Search string

TS = ((mammal* OR fauna OR wildlife OR animal*) AND tenure OR land NEAR/2 (ownership OR right* OR holding* OR title OR administration OR management OR tenan* OR deed* OR pastoral OR private OR commun* OR customary OR state) OR "natural resource" NEAR/2 (ownership OR right* OR management OR regim* OR private OR commun* OR customary OR state) OR "property regime" OR area NEAR/2 (communal OR protected OR communit* OR freehold OR "free leasehold" OR "Wildlife Management") OR ownership NEAR/2 (pastoral OR private OR commun* OR customary OR state) AND (hunt* OR poach* OR bushmeat OR trap* OR snar* OR vulnerabl* OR endangered OR threatened OR risk OR "conservation dependent" OR extinct*)).

The search terms were kept as consistent as possible and all searches were recorded so the searches can be easily repeated in the future.

All the following databases were searched using the subscription of the University of Oxford:

- Agricola [http://agricola.nal.usda.gov].
- AGRIS [http://agris.fao.org/].

- BIOSIS: Biological Abstracts (Accessed via Web of Science—BIOSIS Citation Index-1969-Present).
- CAB Abstracts (Accessed via Ovid).
- PAIS Index (Accessed via ProQuest).
- SCOPUS (http://www.scopus.com).
- Web of Science Core Collection: citation indexes listed in Additional file 2.
- Zoological record (Accessed via Ovid).

Deviations from the protocol

To ensure the expanded focus was encapsulated in the search strategy the search terms were rerun removing keywords relating to tenure. The resulting articles which met the inclusion criteria remained the same. The population criteria were amended to include studies focused on multiple species where it is stated hunting is illegal, but the species hunted is not specified. It was necessary to interpret this criterion liberally as a large number of studies focused on the illegal hunting of multiple species using the umbrella term 'bushmeat'—referring broadly to mammals killed for subsistence.

Article screening

Screening process

The inclusion criteria were applied during the title and abstract screening and all articles were double screened by two authors. Once 20% of articles had been screened, the corresponding authors met to check for consistency between the screening choices. All disagreements during screening were discussed and reconciled between the team of three reviewers. Cohen's kappa statistic was calculated after double screening all articles (12,403) by three authors, resulting in 0.929 and 0.884 (Additional file 2). Articles set aside for inclusion after screening abstracts were single screened at full text with 20% of articles double screened at full text to ensure consistency. All articles screened and excluded at full text were recorded, the methodology was coded and a brief outline of the content and the reason for exclusion is provided (Additional file 3). No articles included in the final synthesis were authored by the reviewers so there is no conflict of interest. None of the articles we screened were unobtainable. The systematic map guidelines were followed via the ROSES checklist (Additional File 4).

Eligibility criteria

Eligible population

The focus is on terrestrial mammals that are listed as vulnerable [21], endangered (EN) or critically endangered (CR) on the IUCN Red List. This is the global authoritative list of species in decline. Species included were further restricted to those for whom the IUCN threat assessment includes hunting and trapping as a key threat of which there are 172 species (listed in Additional file 1). The regional area of focus is Sub-Saharan Africa, as defined by the United Nations inclusive of 46 countries (Additional file 1). Many studies include multiple predator and prey species or use the catch-all expression bushmeat, if one species listed met the inclusion criteria the study was included.

Eligible exposure

The exposure of the populations outlined above to illegal hunting is the focus of this paper. While it is not necessary for a study to explicitly state the reason for the hunt, e.g. local subsistence hunting or transnational trafficking, the location of the kill must be included. The focus is on unregulated illegal hunting, hence studies on trophy hunting were excluded as this is a legal form of regulated hunting where quotas are set considering local population dynamics. Studies looking at mortality from zoonotic disease or other anthropogenic causes were also excluded.

Eligible comparator(s)

Various kinds of study designs are included in the map as shown in the results (Fig. 3). As the search progressed it became evident that including only studies that explicitly mention property rights arrangements would yield very few eligible studies despite shifting land use and ownership being an international cause of concern for wildlife. It was decided that studies would be included so long as the status of the land was mentioned, e.g. protected area, village land, rather than the explicit ownership arrangement. Various environmental and anthropogenic correlates were assessed between studies i.e. proximity of illegal hunting incidences to roads, water bodies, human settlement areas and anti-poaching ranger patrol bases.

Eligible outcomes

The evidence has to be geolocated. The locations of the kill sites were required to include primary data and not via referenced data from other studies. Data collected first hand can include records of carcass locations or signs of hunting, i.e. used shrapnel, snares, hunter arrest records or via hunter follows, interviews and/or surveys. Variation in the number of species consumed or sold is also an eligible outcome if the capture location(s) is included.

Exclusion criteria

Demographic studies containing data only on species abundance and distribution were excluded. Similarly, studies that only contain data on species behaviour in response to a perceived threat, e.g. monitoring flight initiation time were excluded. Studies that infer the level of illegal hunting by providing proxies, e.g. bushmeat price as an indicator of supply were excluded. All articles excluded at full text were recorded with a description of the focus of the article and the reason for exclusion (Additional file 3).

We excluded the following kinds of articles:

- Theoretical or modelling studies and purely qualitative research that does not include any quantitative data.
- Editorials and commentaries.
- Social commentaries that do not include any quantitative data.
- Literature reviews.

Study validity assessment

We did not conduct a study validity assessment on the results of our searches as the purpose of the searches was to cover a broad spectrum of methods. Articles were judged against the eligibility criteria outlined above.

Data coding strategy

Data extraction consisted of two stages carried out by three reviewers. Once articles were screened at the level of title/abstract, 206 articles were put aside to be reviewed at full text. At this stage the title, focus of the study and method used for data collection was recorded, alongside the reason why articles were excluded (Additional file 3). The methods used to collect data on illegal hunting were reviewed and grouped and codes were created (Additional file 5). Once this stage was complete and the 47 articles that met the inclusion criteria remained, we used a separate coding sheet (Additional file 6) to extract the following relevant information:

1. Bibliographic information: publication type, title, publication year, etc.
2. Study context: country, land tenure type, size of study area, number of sites, taxa.
3. Study design: method used for data collection, unit of analysis, sample size, length of data collection.
4. Outcomes: spatial variation in the level of hunting, stated conclusion/finding of study.

To ensure consistency the first 20% of articles was coded by two reviewers. It was necessary to consult the supplementary material in several cases and in four cases to directly contact the authors for information.

Data mapping method

Comparable points of information were extracted to categorise and compare, variables such as proximity to roads, water bodies, distance to human settlements and ranger patrol bases were recorded as were the countries and the list of species included in the study (Additional file 6). To gain an understanding on the different methods in use we created a key of methods in use (Additional file 5), these were grouped and visualised in a bar graph showing included and excluded studies. To show the geographic distribution of studies we grouped these via a choropleth map and the variety of taxa were visualised via a Sankey diagram. This enabled us to identify knowledge gaps. For example, there is a lack of research outside protected areas and geographically there is a lack of studies in central and west Africa.

Results

Number and types of articles

Figure 1 details the step-by-step results of the systematic mapping process. 12,645 articles were screened at title and abstract, 206 articles were read at full text of which 47 met the criteria.

1. What data are available on the spatial distribution of illegal hunting of terrestrial mammals in Sub-Saharan Africa in relation to environmental and anthropogenic correlates i.e. proximity to roads, water bodies, human settlement areas, different land tenure arrangements and anti-poaching ranger patrol bases?

    a. What evidence exists on the impact of transport corridors on the spatial distribution of illegal hunting?

    Studies that include proximity to transport networks in analysis span a diverse range of methods, including recording poaching signs e.g. carcasses, snares, cartridge shells; using tracking data to look at species mortalities; household dietary recall surveys and bushmeat market surveys. In Guinea higher carcass numbers were found in villages bordering a heavily trafficked road compared with rural villages in the same landscape [23]. In Nigeria and Cameroon, the price of bushmeat was found to increase closer to roads as it is thought that this increases access to distant markets [24]. A study in Ghana on the Pangolin trade found hunting frequency increased on busy roadside verges as this provides a point of direct sale to customers [25]. Increased hunting was found to increase in proximity to railway lines

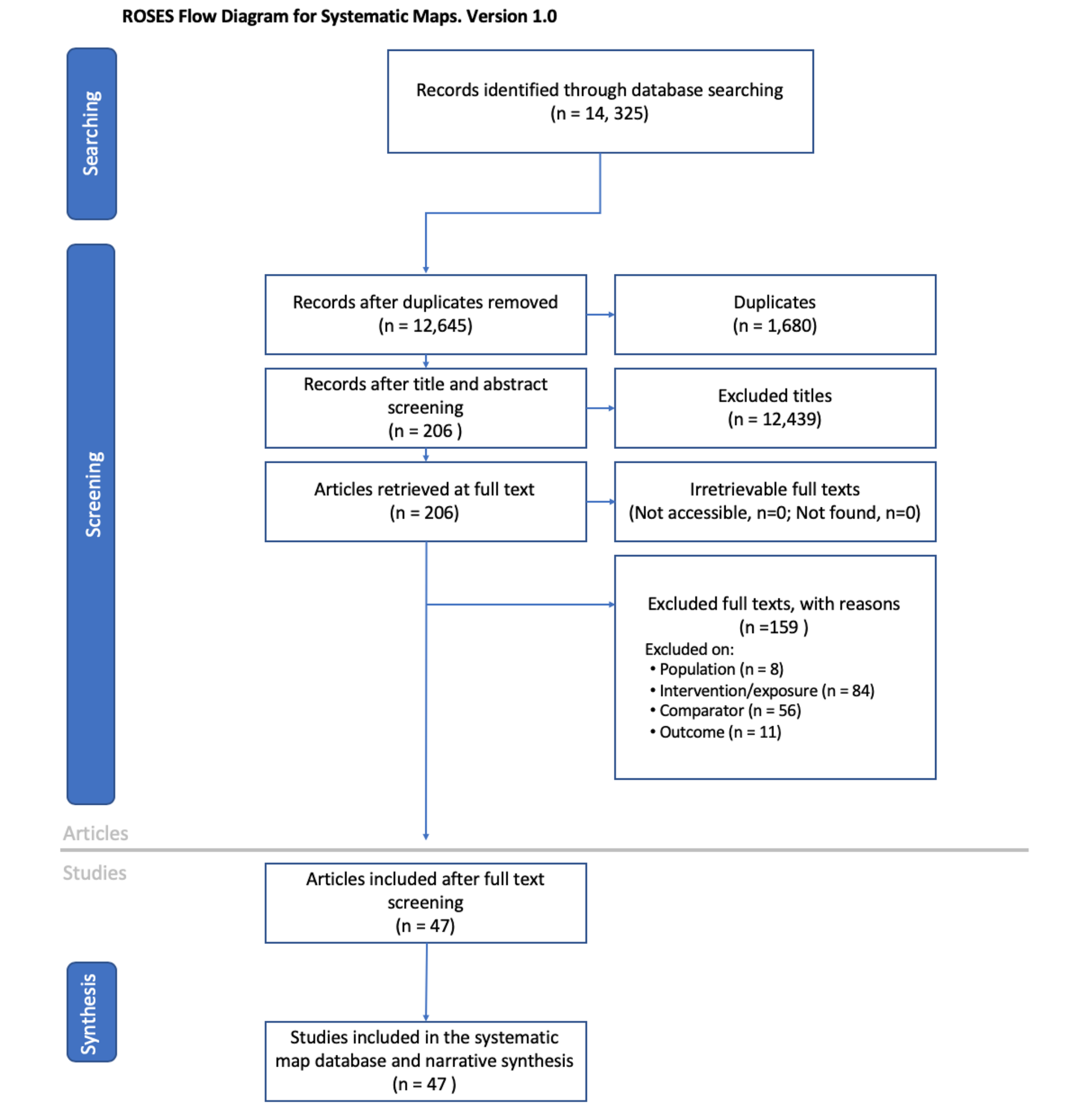

Fig. 1 Search, screening and full-text assessment flow chart [22]

as shown in a study on lions in Zimbabwe [26]. Another common impact of roads is accidental roadkill [27]. Proximity to transport networks was included in several analyses [23–30], exploring whether hunting pressure increases closer to transport networks globally would be amenable to systematic review (Fig. 2).

b. What evidence exists on how seasonal variation and the spatial distribution of water bodies impact upon illegal hunting incidences?
Proximity to water resources is included in several analyses [26, 28, 31–36]. An analysis of 6 years of snare data in Tsavo National Park, Kenya found snare numbers were higher around

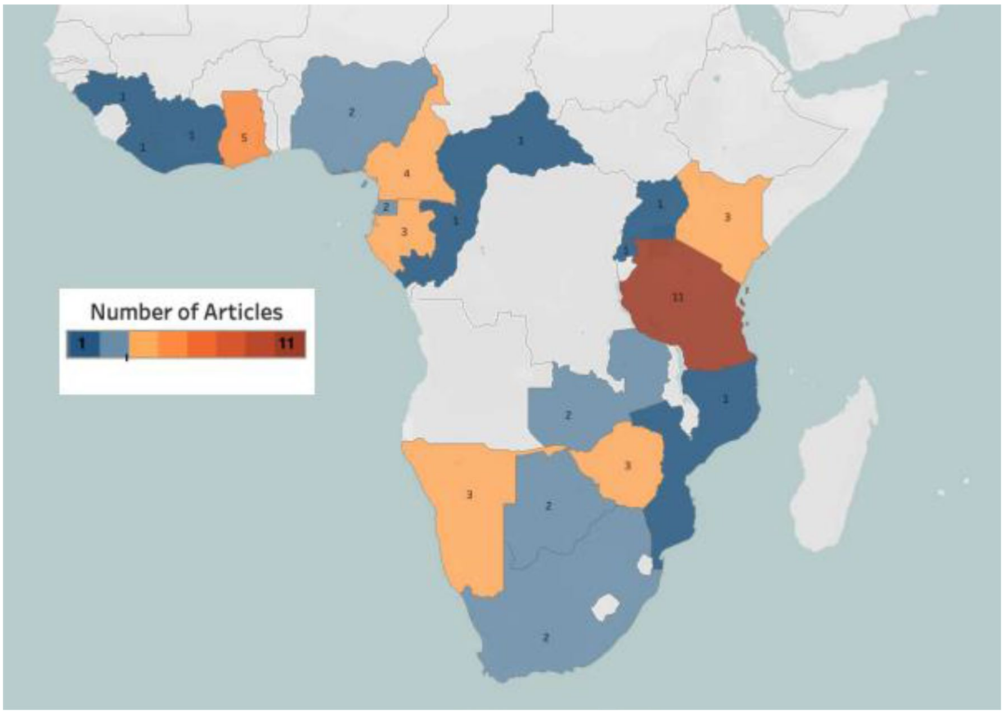

Fig. 2 Chloropleth map of inlcuded articles

water holes [28], the same was found in a study on lions in Zimbabwe [26] and for elephants in Tanzania [34]. Mammals tend to be easier to locate and hunt at water holes as they become stationary when drinking. The impact of seasonal variation on illegal hunting varies between studies, some report increases during the dry season and others during the wet season. Various reasons are given for the differences; the wet season offers an advantage to hunters as large areas of reserves and national parks cannot be accessed by roads which become muddy, washed out and often impassable, reducing access for patrol forces. Poachers can take advantage of the lack of enforcement in the wet season, although difficulty traversing the landscape will increase the unit of effort per catch. Another factor that makes it easier to hunt illegally in the wet season is the closing of tourism operations, i.e. legal trophy hunting operations, this enables poachers to move around with less risk of being caught [37]. In Gabon, hunting increased in the dry season during circumcision ceremonies as there is an increased demand for meat [38].

The rhythm of the agricultural season is mentioned as an influencing factor in several studies. During periods of low agricultural activity, hunting provides a replacement source of income, this was found in Cameroon [39], Ghana [40, 41] and Guinea [23]. During the wet season, hunters are largely occupied by other economic activities. In Guinea hunting varied between seasons for different species, e.g. hunting for ungulates and rodents increases in the dry season, while primates are more highly threatened in the mid-to-late rainy season when they are shot to prevent crop-raiding [23]. The majority of studies were conducted over a year or less, therefore seasonal variation could not be factored in. Seasonal variation is species and context-specific affected by many economic, social and cultural factors.

c. What evidence exists on how proximity to human settlement areas impact illegal hunting?
It is not possible to make an analysis on the impact of tenure as very few studies include more than one land tenure arrangement. Most studies in this map have been conducted in a single protected area looking at hunting incidences on

a gradient from the border to the interior. Other studies analyse illegal hunting in a protected area at varying distances to another site, e.g. game reserve, customary land area, game management area. Logically, the majority of studies have focused on protected areas as this is where wildlife numbers are highest.

One study in Zimbabwe made a comparison between two areas of a conservancy: an area where adjacent land was settled by subsistence farmers after the fast-track land reform programme and another in an unsettled area in the north [42]. The resettled area was more strongly affected by illegal hunting. This halo of defaunation around a human settlement area has been identified in several studies [26, 32, 43, 44]. Increased hunting around a protected area was frequently cited, often referred to as an 'edge effect' [24, 25, 28, 29, 35–37, 45–54]. Different methods are used that find the same effect e.g. recording carcass and snare locations [28, 36, 43–45, 48, 53, 54], one household survey in Tanzania found wild meat consumption increased in villages closer to the park boundary [46] and several studies on bushmeat market surveys found the price decreased closer to protected areas indicating an increase in supply [24, 25]. Other studies using GPS or radio-tracking data to monitor mortalities found hunting was higher on the border of protected areas compared to the interior [24, 25]. Illegal hunting likely increases on the border of protected areas as wildlife numbers increase by virtue of being next to a protected area.

d. What evidence exists to show how anti-poaching ranger patrol posts impact the spatial distribution of illegal hunting incidences?

   Several studies analysed the impact of anti-poaching ranger posts and patrol routes on illegal hunting incidences. One study, looking at hydrocarbon concessions in Central Africa, found, as expected, increased ranger patrols led to reduced poaching at a site [31]. However, in Tanzania mixed results were found: fewer elephant carcasses were discovered near several wildlife ranger posts, while an increase was detected at others—the variance was put down to disparities in resource allocation between posts [34]. To accurately analyse spatial variation in poaching incidences it is necessary to account for patrol effort. Catch Per Unit of Effort (CPUE) calculates the number of illegal activities identified per unit of patrol effort which is often used as a metric to assess deterrence efficacy; however, this can often be difficult to interpret [55].

   An analysis of incidents at several sites where the SMART anti-poaching software is used found anti-poaching patrols had a greater impact in areas with open habitat, likely due to increased visibility [56]. Poaching threat maps that use illegal hunting data can generate understandings of how ranger patrol posts impact upon the spatial distribution of poaching incidences in the landscape. Poaching heat maps of this kind can be used to identify suitable locations where additional ranger posts could be established to reduce poaching. However, it is necessary to be careful with the use of poaching data as the primary focus of rangers is law enforcement, not monitoring [57]. Large portions of protected areas are unpatrolled due to limited resources, which makes inferences on the distribution of illegal activity challenging, at best, if not impossible in many locations. Rangers often cannot survey the landscape evenly as seasonal variation prevents access, i.e. during the wet season roads become washed out and it can be difficult to patrol in open savannah during hot periods. Patrol activity in most sites is badly understood due to a lack of recording and oversight. One recent study analysing spatio-temporal patrol presence in a large number of sites found patrols typically cover insufficient spatial scales to reduce illegal activity [56].

   There have been several attempts to apply Artificial Intelligence (AI) and Machine Learning to patrol data to predict future illegal hunting incidents. The accuracy of predictions is based on biases contained within the collection of training data and should be treated cautiously [58]. Future primary studies regarding the impact of ranger posts on the distribution of illegal hunting incidences are recommended.

2. Which research methodologies have been used to collect quantitative data on illegal hunting and how comparable are these data?

   The variety of methods used to collect quantitative data on illegal hunting is shown in Fig. 3—this shows all the methods that document levels of illegal hunting that were screened at full-text, however several of these do not collect spatially explicit information thus cannot be used to analyse spatial dynamics. The most common method identified in this review is abundance and distribution surveys which infer the severity of hunting by looking at fluctuations in population numbers. It is not possible to reliably attribute fluc-

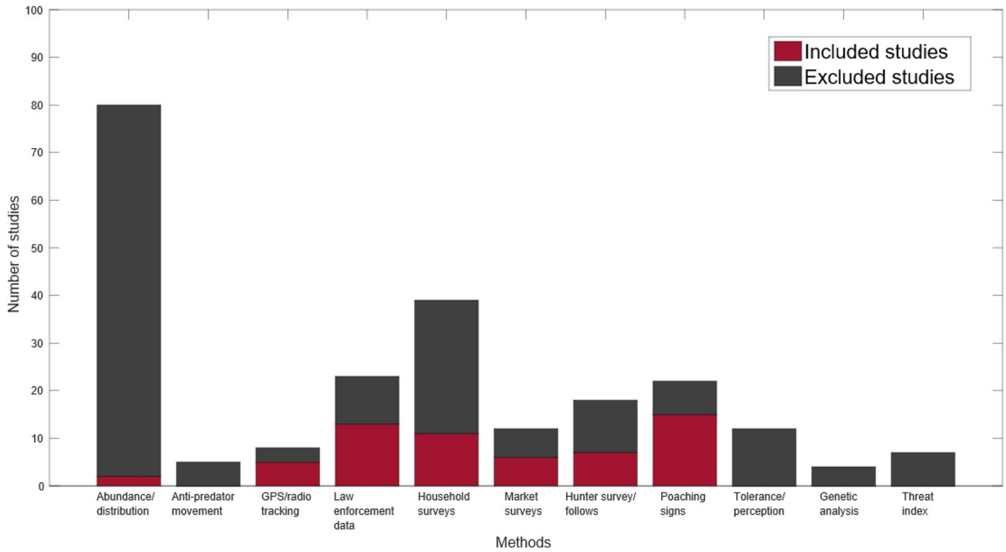

Fig. 3 Methods used to collect data on illegal hunting reviewed at full text

tuations in population numbers to illegal hunting as many variables impact survival rates. There are few longitudinal studies that include more than a year of data collection and no studies that survey the entire extent of a species range. Changes in the population at the site level do not reflect long-term population dynamics. As population numbers are a proxy indicator of hunting pressure and do not provide spatially explicit information, these have been excluded from the final map.

Several methods use animal movement data to assess the speed at which species flee when sensing an audible or visual threat; 'flight initiation' time is monitored visually or via radio or GPS tag to assess anti-predator behaviour [59, 60]. These studies were excluded as they are not a direct measure of illegal hunting. Many studies use bushmeat household and market surveys, however, often the species hunted are not in the IUCN endangered categories and were excluded. Three study designs labelled 'tolerance and perception', 'genetic analysis' and 'threat index' appeared frequently during the title and abstract screening. 'Tolerance and perception' studies aim to gauge the level of local animosity toward wildlife through a variety of survey methods; the results are then used to ascertain the level of hunting risk in the landscape [7, 61–65]. As no quantified data are included, these were excluded. Studies using 'genetic analysis' can be divided into two: studies that look at landscape connectivity and resistance to gene flow caused by human settlement and infrastructure, and studies that genetically analyse seized teeth or bones to locate poaching hotspots [66–68]. It is possible to genetically identify kill locations only at very coarse geographic scales, so these were not included in the final synthesis. 'Threat index' studies take different forms, including modelling the optimal size of national park buffer zones to prevent hunting, modelling species survival rates after release and developing threat indices to establish which properties in the landscape cause greatest threat [69–72]. While these are relevant for assessing the threat of illegal hunting they were excluded as they do not provide hunting locations.

The majority of studies that met our inclusion criteria fall into two categories; they either use pre-existing law enforcement data collected on hunting incidences or the authors of the study collected data on hunting incidences via line transects, aerial counts or hunter follows recording capture locations. An advantage to pre-existing data collected by wildlife authorities is that these are often longitudinal and cover a larger area beyond the capacity of an individual study.

3. Is there a preference in the research body toward particular taxa and countries? Countries

Published data are only available for 19 of the 46 countries that constitute Sub-Saharan Africa, this is a small sample size considering the size of the region. There is a concentration of studies in Tanzania and a bias toward a single protected area—Serengeti National Park. Several of the largest countries in Sub-Saharan Africa contain no studies, i.e. the Democratic Republic of Congo, Sudan, and Chad. In West Africa, the majority of studies have been conducted in Ghana.

Species included in the systematic map

Some data collection methods are not conducive to recording taxa, e.g. analysis of snare data, as the species killed can be difficult to identify. Household surveys and illegal bushmeat market surveys often experience the same problem where consumers or sellers do not know the species being consumed. Figure 4 shows all species included in the final synthesis.

One hundred and seventy-two species in Sub-Saharan Africa are in the IUCN endangered categories listed as being at risk from hunting and trapping. However, spatially referenced quantitative data are only available for 23 of these species. The largest class of threatened taxa is primates who comprise 96 of the 172 listed species. This distribution is reflected in our review as spatially explicit data on hunting location is available for ten primate species—more species than in any other taxonomic group. The taxa covered are relatively representative of the distribution of species of conservation concern. There are some exceptions: no studies on bats met our inclusion criteria despite 14 bat species being listed in the IUCN endangered categories in Sub-Saharan Africa. Bats are relatively easy to hunt; hundreds can be trapped in a few hours as they cluster while roosting and netting are sold cheaply to protect crops. We expected spatially explicit data on the hunting of bats due to their connection with several vector-borne diseases, e.g. Rabies and Ebola. Hunting of certain species occurs for a variety of reasons; for cultural ceremonies, subsistence

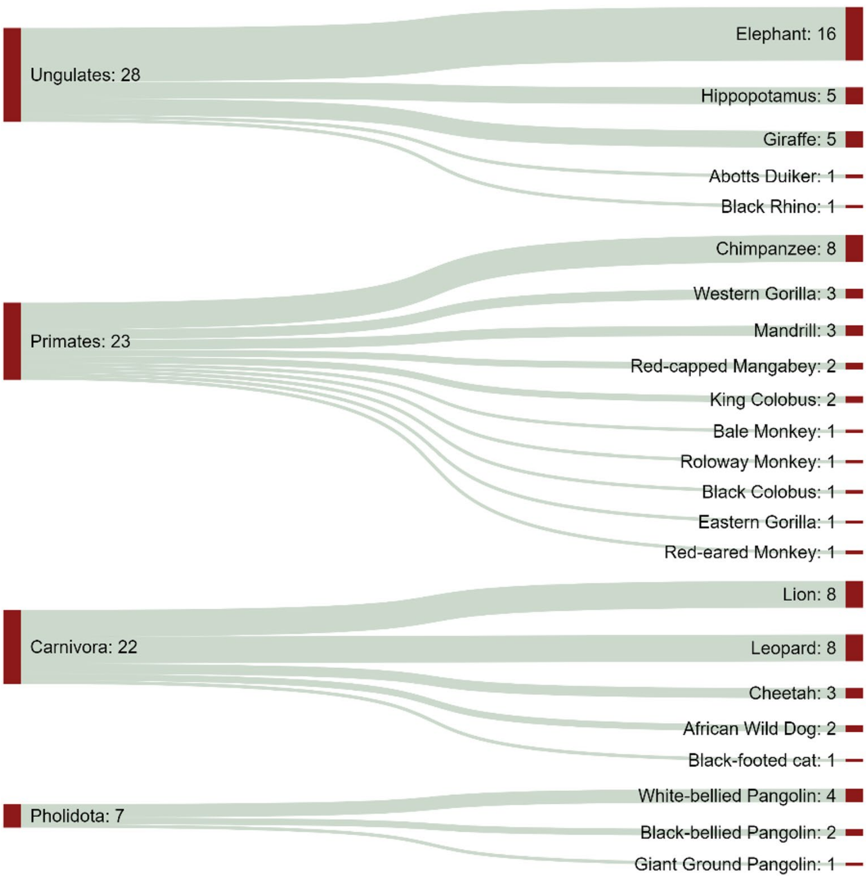

Fig. 4 Sankey diagram of all species included in the systematic map

meat, ornaments, etc. and different parts of the animal are primarily sought, e.g. skin, teeth, bones, meat, organs. Specific cultural beliefs and taboos will also prevent some species being hunted over others.

Limitations of the map

Limitations due to the search strategy

One limitation in our search strategy was that we only consulted academic databases, we test ran the search terms on a number of organisational websites, but these did not yield any relevant results. Google Scholar was not consulted as we were advised by the University of Oxford Bodleian librarian that the peer reviewed articles it would provide would already be captured in the eight selected databases. Searches were only conducted in English as the majority of academic papers are published in English, the bias this introduces is likely to be small.

Limitations due to bias in pool of articles found

Our findings are restricted to Sub-Saharan Africa and to a small sample size. Spatial features included in this review may have a different effect in other locations and biomes. We only included articles on species of conservation concern which reduced the number of articles included. The absence of studies with qualitative data is a limitation as social and cultural factors that drive hunting are not considered. Sociological information is critical for understanding the context in which poaching occurs, but these variables are not easy to compare across diverse geographical locations.

Conclusions

Implications for policy/management

This systematic map categorised all the available evidence relating to the research questions. The intention is that policymakers find the map useful to gauge the extent of available evidence on illegal hunting of species of conservation concern. The key points of policy relevance are as follows:

- Few studies contain systematically collected data on poaching incidences; several applications have been developed to assist with data collection including Kobo Collect and the Spatial Monitoring and Reporting Tool (SMART). Funding these tools would enable the advancement of systematic data collection that would allow weights to be constructed in geospatial models to forecast future poaching incidents.
- Discerning what local spatial biases exist and including these in the design of anti-poaching patrol schedules would help to make best use of, often stretched, patrol resources.
- Seasonal fluctuations in illegal hunting varied between studies as seasonal employment opportunities for local people change. This shifting temporal factor should be considered in anti-poaching conservation programmes when planning annual patrol intensity.
- There is a research bias toward East Africa in the studies collected. It is recommended that conservation funding be directed toward collection of improved illegal hunting datasets in central and west Africa so as to gain a better understanding of illegal hunting dynamics in these regions.

Implication for research

This map identified several understudied subtopics which would benefit from primary research. The research gaps identified were as follows:

- On review of the evidence base it is clear that an analysis on the influence of tenure is not possible as there are too few comparative studies between adjacent land tenure areas. Future longitudinal research studies comparing hunting incidences in adjacent land tenure sites, where other variables remain similar would allow for an assessment of this relationship.
- The studies included in this review show discernible spatial patterns in illegal hunting incidences, however due to variation in methodology and study length it would not be possible to compare studies directly via meta-analysis [69–72]. However, a systematic review could assess the spatial trends in the evidence globally to establish what spatial patterns are consistent across biomes. This information could then be used to guide anti-poaching patrols and optimally position wildlife ranger posts which is particularly relevant as predictive modelling using AI and Machine Learning is advancing.
- Biased collection of biodiversity datasets is well documented [73] as is apparent in this map-research is encouraged in these understudied areas. Several countries have no spatially explicit data available e.g. Angola, Democratic Republic of Congo.
- Future research assessing the relationship between the size of buffer zones and levels of illegal hunting is recommended to establish whether buffer zones act as an important deterrent.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s13750-020-00195-8.

Additional file 1. Inclusion criteria: Countries in Sub-Saharan Africa defined by the United Nations; IUCN search criteria and the list of articles used for benchmarking search strings.

Additional file 2. Search terms, databases consulted, the number of retrieved articles and number of articles screened after duplicates removed.

Additional file 3. Exclusion sheet listing the titles of the articles screened, the method used to gather data on illegal hunting, the focus of the study and the reason for exclusion.

Additional file 4. ROSES Systematic map checklist.

Additional file 5. The key created for the methods used to monitor illegal hunting.

Additional file 6. Details of included studies: Title, country, species name, the research method used for data collection, the main finding of the article, the tenure of the land under investigation, the period of data collection and mention of the following factors: 1. anti-poaching ranger patrol bases, 2. Proximity to water, 3. Season and 4. Proximity to transport networks.

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Authors' contributions
ID conceived the study and developed the parameters of the search strategy and inclusion/exclusion criteria with input from TH, TW, and oversight from DM. All authors contributed to the manuscript, led by ID. The scoping of the search strategy was developed with assistance from Oliver Bridle and Alison Bethel. All authors read and approved the final manuscript.

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Availability of data and materials
All data generated or analysed during this study are included in this published article [and its additional information files].

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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II

Determination of optimal flight altitude for minimizing acoustic drone disturbance to wildlife using species-weighted audiograms

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RESEARCH ARTICLE

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Determination of optimal flight altitude to minimise acoustic drone disturbance to wildlife using species audiograms

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Abstract

1. Unmanned aerial vehicles (UAVs) are increasingly important in wildlife data collection but concern over wildlife disturbance has led several countries to ban their use in National Parks. Disturbance is an animal welfare concern and impedes scientific data collection through provoking aberrant behaviour. Dealing with the issue of disturbance will enable wildlife researchers to use UAV technology more effectively and ethically.
2. Here we present a novel method to determine optimal flight altitude for minimising drone disturbance for wildlife using species audiograms. We recorded sound profiles of seven common UAV systems in the horizontal and vertical planes at 5-m increments up to 120 m. To understand how mammals perceive UAV sound, we used audiograms of 20 species to calculate the loudness of each UAV for each species across the measured distances. These calculations filter the UAV noise based on the sensitivity of species' hearing over the relevant frequency spectrum.
3. We have devised a method to optimise the trade-off between image spatial resolution and flight altitude. We calculated the lowest point at which either the UAV sound level decreases below an acceptable threshold, here chosen as 40 dB, weighted according to species' hearing sensitivity, or disturbance cannot be significantly further minimised by flying higher. The latter is quantified as the point above which each additional 5 m of flight altitude causes on average less than 0.05 dB decrease in sound pressure level.
4. Reliable data on appropriate flight altitudes can guide policy regulations on flying UAVs over wildlife, thus enabling increased use of this technology for scientific data collection and for wildlife conservation purposes. The methodology is readily applicable to other species and UAV systems for which sound recordings and audiograms are available.

Isla Duporge and Marcus P. Spiegel contributed equally to this work.

KEYWORDS
aerial survey, anthrophony, audiogram, audiometry, conservation, remote sensing, sound pressure level, unmanned aerial vehicle (UAV)

1 | INTRODUCTION

The introduction of unmanned aerial vehicles (UAVs) is revolutionising the study of wildlife. Recent applications include gathering biological samples (e.g. blow samples from whales Acevedo-Whitehouse et al., 2010; Dominguez-Sanchez et al., 2018; Geoghegan et al., 2018; Pirotta et al., 2017), monitoring morphometric attributes (Burnett et al., 2019) and collecting behavioural data (Fiori et al., 2020; Graving et al., 2019). In addition UAVs have been used for census surveys (He et al., 2020; Linchant et al., 2018; Vermeulen et al., 2013; Ratcliffe et al., 2015), for anti-poaching surveillance (Marks, 2014; Mulero-Pazmany et al., 2014), for mapping species habitat use and distribution (Goebel et al., 2015; Koh & Wich, 2012; Perryman et al., 2014; Szantoi et al., 2017; van Andel et al., 2015), for locating radio-tagged animals (Muller et al., 2019), for assessing species body mass and condition (Christiansen et al., 2019; Krause et al., 2017), for relocating animals to mitigate human–wildlife conflict (Hahn et al., 2017; Schiffman, 2014) and for kinematic analysis (i.e. recording running giraffes; Basu et al., 2019). This technology also enables behavioural ecologists to study fine-scale wildlife movements that are undetectable from the ground (Fiori et al., 2020). Flying UAVs is less disruptive than collecting data using existing techniques (e.g. manned aircraft Colefax et al., 2019; Yang et al., 2019) or vessels (Pirotta et al., 2017), and can be used to access species in locations that are impractical or unsafe to visit on foot. It is now possible to use automated analysis techniques to speed up detection of species in resulting imagery (Gray et al., 2019). The applications of UAVs to wildlife studies are numerous and continue to grow (Duffy et al., 2020; Hodgson & Koh, 2016). However, there is significant scope for misuse: alarming media coverage has portrayed UAVs as a new source of disturbance in natural habitats (Keane, 2018; Sawer, 2016). Social media videos showing wildlife being harassed have been widely circulated (e.g. a video showing a bear cub highly distressed by a UAV has gathered more than 8.5 million views Bittel, 2018; Youtube, 2018). Although alarmist news articles and social anxiety are common when new technologies become widely available (Bauer, 1995), disturbance should be taken seriously as the noise emitted from UAV systems can distress wildlife in several ways. Disturbance effects include obscuring auditory detection and communication, and eliciting behaviours that displace time and energy from primary survival functions (e.g. feeding, mating and breeding; Mulero-Pazmany et al., 2017). Additionally, disturbance impedes collection of scientific data as unnatural movement is triggered.

Using UAVs for wildlife monitoring and surveying is hampered by a lack of research and clarity on disturbance issues (Jeanneret & Rambaldi, 2016; Rambaldi, 2019). Concerns over the possible adverse effects of UAV use on wildlife have caused several countries to ban UAVs in National Parks, including in the United States (Baltrus, 2014) and South Africa (Drone Laws in South Africa, 2021).

There is a growing body of literature discussing the impact of UAV-generated disturbance on large mammals based primarily on visual observation of aberrant behaviour (Arona et al., 2018; Hodgson & Koh, 2016). Guidelines on advised flight altitudes based on visual observations are presented in several studies, for example, 25–40 m above water level (AWL) for bottlenose dolphins (Fettermann et al., 2019) and 80–100 m above-ground level (AGL) for snub-nosed monkeys (He et al., 2020). All guidelines require nuance as different UAV designs generate different sound profiles, and sound propagation loss (sound wave dissemination) is affected by numerous environmental and situational factors (e.g. vegetation) and atmospheric conditions (e.g. wind speed and direction; Bennitt et al., 2019).

Current evidence indicates substantial inter- and intraspecific variability in the flight altitude at which a disturbance is detected when using the same UAV system (Brisson-Curadeau et al., 2017). For example, sea turtles have been found to be undisturbed by UAVs flown as low as 10 m (AWL; Biserkov & Lukanov, 2017) whereas crocodiles react visibly to UAVs at 50 m (AGL; Bevan et al., 2018). Adélie penguins *Pygoscelis adeliae* are more readily disturbed than gentoo penguins *Pygoscelis papua* during flights over their nest sites conducted at the same altitude (Rummler et al., 2018). One study comparing sound from two UAVs with the hearing thresholds of odontocete and mysticete whales and pinnipeds showed that the noise could only be quantified above ocean ambient sound at 1 m depth when flying at 10 m, therefore, disturbance is only a concern when UAVs are flown very close to the water surface (Christiansen et al., 2016).

However, the concept of disturbance remains ill defined. Species may not immediately change their behaviour when they are disturbed or stressed, yet existing studies have largely focused on assessing animals' responses through visual observation (Fettermann et al., 2019; Ramos et al., 2018; Rümmler et al., 2015; Vas et al., 2015). However, without physiological information or baseline behavioural data from which to understand anomalies, it is difficult to gauge whether disturbance has occurred. For example, the heart rate of black bears increased by 300% when a UAV was flown overhead although no other discernible behavioural response was detected (Ditmer et al., 2015). Sensitivity to noise varies across taxa and within species groups depending on sex, age, life history, breeding season and the level of habituation to noise (Bennitt et al., 2019; Ratcliffe et al., 2015). In a follow-up study on the same black bears, it was found that the elevation of heart rates dropped as the bears became habituated to the sound after 4 weeks of exposure (Ditmer et al., 2019). It is time-, labour-, and cost intensive to gather physiological and behavioural baselines against which to measure disturbance, although these can be revealing.

Planning UAV flights always entails trade-offs between flight altitude and image spatial resolution with the goal of maximising image resolution while minimising disturbance. Image resolution is defined by the ground sampling distance (GSD, distance between pixel centres on the ground), which is linearly related to the height above-ground level for cameras with a fixed focal length. For example, GSD for a survey with the Mavic Pro Platinum over ground is 1.24 cm/pixel, 2.48 cm/pixel and 3.72 cm/pixel for flights at 40, 80 and 120 m respectively. Flight altitude must provide the GSD to meet research aims while the potential for disturbing species is acceptably minimised.

Existing studies assessing UAV disturbance on wildlife often use A-weighted decibels, dB(A), which weight frequency-specific levels according to the sensitivity of human hearing (Ditmer et al., 2015; Hodgson et al., 2013; Wegdell et al., 2019). This method is problematic, as this weighting is based on human perception rather than the hearing sensitivity of the species of interest. Mammalian hearing is very diverse. For example, bats and dolphins hear in the ultrasonic range (>20 kHz), while whales and elephants hear in the infrasonic range (<20 Hz), rendering A-weighted measurements misleading for these species.

Here, we present a new method that calculates advisable flight altitudes based on an interpretation of UAV noise that incorporates species' hearing. We used audiometry—a measurement of the range and sensitivity of hearing generated for different species—and cross-reference these with sound measurements from seven commonly used UAVs. Our method does not rely on longitudinal behavioural datasets to understand disturbance but can be integrated with in-situ behavioural observations. We generated sound profiles for seven commonly used UAVs and applied our method to 20 species for which audiograms were available. The three main research objectives were:

1. Describe the noise profile of seven commonly used UAV systems.
2. Use available audiograms to create species-weighted measurements to demonstrate how different UAVs are heard by various species.
3. Generate advisable flight altitudes for flying each UAV over these species by calculating the lowest altitude at which the loudness is either below an acceptable threshold or no longer decreases significantly with altitude, thus minimising disturbance while maximising image resolution.

2 | MATERIALS AND METHODS

2.1 | UAV audio recording collection

Unmanned aerial vehicles audio recordings were taken for seven commonly used UAV systems from DJI (Shenzhen DJI Sciences and Technologies Ltd.): Inspire 2, Phantom 4, Mavic 2, Mavic Pro, Mavic Pro Platinum, Mavic Mini, and Spark. Recordings were taken 14–25 May 2020 in an open field in Wytham, a research facility belonging to the University of Oxford, UK. Recordings were taken between 23.00 and 03.00 (GMT) on nights when zero wind speed was detected on the anemometer, and ambient background sound levels were low. Flights were conducted by a certified UAV pilot with permission from the UK Civil Aviation Authority.

The sound from each UAV was recorded along a single transect in two principal directions: vertical, with the drone directly overhead, and horizontal, with the drone displaced from the microphone at a fixed height. As we explain later in this section, only the vertical recordings were used to ultimately arrive at advisable flight altitudes. The horizontal recordings were taken to provide a comparison for how UAV noise propagates differently in the horizontal and vertical planes.

Vertical recordings were taken with the microphone at ground level. The internal UAV GPS was used to hover the UAV at the desired altitude during recording. All vertical recordings were taken when there were not any wind gusts or transient noise. For the horizontal recordings, the UAV was fixed to a 1.5 m high speaker stand, and the microphone was held at the same height. The stand provided a consistent setup for our recordings that would not be affected by gusts of wind and enabled us to easily pause measurements when there was transient noise (e.g. owls, aircrafts). Given the flying settings, the recordings are reflective of the UAV hover mode in windless conditions, consistent with the vertical recordings.

Recordings were taken vertically and horizontally at 5-m intervals up to a maximum distance of 120 m—the legal limit for UAV flight altitude in the United Kingdom. Three ambient background sound recordings were taken prior to the UAV recording at 5, 50 and 100 m. Each measurement was repeated three times at each distance to ensure consistency. The audio data were recorded using the Signalscope X Pro Advanced Toolset Application (version 10.8.4) from Faber Acoustical (http://faberacoustical.com/) in combination with a calibrated omnidirectional electret condenser microphone micW i437L, Class 2 - sensitivity 7.5 dBFS (94 dB SPL @ 1 kHz) [http://www.micwaudio.com]. The application was run on an Apple iPhone Xs using iOS.13.5.1. We use calibrated recordings from the microphone from 100 Hz to 20 kHz, logging audio spectrograms in 10 Hz bins via the Fast Fourier Transform (FFT) Spectrum Analyser. The total record length was 250 ms, consisting of four exponentially averaged FFT recordings of 100 ms (50% overlap). The noise floor of the measurement system was 32 dB(A).

2.2 | Audiogram data collection

The species audiograms in this paper were taken from an open portal provided by The University of Toledo, Ohio, USA (Heffner, 2020) and a portal on Marine Mammal audiograms created at the Museum für Naturkunde, Berlin, Germany (Animal Audiogram Database, 2021). Each species has a frequency range where its hearing is most sensitive. Audiograms or hearing curves, as shown in this paper, display an individual's hearing range at various frequencies. The audiograms vary in terms of design and the number of individuals measured but should be representative of the species to which the individuals belong. The audiograms were collected under laboratory conditions using either the behavioural psychophysical method or auditory brainstem response (ABR) experiments. The former relies on training animals to react to a sound using either appetitive operant conditioning—recording an animal's response elicited by sound to gain rewards of food or water (Elder, 1934; Hienz et al., 1982; Kastak & Schusterman, 1998; Kojima, 1990; Owren et al., 1988), positive reinforcement training (Schusterman, 1974) or conditioned avoidance (Flydal et al., 2001; Heffner & Heffner, 1990; Heffner et al., 2014). In behavioural psychophysical experiments, species are exposed to sound frequencies of varying amplitude. The hearing threshold is defined as the levels at which the species cease to respond (Jackson et al., 1999). In contrast, ABR does not necessitate training animals but rather measures brain activity (auditory evoked potentials—AEPs) in response to auditory stimuli—electrodes are placed on the skin to record small variations in voltage that are elicited when playing sound of varying frequency and intensity (Sohmer et al., 1991). All the audiograms in this study measured animals' hearing thresholds while varying frequencies in octave intervals.

2.3 | UAV audio processing

Recordings were analysed using the R project for statistical computing (R Core Team, 2020). We used the 10 Hz sound pressure levels (SPLs) generated by the FFT application to calculate third-octave band (TOB) levels and create power spectral density curves (PSDs) representing the frequency profile of each UAV's noise at each distance. We also binned the SPLs into octave bands to match the frequency intervals of the species audiograms, enabling an integrated analysis. Separating the frequency range into octave and TOBs is common in sound analysis to create natural groupings of individual frequencies or narrowband sounds. The bands are unequal in width, such that the upper frequency in an octave band is twice the lower band frequency and the upper frequency in a TOB is the cube root of two times the lower frequency. For example, the 1 kHz centre frequency octave and TOBs range from 710–1,420 Hz and 891–1,122 Hz, respectively, while the 16 Hz octave and TOBs range from 11–22 Hz and 14.1–17.8 Hz respectively.

To calculate the SPL at each band, we added together the 10 Hz SPLs falling within the band's frequency range. Since the sounds at separate frequencies have no correlative relationship, we binned SPLs by adding levels as incoherent sources:

$$\mathrm{SPL}_1 + \mathrm{SPL}_2 + \ldots + \mathrm{SPL}_n = 10\log_{10}\left(10^{\mathrm{SPL}_1/10} + 10^{\mathrm{SPL}_2/10} + \ldots + 10^{\mathrm{SPL}_n/10}\right). \quad (1)$$

For each TOB calculation, we also corrected for the differences between TOB bandwidths and the range of the n assigned 10 Hz SPLs:

$$\text{TOB level} = \sum_{i=1}^{n} (10\ \text{Hz SPL})_i - 10\log_{10}(10n) + 10\log_{10}(\text{TOB Bandwidth}), \quad (2)$$

where the summation is done as in Equation (1). To calculate PSDs, we subtracted $10\log_{10}(\text{TOB Bandwidth})$ from each TOB level, which is equivalent to the computation in Equation (2) without the addition of the final term.

We compiled a single ambient curve for the field site that included the minimum SPL at each 10 Hz bin from all the ambient recordings. We use the lowest magnitude recording to represent persistent ambient noise. Similarly, for each of the three UAV recordings at a given distance, we chose the lowest amplitude sound measurement at each frequency to eliminate spikes caused by transient background noise. The sound curves were trimmed to the 100–20,000 Hz range, as the sensitivity of the microphone at these frequencies below 100 Hz was insufficient. In addition, the majority of species investigated in this study do not hear well below 100 Hz. We compared the ambient and UAV recording PSDs to the sound floor PSD of the microphone, which was provided by the manufacturer, to ensure that the UAV sound was audible above the microphone.

2.4 | Integrating species audiograms with UAV recordings

All UAV recordings were weighted by the species audiograms to provide a measure of how different species perceive the sound level of each UAV based on their hearing sensitivity across the relevant frequency spectrum. The weighting was done by subtracting the species' hearing threshold from the corresponding octave-band level for each octave. Any negative values were set to 0 dB, as these indicate frequencies where the UAV SPL was below the species' hearing threshold. Weighted sound levels for all octave bands were summed to create a single, overall species-weighted sound level. Thus, the loudness of UAV d for species α at a given distance was calculated as:

$$\mathrm{dB}(\alpha)_d = \text{ioctavebands} - \sum max\left(\text{recording}_{d,i} - \text{audiogram}_{\alpha,i}, 0\right), \quad (3)$$

where the summation is done logarithmically as in Equation (1).

An advisable flight altitude for each UAV over each species was determined using the vertical species-weighted levels depicting how UAV loudness varies with altitude. The advisable altitude is not the point at which the UAV becomes inaudible to a species, as nearly all UAV models are still audible to most species even at 120 m. Rather, we calculated the point at which either the sound level is below 40 dB(species) or flying higher does not yield significant benefits in noise reduction. The 40 dB(species) threshold was chosen because 40 dB(A) LAeq is the sound floor above which sound is considered a disturbance to humans (i.e. World Health Organisation, 1999). There is no similar guideline for animals so we adopt the human threshold dB(A). In some cases, the UAV loudness at a certain altitude may not be below the threshold for a species, but the relationship between sound level and altitude has flattened such that the decrease in loudness achieved by flying higher is minimal. To calculate the altitude above which this relationship flattens, we fit a linear least-squares line through each species-weighted sound curve and iteratively removed the lowest altitude until the slope exceeded (was less negative than) −0.05 dB(species)/5 m, as shown in Figure 1. We designated the

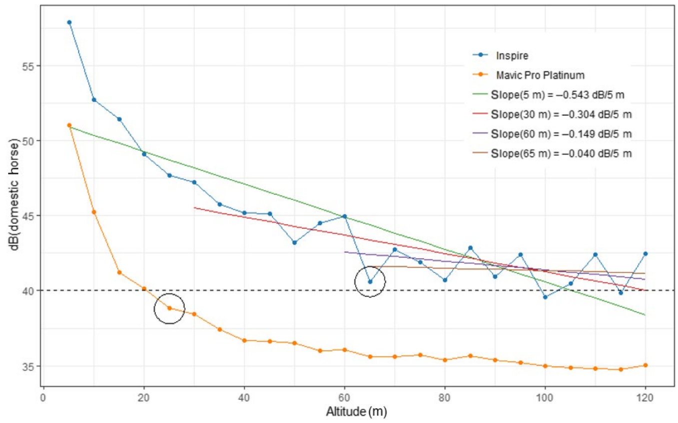

FIGURE 1 Demonstration of calculating the advisable altitudes (circled) for flying the Inspire and Mavic Pro Platinum over the domestic horse. The point where sound level no longer significantly declines with higher altitude (least-squares line slope >−0.05 dB/5 m) before the sound level is below the 40 dB(species) is circled (i.e. Inspire 65 m, Mavic Pro Platinum 25 m). In the latter example the curve has not flattened out, but the sound level (38.8 dB(domestic horse)) is below the threshold

lowest remaining altitude as the advisable altitude for that species and UAV if the UAV sound level was not already below 40 dB(species). We selected 0.05 dB (species)/5 m as the threshold based on our independent visual interpretation of where the sound curves flatten out. A sensitivity analysis confirmed that varying this threshold locally did not significantly change the advisable altitude (Figure S1).

3 | RESULTS

3.1 | The sound profile of UAV systems

Figures 2 and 3 illustrate the different sound profiles of seven commonly used commercial UAV models across the 100–20,000 Hz spectrum. The ambient background sound level was measured at 40.8 dB(A). The UAV sound signal was present above the ambient noise and the microphone noise floor over the entire frequency spectrum. Sound propagation is frequency dependent (i.e. lower frequencies propagate farther than higher frequencies). The variation between UAV systems is not consistent at all frequencies. The difference in amplitude is higher at lower frequencies, and there is more variation at short distances. As the distance increases to >100 m, the sound levels of all the UAVs converge (Figures 2 and 3) and are close to the observed ambient background sound levels. In the horizontal plane (Figure 3), sound does not propagate as far as in the vertical plane (Figure 2). The systems converge with the ambient recording at lower frequencies sooner in the horizontal plane than the vertical. Even at 120 m there is little convergence in the lower frequencies in the vertical plane, while they converge in the horizontal plane after 70 m.

3.2 | Species-weighted measurements of hearing sensitivity based on audiograms

Measurements of four different mammals' sensitivity to sound with distance from its source are shown in Figures 4 and 5. Consistent with an inverse-square law, the UAV loudness generally decreases by a constant weighted decibel value with each doubling of altitude or range. At larger distances, the decrease in noise with distance becomes negligible. In the vertical plane, the same drone is heard approximately 5 dB louder by the reindeer *Rangifer tarandus* as compared with the Indian elephant *Elephas maximus indicus* which hears approximately 10 dB louder than the California sea lion *Zalophus californianus*. Note, an increase of 10 dB is perceived by humans as a doubling in loudness.

There is significant variability in sound propagation between the vertical and horizontal plane. In the horizontal plane the Spark is largely the quietest system, while in the vertical plane, the Mavic 2 Pro or the Mavic Mini is often the quietest. The difference between how loud species hear UAV noise is higher when the UAV is flown at close range, as there is more amplitude variation over the lower frequencies (<1,000 Hz).

3.3 | Optimal flight altitude by UAV system and species

Advisable flight altitudes in Table 1 were calculated for seven UAV systems based on the relationship between noise and altitude (for further exploration see https://tinyurl.com/UAVdisturbance). The method addresses the trade-off between image resolution and minimising disturbance. The advisable altitude is not the point at which the UAV becomes inaudible. Rather, given that a UAV will be flown over a particular species, the method calculates the point at which either the loudness, weighted according to the species' hearing, is below an acceptable threshold or flying any higher will not significantly further minimise disturbance, defined as an average decrease in sound level of equal to or less than 0.05 dB(species) per additional 5 m. Unweighted advisable altitudes for each drone, calculated as if the hearing threshold at all frequencies is 0 dB, have also been included in the table and can be applied cautiously if surveying over any species for which audiograms are not available. The advisable

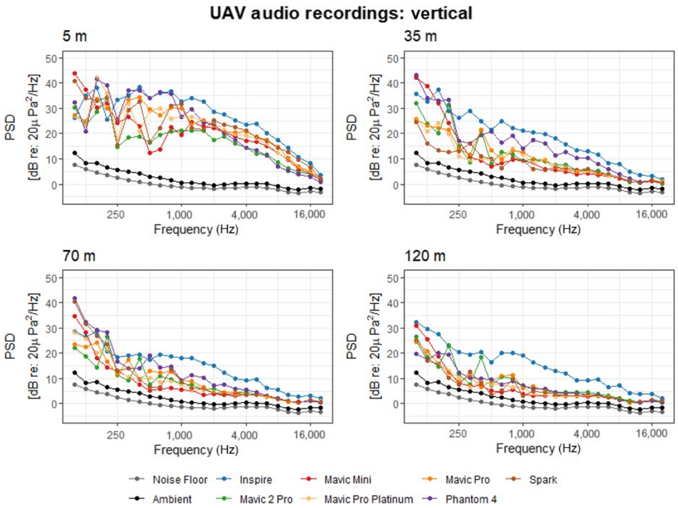

FIGURE 2 Power spectral density (PSD) curves in third-octave bins for seven UAV systems tested at four altitudes. Note the log scale *x*-axis

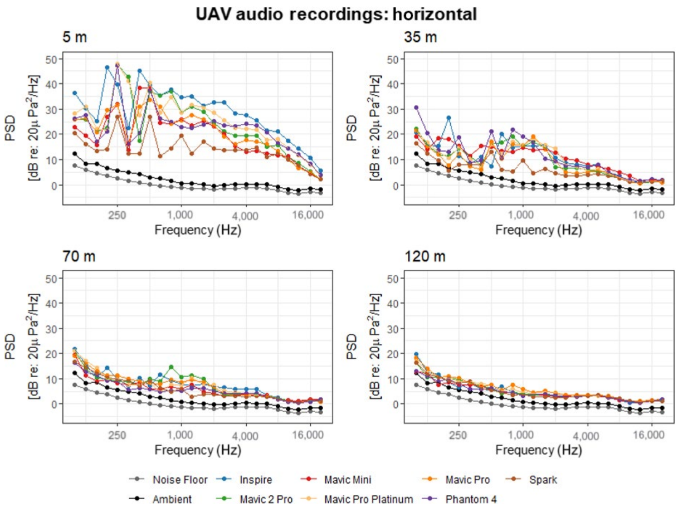

FIGURE 3 Power spectral density (PSD) curves in third-octave bins for seven UAV systems in the horizontal plane. Note the log scale *x*-axis

altitude is generally higher for louder drones, such as the Inspire or Phantom 4, as their sound profiles flatten out only at higher altitudes. For example, to meet the proposed criterion, the Phantom 4 would need to be flown at 120 m above a yellow baboon or De Brazza's monkey while the Mavic Mini could be flown as low as 35 m over these species. The calculation also depends on the hearing sensitivity of the animals. For example, we would advise flying the Inspire at 90 m over a spotted seal, but only 5 m over a harp seal. Table 1 displays the corresponding weighted sound level (dB(species)) at each advisable altitude to facilitate comparisons between different species and UAV systems.

4 | DISCUSSION

This study provides a method to calculate the minimum advisable altitude by integrating measurements of UAV sounds with species-specific hearing sensitivity. The results demonstrate that noise emitted by different UAV models varies in overall loudness and volume across the frequency spectrum. Sound propagation differs between the horizontal and vertical planes. While sound decays more rapidly with distance in the horizontal for all UAVs, the ordering of UAVs when comparing overall loudness differs between the vertical and horizontal. This is likely due to differences in how the sound

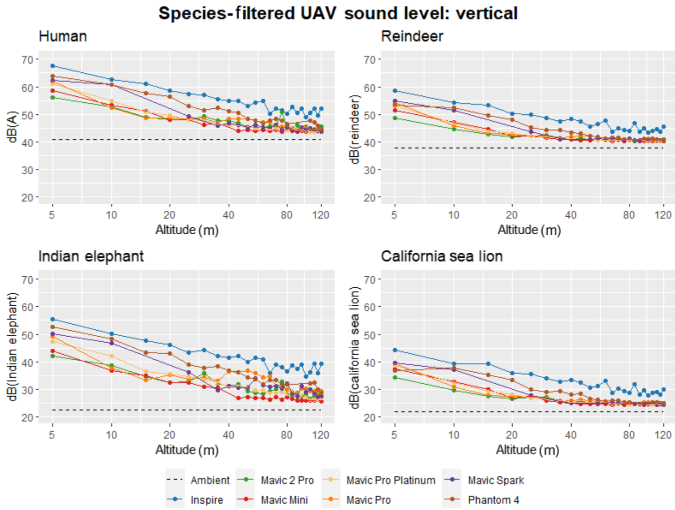

FIGURE 4 Changes with altitude of perceived noise from seven commonly used UAV systems by four mammalian species

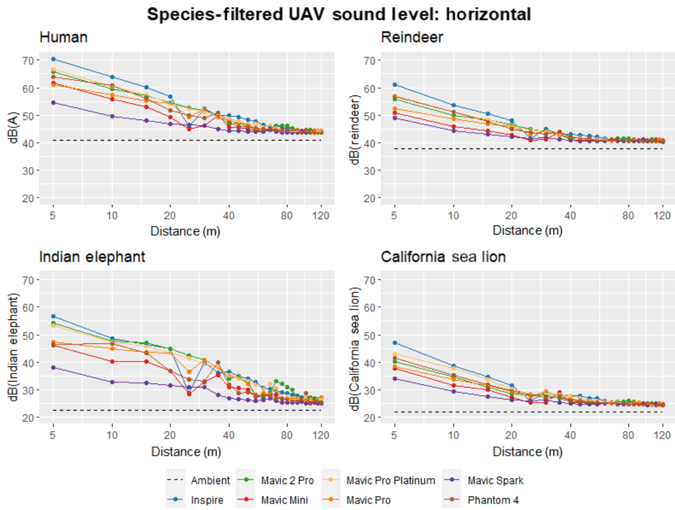

FIGURE 5 Changes with horizontal distance of perceived noise from seven commonly used UAV systems

is directed resulting from variation in propeller design. Some of the variation in sound propagation between the horizontal and vertical planes was likely due to greater attenuation from grass during the horizontal measurements. However, the reduction in noise when standing next to, compared to standing below, a UAV for a given displacement is consistent with previous studies (He et al., 2020). UAVs will be loudest when directly overhead, so we present advisable altitudes derived from only the vertical recordings, which are sufficient even if flying over species with a horizontal offset. Recent improvements in technology have enabled UAVs to operate more quietly, thus leading to a lower advisable altitude, which improves image quality and flight time. For example, the Mavic 2 Pro, despite being heavier than the Mavic Pro (907 g vs. 734 g), is consistently quieter, likely due to its low-noise propellers and newly designed chassis. This translates into substantial differences in the advisable altitudes for the two drones over some of the primates and ungulates.

The difference in the acoustic profile of UAVs is of higher relevance when flown close to the target species, and the choice of UAV system is more relevant when flying over species such as elephants, whose hearing sensitivity is higher at very low frequencies (Heffner & Heffner, 1982). UAV sound level converges in the upper frequencies; therefore, the choice of the system has less relevance when flying

TABLE 1 Advisable flight altitude (metres, upper row) and corresponding sound level (dB(species), lower row) based on drone recordings and species audiograms. Bold italics and italics indicate that the curve has levelled off at this altitude, sometimes in addition to the sound level falling below 40 dB. See Table S1 for the altitudes at which the levelling off occurs for all species, including where this point is after the sound level has decreased below 40 dB

Target species		UAV system						
		Inspire	Mavic 2 Pro	Mavic Mini	Mavic Pro	Mavic Pro Platinum	Spark	Phantom 4
Common name and species	**Classification**	**Upper rows: Advisable altitude to fly (metres) Lower rows: dB(*species*) at the advisable altitude**						
Common harbour seal (*Phoca vitulina*)	Carnivora Pinnipedia Phocidae	10 38.6	5 33.6	5 36.4	5 38.1	5 37.8	5 38.7	5 36.5
California sea lion (*Zalophus californianus*)	Carnivora Pinnipedia Otariidae	**10** 39.5	**5** 34.5	**5** 37.5	**5** 39.2	**5** 38.7	**5** 39.8	**5** 36.7
Northern fur seal (*Callorhinus ursinus*)	Carnivora Pinnipedia Otariidae	**30** 38.9	**5** 39.3	**10** 37.6	**10** 35.8	**10** 37.4	**25** 34.2	**15** 39.7
Harp seal (*Pagophilus groenlandicus*)	Carnivora Pinnipedia Phocidae	**5** 34.2	**5** 23.1	**5** 25.9	**5** 28.9	**5** 27.9	**5** 29.7	**5** 29
Spotted seal (*Phoca largha*)	Carnivora Pinnipedia Phocidae	***90*** *54.2*	***65*** *50*	***45*** *49.4*	***105*** *49.3*	***80*** *49.2*	***85*** *49.6*	***120*** *50.4*
Sea Otter (*Enhydra lutris*)	Carnivora Mustelidae	***65*** *45.6*	***35*** *43.1*	***30*** *43.1*	***35*** *43.1*	***35*** *43.1*	***35*** *43.1*	***60*** *42.9*
Rhesus macaque (*Macaca mulatta*)	Primates Cercopithecidae	***65*** *42.4*	**35** 39.8	***30*** *39.5*	**35** 39.8	**35** 39.7	***35*** *39.3*	**60** 39.5
Japanese macaque (*Macaca fuscata*)	Primates Cercopithecidae	***65*** *47*	***80*** *42.9*	***45*** *42.3*	***105*** *42.7*	***100*** *42.3*	***85*** *42.5*	***120*** *43.5*
Vervet monkey (*Chlorocebus pygerythrus*)	Primates Cercopithecidae	***65*** *47.7*	***75*** *42.4*	***60*** *40.6*	***85*** *42*	***100*** *40.6*	***115*** *40.7*	***120*** *42.1*
De Brazza's monkey (*Cercopithecus neglectus*)	Primates Cercopithecidae	***65*** *43.7*	***50*** *40.1*	***35*** *40.2*	***70*** *40.6*	***65*** *39.9*	***85*** *39.8*	***120*** *40*
Yellow baboon (*Papio cynocephalus*)	Primates Cercopithecidae	***65*** *47.3*	***50*** *43.9*	***35*** *44.5*	***70*** *44*	***95*** *43.4*	***85*** *43.4*	***120*** *43.9*
Chimpanzee (*Pan troglodytes*)	Primates Homininae	***65*** *43.4*	**50** 39.2	***30*** *39.9*	***70*** 39.6	**40** 39.7	***35*** *39.5*	**75** 39.8
Reindeer (*Rangifer tarandus*)	Cetartiodactyla Cervidae	***65*** *43.8*	***35*** *41.4*	***30*** *41.4*	***60*** *41.4*	***35*** *41.4*	***35*** *41.4*	***75*** *41*
White-tailed deer (*Odocoileus virginianus*)	Cetartiodactyla Cervidae	***65*** *46.9*	***35*** *44.5*	***30*** *44.6*	***60*** *44.2*	***35*** *44.4*	***35*** *44.5*	***75*** *44.1*
Domestic goat (*Capra hircus*)	Cetartiodactyla Bovidae	***90*** *55.6*	***75*** *50.9*	***55*** *49.9*	***105*** *49.9*	***95*** *49.6*	***110*** *49.8*	***120*** *50.9*
Domestic cattle (*Bos Taurus*)	Cetartiodactyla Bovidae	***65*** *54.8*	***35*** *52.3*	***30*** *52.4*	***50*** *52.2*	***35*** *52.2*	***35*** *52.4*	***75*** *51.9*
Alpaca (*Vicugna pacos*)	Cetartiodactyla Camelidae	***65*** *45.1*	***40*** *42.7*	***30*** *42.6*	***65*** *42.4*	***40*** *42.1*	***35*** *42.6*	***75*** *42.3*
Indian elephant (*Elephas maximus*)	Proboscidea Elephantidae	**50** 39.9	**10** 38.8	**10** 36.7	**10** 37.8	**15** 36.5	**25** 36.2	**25** 39

(Continues)

TABLE 1 (Continued)

Target species		UAV system						
		Inspire	Mavic 2 Pro	Mavic Mini	Mavic Pro	Mavic Pro Platinum	Spark	Phantom 4
Common name and species	**Classification**	**Upper rows: Advisable altitude to fly (metres) Lower rows: dB(*species*) at the advisable altitude**						
Domestic horse (*Equus caballus*)	Perissodactyla Equidae	***65***	**15**	**20**	**25**	**25**	**25**	**50**
		40.6	38.7	38.2	38.8	38.8	39.7	38.7
Unweighted		***60***	***105***	***45***	***105***	***80***	***75***	***45***
		57.5	*47.3*	*46.4*	*47.3*	*47.2*	*46.6*	*57.6*

over species with greater high frequency sensitivity (e.g. Felidae and Carnivora species that hunt mainly by sound). The choice of UAV system is especially important for species whose hearing sensitivity is highest between 1.5 and 6 kHz, as UAV sound is concentrated in this bandwidth. As shown in the audiograms, some species hear well across the entire frequency spectrum, while the hearing sensitivity of other species is concentrated at particular frequencies. In addition, some species have an aversion to specific audio frequencies when the sound resembles other noises. For example, elephants are highly sensitive to bee sound, thus UAV sound which is similar to bee sound has been used to move elephants away from cropland (King et al., 2007). To reduce general UAV disturbance to elephants, our results show it would be advisable to use a Mavic Pro, Mavic 2 Pro or Mavic Mini. However, to specifically avoid acoustic similarity to bees, the Mavic Pro Platinum would be optimal. While it is louder overall, it is not as loud at specific bee frequencies (i.e. 200–500 Hz; Islam et al., 2017). Thus, using this method, aversion to specific audio frequencies by certain species can also be factored into UAV study design.

While weather conditions, particularly wind, influence sound propagation, testing varying environmental conditions was outside the scope of this study. However, windless conditions, as well as the open field environment, are both favourable for sound propagation. Consequently, our recommendations are conservative and can be applied across different weather conditions and vegetated surfaces. While windy conditions may require the rotor speed to increase as the UAV hovers, the sound of the wind typically obscures the additional sound. Less UAV sound reaches wildlife in highly vegetated areas as compared with open field, as trees and other vegetation impede sound propagation (Tarrero et al., 2008). However, if flying over less porous surfaces, such as ice, additional altitude may be needed to offset the reduction in sound absorbance.

As auditory sensitivity and sound perception has been studied in few wild mammals, it is difficult to extrapolate these findings within taxonomic groups. Certain species have hearing sensitivity concentrated at the extremes, such as ultrasonic sound perception in bats and small rodents and infrasound reception for elephants (Heffner & Heffner, 1982). However, there are not enough data to assess whether there is a natural similarity in auditory sensitivity within taxonomic groups, hence it is not possible to say to which close taxonomic relatives these audiograms can be extrapolated. Future research could use allometry to predict approximate auditory sensitivity from body mass (which applies for some species) or use analysis of the frequency composition and modulation of species' natural calls to inform predictions of noise perception, as vocalisation ranges are similar to ranges of perception. For species not covered in these guidelines and for whom audiograms, allometry or call data cannot be acquired, we have included advisable altitudes in Table 1 based on unweighted calculations of sound levels. These altitudes should be used cautiously, as the unweighted sound level for all UAVs still exceeds 40 dB at the point where the sound decay flattens out. In these situations, we recommend using a quiet drone, such as the Mavic Mini or Spark, when possible.

The method developed in this paper is applicable to assessing other sources of anthrophony. While herd structure, social dominance dynamics and mating strategies that rely on auditory cues have evolved over millennia, anthrophony is comparatively recent and is increasing in both terrestrial and marine habitats. During the last 50 years, low-frequency noise from ships has increased 32-fold along major routes (Miksis-Olds & Nichols, 2016). This is despite the fact that regarding marine operations is more highly regulated than land-based activities. The U.S. Marine Mammal Protection Act categorises marine noise pollution into harassment levels A and B, yet there is little comparable legislation for land-based activities. To put effective anthrophony regulation in place, we need to understand more about the hearing sensitivity of mammals and the impact of noise. This paper presents a method to quantify sources of anthrophony based on individual species' auditory sensitivity and highlights the need for more reliable audiograms for more species.

The method presented here would benefit from additional in-situ behavioural data to assess whether flying at the lowest advisable flight altitude still causes a change in behaviour, due to auditory or visual disturbance. If so, observations from UAVs may not be appropriate. Gathering longitudinal physiological data such as stress hormones or behavioural data to understand responses to UAV flights is useful to comprehensively understand disturbance but it is time intensive and costly to collect. This research is only concerned with auditory disturbance but visual disturbance is also important. Visual disturbance is particularly relevant for species who are aerially predated upon (Barasona et al., 2014; Mesquita et al., 2021). Thus, areas of future recommended research include assessing visual and auditory disturbance from UAVs and comparing disturbance from UAV surveys with other wildlife monitoring methods, such as line transect surveys carried out on foot or by vehicle.

Disturbance caused by UAV is an animal welfare concern and impedes scientific data collection through provoking aberrant behaviour. Information on appropriate altitudes at which to fly over different species will enable UAV technology to be used more reliably and responsibly for both scientific data collection and wildlife conservation purposes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

I.D. conceived and designed the study methodology with guidance from H.K.; Preparation of audiograms carried out by T.C. and I.D.; UAV sound data collection carried out by I.D. with support from ERT and C.L.; Processing the collected data in R Studio carried out by M.P.S.; I.D. led the writing of the manuscript; C.P., D.W.M. and T.W. edited the manuscript and all authors contributed critically to drafts and approved the final manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code are provided in an open repository https://doi.org/10.5281/zenodo.5119659 and Oxford University Research Archive (https://doi.org/10.5287/bodleian:6gxAJamnj).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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III

Using very-high-resolution satellite imagery and deep learning to detect and count African elephants in heterogeneous landscapes

Remote Sensing in Ecology and Conservation
Open Access

ORIGINAL RESEARCH

Using very-high-resolution satellite imagery and deep learning to detect and count African elephants in heterogeneous landscapes

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Abstract

Satellites allow large-scale surveys to be conducted in short time periods with repeat surveys possible at intervals of <24 h. Very-high-resolution satellite imagery has been successfully used to detect and count a number of wildlife species in open, homogeneous landscapes and seascapes where target animals have a strong contrast with their environment. However, no research to date has detected animals in complex heterogeneous environments or detected elephants from space using very-high-resolution satellite imagery and deep learning. In this study, we apply a Convolution Neural Network (CNN) model to automatically detect and count African elephants in a woodland savanna ecosystem in South Africa. We use WorldView-3 and 4 satellite data –the highest resolution satellite imagery commercially available. We train and test the model on 11 images from 2014 to 2019. We compare the performance accuracy of the CNN against human accuracy. Additionally, we apply the model on a coarser resolution satellite image (GeoEye-1) captured in Kenya, without any additional training data, to test if the algorithm can generalize to an elephant population outside of the training area. Our results show that the CNN performs with high accuracy, comparable to human detection capabilities. The detection accuracy (i.e., F2 score) of the CNN models was 0.78 in heterogeneous areas and 0.73 in homogenous areas. This compares with the detection accuracy of the human labels with an averaged F2 score 0.77 in heterogeneous areas and 0.80 in homogenous areas. The CNN model can generalize to detect elephants in a different geographical location and from a lower resolution satellite. Our study demonstrates the feasibility of applying state-of-the-art satellite remote sensing and deep learning technologies for detecting and counting African elephants in heterogeneous landscapes. The study showcases the feasibility of using high resolution satellite imagery as a promising new wildlife surveying technique. Through creation of a customized training dataset and application of a Convolutional Neural Network, we have automated the detection of elephants in satellite imagery with accuracy as high as human detection capabilities. The success of the model to detect elephants outside of the training data site demonstrates the generalizability of the technique.

Introduction

The planet is in the geological era of the Anthropocene, during which human activity is the driving force of change. Many wildlife species are under threat across their geographical range as we are currently undergoing the sixth-mass extinction (Barnosky et al., 2014; Cardinale, 2012; Skogen et al., 2018). Reliable, accurate, and up-to-date data on wildlife numbers is essential to monitor population fluctuations and identify causes of decline. Various methods are used for conducting population counts, including, but not limited to line transect surveys (Emmanuel et al., 2017), dung and track counts (Barnes et al., 1997), bio-acoustic monitoring (Shiu et al., 2014), camera trap grids (Smit et al., 2017) and aerial surveys (Schlossberg et al., 2016), among others.

Satellite remote sensing has recently emerged as a new viable monitoring technique for detecting wildlife. It has been used to successfully identify and count several wildlife species in open, homogeneous landscapes and seascapes. The benefits of this monitoring technique are numerous; large spatial extents can be covered in short time periods making repeat surveys and reassessments possible at short intervals. For example, the satellite used in this study, Worldview-3 has an average revisit time of less than one day. It can collect up to 680,000 square kilometres every 24 h. Satellite images are captured over large areas in one shot so issues with double counting and miscounts are largely eliminated. Satellite remote sensing is unobtrusive as it requires no human presence, eliminating the risk of disturbing the species being surveyed. Disturbance remains a key concern in other surveying techniques (Mulero-Pazmany et al., 2017). Image acquisition is automated and less logistically complicated compared with traditional aerial surveys (Stapleton et al., 2014) and setting up camera trap grids or audio loggers. Censuses can be carried out without concern for human safety providing an ability to survey previously inaccessible areas. For example, in the case of the Emperor penguin, new colony locations were detected in a pan-continental survey of the Antarctic coast (Abileah, 2002; Smit et al., 2017). Additionally, cross border areas can be surveyed without requiring multiple national civil aviation permissions.

Detecting wild animals in satellite imagery is influenced by body size, background complexity and contrast between species and surrounding habitat. Seascapes provide a uniform high contrast background context against which whales have been identified in known breeding, calving and feeding grounds (Abileah, 2002; Cubaynes et al., 2018; Fretwell et al., 2014) and flamingos have been identified on a lake (Sasamal et al., 2008). Spectrally uniform rocky outcrops and ice have been used to identify several marine species, including Emperor and Adelie penguins (Barber-Meyer et al., 2007; Fretwell et al., 2012; Fretwell & Trathan, 2009; LaRue et al., 2014; Lynch & LaRue, 2014), Elephant and Weddell seals (LaRue et al., 2011; McMahon et al., 2014), Masked Boobies (Hughes et al., 2011) and Albatross (Fretwell et al., 2017). Several Arctic species have been identified against snow using shadow and body contrast for detection (e.g. Polar bears LaRue & Stapleton, 2018; LaRue et al., 2017; LaRue et al., 2015; Stapleton et al., 2014) and muskoxen (LaRue et al., 2017)). On the African continent only two studies have detected mammals (wildebeest and zebra) using satellite imagery in open savannah (Xue et al., 2017; Yang et al., 2014), both in homogeneous monochrome environments. No study has yet, to the best of our knowledge, detected species in complex heterogeneous landscapes from space.

Various methods have been used to detect species in satellite imagery. The majority of studies have manually counted species in imagery using several observers for cross-validation. However, manual methods are unfeasible if large areas are surveyed, as counting is labour and time intensive and counts tend to be error-prone (Hollings et al., 2018). Several studies have relied on environmental proxies and indirect ecological signs of animal presence e.g. burrows (Löffler & Margules, 1980), mounds (Velasco, 2009), changes in vegetation from nest signatures (Hughes et al., 2011) and faecal stains in the case of penguins (Barber-Meyer et al., 2007; Fretwell et al., 2012; Fretwell & Trathan, 2009; LaRue et al., 2014; Lynch & LaRue, 2014; Lynch et al., 2012). Image differencing is a technique where satellite images are captured in the same location at different times. This technique is used for environmental change detection (Lu et al., 2010) e.g. deforestation and land use change (Kiage et al., 2007; Kusimi, 2008; Meng & Meentemeyer, 2011), identification of fire (Carvalho Júnior et al., 2015; Meng & Meentemeyer, 2011), droughts (Buma & Lee, 2019; Rulinda et al., 2010) or floods (Oliveira et al., 2019; Thito et al., 2016). Three studies used short-time image differencing to detect polar bears from space (LaRue & Stapleton, 2018; LaRue et al., 2015; Stapleton et al., 2014). Image differencing is possible in cases where multi-temporal imagery is available, and species can be differentiated from static objects. e.g. rocks. Images can be acquired via targeted satellite tasking on specific days; however, this is more costly than using archive imagery. Cloud cover, environmental variability and changing sea states can impede ground visibility which is problematic when image differencing and tasking is used.

Several studies have applied a form of supervised or semi-supervised classification approaches to detect species in satellite imagery. One form of image segmentation using semi-supervised classification is thresholding method. Pixel values are classified relative to a set of threshold values that distinguish species from background. Thresholding method does not make use of geometric information but rather relies on spectral signatures (pixel value combinations).Thresholding method is reliant on the human classifier to set accurate thresholds which is helped by familiarity with the species and environment (Xue et al., 2017). This technique is effective in date data on wildlife numbers is essential to monitor population fluctuations and identify causes of decline. Various methods are used for conducting population counts, including, but not limited to line transect surveys (Emmanuel et al., 2017), dung and track counts (Barnes et al., 1997), bio-acoustic monitoring (Shiu et al., 2014), camera trap grids (Smit et al., 2017) and aerial surveys (Schlossberg et al., 2016), among others.

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The introduction of Convolutional Neural Networks (CNN) in machine learning has revolutionized the field of computer vision since 2012 (Krizhevsky et al., 2012). Machine learning has become a new essential tool used by ecologists to detect wildlife in imagery e.g. camera trap images, aerial survey images and unmanned aerial vehicle (UAV) images (Bruijning et al., 2018; Chabot & Bird, 2015; Ferreira et al., 2020; Petersen et al., 2019; Torney et al., 2019; Weinstein, 2018). However, automated detection of wildlife from satellite imagery is still in its infancy. To the best of our knowledge only three species have been detected in satellite imagery using deep learning: albatross (Bowler et al., 2019), whales (Borowicz et al., 2019; Guirado et al., 2019) and pack-ice seals (Gonçalves et al., 2020). Object detection applications are now easier to develop than ever before. High-performance off-the-shelf solutions have made machine learning solutions accessible to non-specialists. These techniques can now leverage massive image datasets e.g. ImageNet (>14 million images across 20,000 classes)obtaining significant performance improvements compared to previous methods based on manually engineered features (Russakovsky et al., 2015). A Convolutional Neural Network (CNN) is a deep learning artificial neural network architecture that has been extensively used for object detection and recognition in recent years. The 'deep' stems from the use of multiple layers in the network. In this study, we test whether it is possible to detect the world's largest terrestrial mammal – the African elephant – using deep learning via a CNN.

The population of African elephants (*Loxodonta africana*) has plummeted over the last century due to poaching, retaliatory killing from crop raiding and habitat fragmentation (Gara, 2016; Poulsen et al., 2017; Sibanda & Murwira, 2012). To ensure conservation is achieved accurate monitoring is vital. Inaccurate counts can result in misallocation of scarce conservation resources and misunderstanding population trends. Existing techniques are prone to miscounting. The most common survey technique for elephant populations in savannah environments is aerial counts from manned aircraft (Schlossberg et al., 2016). Aerial surveys are conducted either as total counts – flying closely spaced transects, or sample counts, covering 5-20% of an area and extrapolating to a larger area. Several studies have shown that observers on aerial surveys often miscount due to fatigue and visibility issues resulting in over-estimates (Caughley et al., 1976; Jachmann, 2002; Koneff et al., 2008). Aerial surveys can be costly, logistically challenging in terms of finding suitable runways and refuelling stops and time consuming in terms of getting appropriate permissions. This is particularly relevant in cross-border areas where multiple national permissions are required. Remotely sensing elephants using satellite imagery and automating detection via deep learning may provide a novel avenue for surveying while mitigating several of the challenges outlined above.

In this study, we investigate the feasibility of using very-high-resolution satellite imagery to detect wildlife species in heterogenous environments with deep learning. To test this, we use a population in Addo Elephant National Park, South Africa where herds move between open savannah habitat and closed heterogeneous woodland and thicket.

Methods

Study Site

Addo Elephant National Park in South Africa was chosen as the study site. It provides a spectrally complex heterogeneous background with a high concentration of elephants. The park is the third largest park in South Africa at 1640 km^2. Different areas of the park have been sectioned off for conservation purposes- elephants were identified in the Main Camp section of the park surrounding Hapoor Dam (Figure 1).The Main Camp is a combination of dense shrubland and low forest e.g.porkbush (*Portulcariaafra)*, White milkwood *(Sideroxyloninerme)*, Cape leadwort(*Plumbago auriculate*) and open grassland (Kakembo et al., 2015; Tambling et al., 2012). Over six hundred elephants move between these habitats (Du Toit & O'Connor, 2014; Wilgen et al., 2016). Elephants cover themselves in mud to cool down and adopt a range of postures when foraging, playing, sleeping (Soltis et al., 2016; Wickler & Seibt, 1997) so their shape and colour is continually changing. The background environment is also changing as they move between open savannah and woodland and take shelter under trees in the mid-day sun.

The park has rainfall year-round (Fullman et al., 2017) and four seasons can be broadly delineated as early wet season (Oct -Dec), late wet season (Jan-March), early dry (Apr-Jun) and late dry season (July-Sept) (Du Toit & O'Connor, 2014; Wilgen et al., 2016).To ensure a representative and diverse sample of elephants in the park we include training and test labels from images captured in different seasons and years (Table 1).

Dataset generation and satellite image preprocessing

WorldView-3 and WorldView-4 are the highest resolution satellite imagery commercially available. They provide

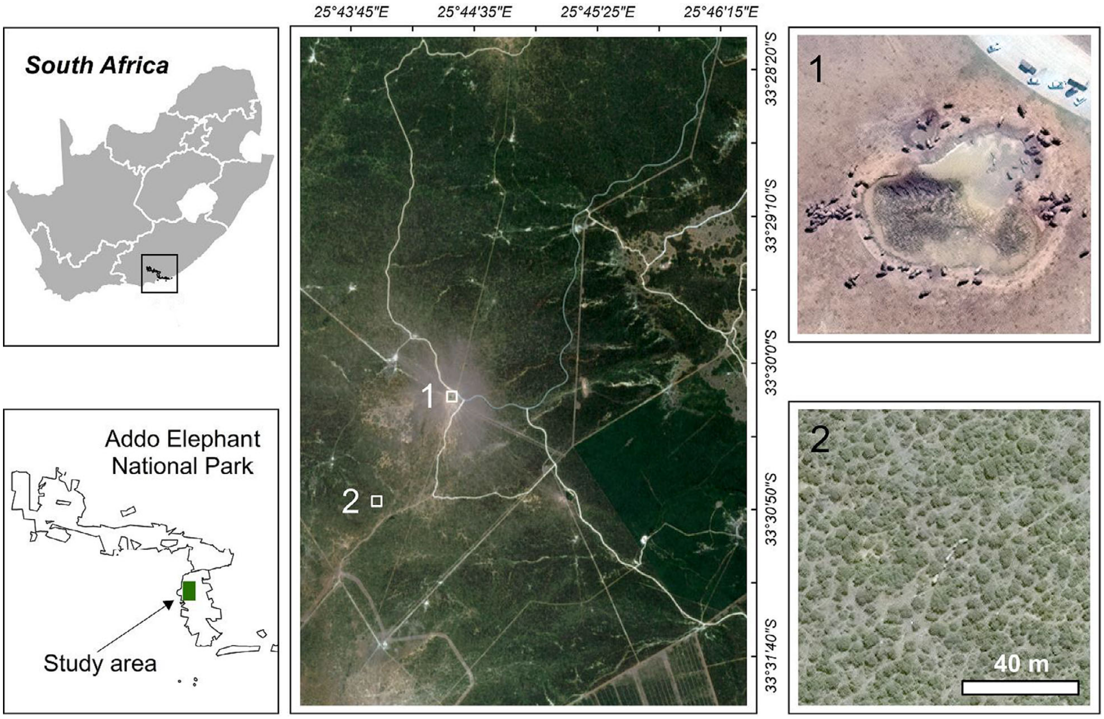

FIGURE 1. Location of the study area in -Addo Elephant National Park, South Africa. Two example WorldView-3 images showing 1) Elephants in open homogeneous area around Hapoor Dam, 2) Elephants in heterogenous woodland and thicket area. Satellite image (c) 2020 Maxar Technologies

TABLE 1. List of satellite images used in the training and test dataset

Date of acquisition	Satellite	Elephant labels in training dataset	Elephant labels in validation dataset	Elephant labels in test dataset
01_12_2014	WV3	197	52	10
29_01_2016	WV3	178	9	11
10_02_2016	WV3	259	19	32
03_04_2017	WV3	26	19	5
22_11_2017	WV4	10	0	0
11_01_2018	WV4	117	0	23
27_03_2018	WV4	236	16	24
08_10_2018	WV4	119	1	59
20_01_2019	WV3	22	0	0
11_08_2009	GeoEye−1	0	0	32

imagery at 31 cm resolution - WorldView-4 is now out of action but two years of archive imagery is available. The image archive for all WorldView 3 & 4 satellite images from Maxar Technologies (formerly DigitalGlobe) was searched via the Secure Watch Platform [https://www.digitalglobe.com/products/securewatch]. We restricted the search to images that contain less than 20% cloud cover and acquired less than 25% off-nadir (degree off centre of image captured). We selected eleven images that met these specifications between 2014 and 2019. The satellite is on a sun synchronous orbital path, so each satellite image of the study area is captured between 10.10 and 10.45 am local time ensuring regular illumination conditions. The bright morning light improves image clarity as elephants gather at water holes in the morning which makes them easy to identify (Figure 1).

Each image was downloaded in two formats: orthorectified images in natural colour and orthorectified panchromatic image. We processed the images using a pan-sharpening algorithm from ERDAS IMAGINE software package (ERDAS, Inc., Atlanta, GA, USA) Pan-sharpening is an automatic image fusion process that uses the multispectral bands red (620–750 nm), green (495–570 nm), blue (450–495 nm) at 1.24 m resolution and the higher resolution panchromatic band at 31 cm to produce a high-resolution multispectral image. We tested several pan-sharpening algorithms using visual inspection method- the

Gram-Schmidt pan-sharpening algorithm provided the cleanest visual result in terms of spectral and spatial fidelity and was applied to all images. This is consistent with prior quantitative assessment of pan-sharpening algorithms that found Gram-Schmidt provides the highest spectral and spatial fidelity for identification of wildlife (Witharana et al., 2016). The satellite images were converted so that pixel values were in the range of [0,255] and the images were sliced into 600x600 pixel sub images to make them compatible with the deep learning software.

Labelling training data in satellite images

The images were visually scanned for elephants before sub-setting into smaller areas where we identified congregations of elephants. In total, 1125 elephants were identified in the training image dataset. To ensure training labels are representative of elephants at different times, images were selected for different seasons and years in both closed i.e. dense shrubland and forest. and open areas of the park i.e. grassland and bare land. Images were labelled by defining bounding boxes around each individual elephant using the graphical image annotation tool Labelling [https://github.com/tzutalin/labelImg] (Tzutalin, 2015) shown in Figure 2.

The baseline we deem as the true number of elephants is a labelled dataset doubled screened by two annotators – an Ecologist and Machine Learning Scientist. Any ambiguous labels that were not identified by both annotators were removed. We use the method of comparing the accuracy of detections from human volunteer annotators and CNN performance against this baseline control count (Ginosar et al., 2014; Torney et al., 2019).The same test images used to evaluate CNN performance were sent to 51 human volunteer annotators. The images were labelled by the volunteers using the VGG Annotation Tool [http://www.robots.ox.ac.uk/~vgg/software/via/] (Dutta & Zisserman, 2019). Volunteer annotators represent a cross-section of machine learning scientists, biologists, general public and park rangers who work with elephants in Southern Africa. The labellers vary in terms of computer literacy and familiarity with elephant behaviour and habitat preference. Each participant was provided with a detailed training sheet and an example of how elephants look in satellite images prior to labelling. The experiment involving human participants was approved by the University of Oxford CUREC Ethical Committee [R64699].

Training and validating the Convolutional Neural Network model

A CNN is a feed-forward neural network designed to process large-scale images by considering their local and global characteristics (LeCun et al., 2015). A neural network is typically comprised of multiple layers connected by a set of learnable weights and biases (Romero et al., 2013). Convolutional layers represent a set of filters, each able to identify a particular feature in the image. These filters are fed small image patches whilst they scan across the image and generate feature maps for analysis by the next layer. The CNN comprises an alternating sequence of convolutional and pooling layers. Pooling layers are used to reduce the dimensionality of the feature maps to improve computational efficiency. Nonlinear activations are stacked between convolutional layers to enrich their representational power (Strigl et al., 2010). The last layer of the network is fully connected and performs classification (Schmidhuber, 2015). Convolutional neural networks have become a key tool in image classification. They are now comparable to human performance in a number of challenging image classification tasks e.g. face verification, various medical imaging tasks (Gulshan et al., 2016; Olczak et al., 2017).

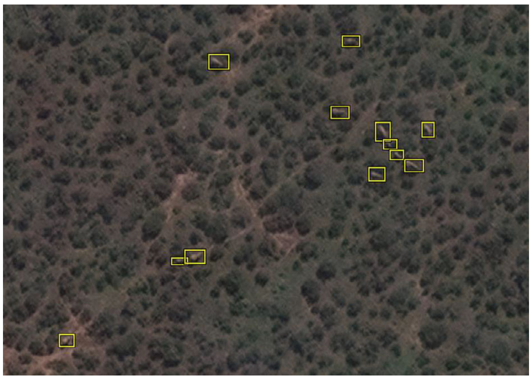

FIGURE 2. Example of elephant labels in a heterogenous area, Addo Elephant National Park, South Africa. Satellite image (c) 2020 Maxar Technologies

We used the TensorFlow Object Detection API [https://github.com/tensorflow/models/tree/master/research/object_detection] to build our model (Huang et al., 2017). This API provides implementations of different deep learning object detection algorithms. In a preliminary assessment of the models available, we selected the model referred to as faster_rcnn_inception_resnet_v2_atrous_coco as it provided the best result and it was used for all the experiments presented. This model is a Faster Region CNN (RCNN) model – after layers that are used to extract features there is a subbranch to propose regions that may contain objects and a subbranch that predicts the final object class and bounding box for each of these regions (Ren et al., 2017). The model we used has an Inception

ResNet (Szegedy et al., 2017) backbone – this is the underlying CNN that is used for feature extraction. We used the model pretrained on the Common Objects in Context (COCO) dataset for object detection [https://cocodataset.org/] (Lin, 2014). We used default values for hyperparameters of this model from the API.

Training a CNN requires images to be split into training, validation and test sets. In total, 188 sub images from nine different satellite images were used for training. These training images contain 1270 elephant labels of which 1125 are unique elephants. There is an overlap of 50 pixels between sub images, when elephants appear at the edge of one sub image the overlap ensures they appear in whole on the neighbouring sub image. Twelve sub images containing 116 elephant labels were left out as a validation dataset. The validation dataset is used to tune the hyperparameters, to define the confidence threshold (above which predictions from the model are counted as detections) and to identify the optimal length of CNN training (see Figure 3).

Test dataset

The test dataset used to test the CNN against human annotator performance contains 164 elephants across seven different satellite images. These images do not overlap with any of the training or validation subimages. The test subimages cover both heterogeneous and homogeneous areas of the park from different seasons and years (see Table 1).

In addition, an image from the Maasai Mara in Kenya was used to test the generalizability of the CNN for broader image conditions - no additional training data were included for this test. The image comes from Geoeye-1 a lower resolution satellite (41 cm) compared to the images used for training which come from Worldview 3 & 4 (31 cm).The GeoEye-1 image was captured at about 10:30 am local time on 11th August 2009. This image allowed us to test the generalizability of our algorithm to a different environment and satellite.

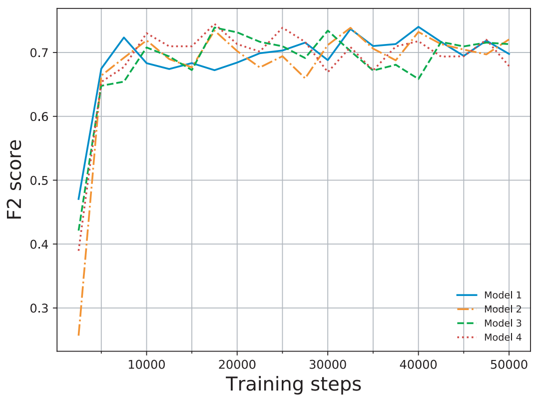

FIGURE 3. F2 score obtained by each of the four models considered over training steps on the validation dataset. All models converged during the first 50 000 training steps

Accuracy assessment

We compare the accuracy of detections from the human volunteer annotators and CNN against our count which we deem as the baseline i.e. the true number of elephants in the images. To calculate the deviation from this baseline we generate an F2 score.

Object detection performance is usually evaluated by *precision* and *recall*:

$$\text{Precision} = \frac{\text{TP}}{\text{TP}+\text{FP}} \text{ and Recall} = \frac{\text{TP}}{\text{TP}+\text{FN}}$$

where TP stands for true positives (correctly predicted elephants), FP stands for false positives (predicted elephants that are not actually elephants, also called false detections), FN– false negatives (elephants that are not detected by the model, also called missed detections).

The CNN gives an output in the form of bounding boxes, the same format we use for the training labels. We count any intersection between predicted and true bounding boxes as a true positive (i.e. the intersection over union threshold used to determine correct predictions was set to 0). Human volunteer annotators provide point detections for elephants. If these point detections were inside true bounding boxes, they were counted as true positives.

In precision and recall both types of errors – false positives and false negatives – are weighted equally. However, as it is more time consuming for a human annotator to check an entire image for missing elephants (false negatives) as compared with reviewing detected elephants and eliminating false positives we decided to use an F2 (F_β- with $\beta = 2$) score. The F2 combines precision and recall in such a way that more emphasis is put on false negatives (Dascalu & David, 2019; Hordiiuk et al., 2019):

$$F_\beta = \left(1+\beta^2\right)\frac{\text{Precision}*\text{Recall}}{\beta^2*\text{Precision}+\text{Recall}} = \frac{\left(1+\beta^2\right)\text{TP}}{\left(1+\beta^2\right)\text{TP}+\beta^2\text{FN}+\text{FP}},$$

which for $\beta = 2$ is equivalent to

$$F_2 = 5\frac{\text{Precision}*\text{Recall}}{4*\text{Precision}+\text{Recall}} = \frac{5\text{TP}}{5\text{TP}+4\text{FN}+\text{FP}}$$

Performance of object detection algorithms are often measured by *average precision* (Huang et al., 2017) i.e. the area under a precision-recall curve that is obtained by varying the threshold of the confidence score. This threshold determines which of the predicted bounding boxes are considered as final detections. Average precision allows comparison between different algorithms without the need to specify this threshold. Since our goal was to compare the algorithm performance with human performance and humans did not provide a confidence score for their detections, we could not use this metric.

The training process is stochastic due to the stochastic gradient descent algorithm used for optimization of neural network weights. We ran the CNN four times to explore how stable the algorithm output is with respect to the stochastic training process. Neural networks models are commonly run as many times as time and availability of computational resources allow. Each of the models ran for 50,000 training steps (i.e. the number of times the weights were updated by the gradient descent algorithm) on the training dataset and the performance was evaluated on the validation dataset every 2500 training steps (Figure 3). All the models reached a plateau in F2 score after around 10,000 training steps on the validation dataset. For each of the models we chose the weights obtained at the number of training steps that gave the best performance on the validation dataset.

RESULTS

Human detection accuracy compared with CNN performance

The results show that overall for the CNN in both homogeneous & heterogeneous are as we received an F2 score of 0.75.The CNN performed better in heterogeneous areas with an F2 score of 0.778 compared to 0.73 in homogeneous areas. The human annotator median F2 score was 0.78 and performance was better in homogeneous areas – 0.80 compared to 0.766 in heterogeneous areas. These results show that the CNN performed with high comparable accuracy compared to human detection capabilities. Visualization of one of the model detections is shown in Figure 4.

Testing detection under different image conditions

To test the applicability of the trained CNN model on an elephant population outside of our study area we test, without further training, on a known elephant population in the Maasai Mara in Kenya (Figure 5). The image covers 0.3 km^2 in which 32 elephants were identified. The CNN managed to detect more than half the elephants in this image (18 true positives) and the resulting F2 score was 0.57. Figure 5 provides visualization of some example CNN detections.

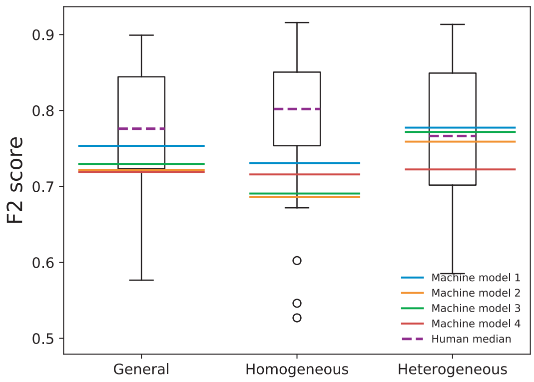

FIGURE 4. CNN detections: The images on the left are the raw images and images on the right are CNN detections (green boxes) and ground truth labels (red boxes). Satellite image (c) 2020 Maxar Technologies

Discussion

Our results demonstrate, for the first time, that it is possible to automate detection of African elephants in very-high-resolution satellite imagery in both heterogeneous and homogeneous backgrounds using deep learning. We have automated the detection of elephants with as high accuracy as human detection capabilities. For a number of species remote sensing via satellite imagery is already a viable monitoring technique. However, the resolution required to identify individuals is not yet available for the vast majority of species but can be used to identify aggregations or environmental signs of presence, for example, guano stain, shadow, mounds from burrows and nests (Barber-Meyer et al., 2007; Fretwell et al., 2012; Fretwell & Trathan, 2009; Hughes et al., 2011; LaRue et al., 2014; Löffler & Margules, 1980; Lynch & LaRue, 2014; Velasco, 2009). Fortunately, a new constellation of six satellites from Maxar, Worldview Legion, will launch in 2021 that will provide imagery for the same location more than 15 times per day at 31 cm resolution. This constellation will have a tropical circle mid-inclined orbit, rather than polar orbit and will broaden the range of species that can be detected and increase detection area.

Previous studies have largely focused on marine species due both to their inaccessibility via other monitoring techniques and the high contrast of their bodies against mainly homogenous backgrounds (Barber-Meyer et al., 2007; Bowler et al., 2019; Cubaynes et al., 2018; Fretwell et al., 2017; Fretwell et al., 2014; Guirado et al., 2019; LaRue et al., 2011; LaRue & Stapleton, 2018; LaRue et al., 2015; McMahon et al., 2014; Stapleton et al., 2014). The advantages of using satellite imagery are numerous. Large

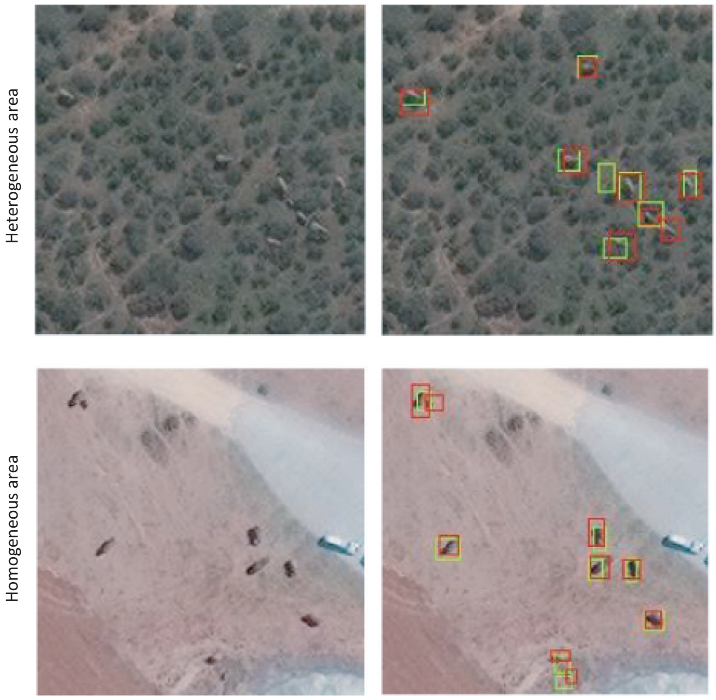

FIGURE 5. Example of CNN detections in Maasai Mara, Kenya from Geoeye-1 Satellite. Raw images on left and images with CNN detections (green boxes) and ground truth labels (red boxes) on right. Satellite image (c)2020 Maxar Technologies

areas can be covered in one pass, reducing the risk of double counting and eliminating the need for repeat surveys at short intervals. Satellite monitoring is an unobtrusive technique requiring no ground presence, and thus eliminating the risk of disturbing species, or of concern for human safety during data collection. Previously inaccessible areas are rendered accessible, and cross-border areas – often crucial to conservation planning - can be surveyed without the often time-consuming and bureaucratically problematic requirements of terrestrial permits.

One challenge with satellite monitoring is the high cost of commercial satellite imagery. Worldview-3 costs $17.50 per km^2 for archive imagery and tasking new imagery costs $27.50 per km^2, with a minimum order of 100 km^2(2020 pricing). Another key challenge is processing the large quantity of imagery generated. However, expediting identification of species by automating detection can allow for large-scale application of satellite-based wildlife surveying (LaRue et al., 2015; Torney et al., 2019). A detection process that would formally have taken weeks can thus be completed in a matter of hours. Furthermore, observer variability means errors in human-labelled datasets are inconsistently biased while in contrast, false negatives and false positives in deep learning algorithms are consistent and can be rectified by systematically improving models. The use of Convolution Neural Networks (CNN) to automate detection of wildlife has been successfully applied on imagery from a variety sensors including, UAVs (Bowley et al., 2018; Christie et al., 2016; Gray et al., 2018; Kellenberger et al., 2019; Kellenberger et al., 2018; Mairea et al., 2013), manned aircraft (Borowicz et al., 2019; Eikelboom et al., 2019; Maire et al., 2015; Sharma et al.,; Torney et al., 2019), multibeam imaging sonar (Toshihiro et al., 2019) and camera trap imagery (Miao et al., 2019; Schneider et al., 2020; Schneider et al.,; Willi et al., 2018). To the best of our knowledge, only three studies have applied a CNN to satellite imagery in the case of albatross (Bowler et al., 2019), whales (Borowicz et al., 2019; Guirado et al., 2019) and pack-ice seals (Gonçalves et al., 2020).

Automating detection is becoming easier as off-the-shelf object detection tools are increasingly accessible to non-experts; however, the biggest obstacle is obtaining sufficiently large training datasets. Crowdsourced labelling platforms, e.g. Zooniverse [https://www.zooniverse.org/], Amazon Mechanical Turk [https://www.mturk.com/] can help in the creation of these bespoke training datasets using the 'Wisdom of the crowd' (Kao et al., 2018; Mierswa, 2016).

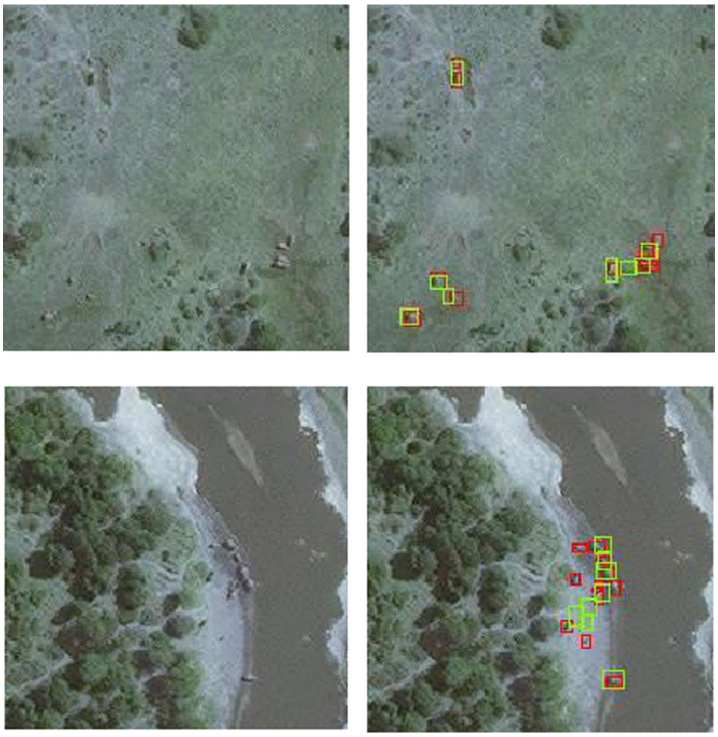

FIGURE 6. Results of human annotation compared with CNN detection for all images (general) and in homogenous and heterogeneous areas. The boxplots show the human results (circles represent outliers); lines are results from the four different CNN models

Our study shows the applicability of this monitoring technique to the case of the African Elephant and demonstrate, for the first time, that it is possible to automate detection of African elephants in very-high-resolution satellite imagery in both heterogeneous and homogeneous backgrounds using deep learning. Not only is the detection accuracy we achieve for elephants as high as that of humans, but there is less variation in the consistency of detection for the CNN compared to human detection performance (as shown in Figure 6).

In addition, we show that it is possible to generalize detection to elephant populations outside of the site of training data. The generalizability of the CNN is promising, as a small amount of training data from this locality or satellite would further increase accuracy. Elephant calves were accurately detected, despite their absence in the training dataset.

Areas of future research to expand this technique include testing whether performance improvements for detecting elephants can be achieved by including the near infrared band and testing to discover for which other species this is already a viable monitoring technique. In our study site vegetation cover was not heavy enough to hinder identification but this is a common challenge when using aerial surveying techniques and would be an obstacle for forest elephants or elephants in other sites.

More broadly, deep learning methods for detecting small objects can be further improved (Cao et al., 2019; Pang et al., 2019) and large training datasets containing images of wildlife from an aerial perspective should be developed. If satellite monitoring is applied at scale then developing methods to ensure standardized and occasional ground-truthing will be required to ensure image interpretation is accurate (LaRue et al., 2017). Using high resolution satellite imagery as a wildlife surveying tool will inevitably increase in the future as image resolution improves and costs fall. Developing automated detection tools to enable larger scale application of this wildlife monitoring technique is highly valuable as satellite image surveying capabilities expand.

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Authors' contributions

I.D. conceived the idea of the paper and designed the methodology with oversight from T.W.; I.D. acquired the image data, processed, analysed and labelled the satellite images; O.I. ran the code in Tensorflow with input from S.R.; I.D. and O.I. organized and analysed the human labels. I.D. led the writing of the manuscript with input from O.I., S.R., D.M. & T.W. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

We are not at liberty to share the raw satellite imagery due to the restrictions defined in the contract with Maxar Technologies and the European Space Agency under which the image grants were awarded.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Image list.
Appendix S2. Comparison of human and machine results on individual images.

IV

A satellite perspective on the movement of African elephants in relation to nomadic pastoralists

A satellite perspective on the movement of African elephants in relation to nomadic pastoralists

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Abstract

The African savannah ecosystem is populated by nomadic pastoralists who herd livestock in the day, as they forage over the landscape, and corral them at night in temporary enclosures, called bomas, to protect them. The number and distribution of bomas in the savannah are important from an ecological perspective and may have a significant impact on wildlife movements. However, no studies have yet examined the spatial-temporal dynamics of bomas and their relationship to wildlife. Here, using very high-resolution satellite imagery and a two-phase approach, we quantify changes in boma distribution and density across an area of 3377 km² in the Laikipia-Samburu ecosystem of northern Kenya between 2011 and 2019. To assess wildlife movement in relation to bomas we use a GPS dataset on elephant movement from 27 collared matriarchs representing herds of 9-15, covering 4,722 GPS fixes over 31 months between 2018 and 2020. Our results show a more than 46% increase in the total number of human-built structures between 2011 and 2019, the majority of which are bomas. This represents a 21.9% increase in human-modified land area. Elephants readily adapt their foraging habits and itineraries in habitats shared with humans, who are also nomadic in space and time. Assessing night-day activity ratio we find elephants move more nocturnally when in closer proximity to bomas. This temporal separation means elephants avoid the times humans are active in and around bomas while still accessing required resources - water and forage. Using daily travel distance as a metric, we show elephants move further in closer proximity to bomas which is likely linked to the need to travel between forage patches. This conclusion supports previous findings where human activity is shown to a have greater impact on animal space use compared to habitat modification. This paper is the first proof of concept that satellite remote sensing can be used to monitor pastoralists and elephants and offers fine-scale insight into the movement strategies of elephants in a shared habitat.

Introduction

Sixty-five percent of the African continent is composed of savannah [1]. Over millennia, the savannah ecosystem has been populated by nomadic pastoralists [2], termed as such, as they relocate seasonally, moving with their livestock to fresh pasture when land no longer provides adequate grazing [3]. Pastoralists guard livestock during the day as they forage, and corral them at night in temporary enclosures that exclude nocturnal predators. In sub-Saharan Africa these enclosures, often called bomas (as in this paper), range from 50-100 m in diameter, protected by fences built largely from acacia thorn trees (*Vachellia tortilis*, formerly *Acacia tortilis*) and associated shrubs [4-6]. Bomas can be occupied for several months or years before being abandoned when the adjacent grazing ground is not suitable for grazing or the dung build up and parasite load become detrimental to livestock [7, 8]. The establishment and abandonment of bomas redistribute organic matter by shifting soil and foliar nutrients due to the patterns of livestock grazing and dung deposition, thus altering plant community composition [7, 9-12] and maintaining the functional heterogeneity of the ecosystem [12-15].

The number and distribution of bomas in the savannah is ecologically significant; however, no ground-based or remotely sensed dataset exists that shows the number, size or duration of use of these structures at a landscape scale. Previous studies have relied on series of aerial photographs covering <50 bomas [7]. The commonly used Human Footprint Index (HFI) is an index of human pressure in the landscape [16, 17] often used to assess wildlife movement in relation to human presence [18-23]. Bomas are not factored into this index, despite being an important feature in rural savannah landscapes in much of sub-Saharan Africa. It is not easy to measure changes in number or distribution of bomas using freely available satellite imagery due to limitations in spatial resolution (>1 m), the small size of structures, and their temporary nature. While many studies examining the rising number of pastoralists in the savannah have stressed the negative effects of livestock, attributing degradation of arid and semi-arid lands to overuse by pastoralists [24-26], understanding long-term ecological impacts requires nuance and evidence. Without data on the density and distribution of bomas, the long-term changes taking place cannot be studied at the landscape scale.

An estimated 50 to 70% of the Earth's land surface is now modified by human activity [27, 28], which is significantly influencing wildlife populations, particularly their long-distance movements [29, 30]. The African savannah harbours the highest density and greatest diversity of ungulate herbivores in the world [31, 32] but the fauna is currently undergoing a severe decline in its populations of mega-herbivores (weighing more than 1000 kg) - in particular African bush elephants (*Loxodonta africana*) [33, 34]. This decline is part of the broader human-driven sixth extinction event the planet is undergoing - as discernible from the fossil record [35-38]. Elephant populations are threatened by habitat fragmentation, illegal hunting for ivory and retaliatory killing for crop raiding [39, 40]. Concurrently the human population is expanding. Africa has the highest population growth rate of any continent [41] with an associated rise in numbers of domesticated livestock [42].

Elephants are the largest herbivore in the savannah and are important ecological engineers [43]. They maintain open woodland by debarking and knocking down trees, opening the landscape for grasses that attracts other grazers [44, 45]. Where elephants share foraging areas with livestock, they reverse at least some of the negative impact of livestock grazing on soil chemistry (i.e., depletion of carbon, nitrogen and phosphorus (CNP)) as dung deposition – among other mechanisms – replenishes the depleted C and N in the soil [46]. Dung deposits from livestock and wild herbivores support distinctive, nutrient-rich plant communities that persist as long-term hotspots of highly fertilized soil in and around boma sites [4, 9, 47, 48]. Studies using soil sampling and dung pile counts have shown that former boma sites contain elevated foliar nitrogen, phosphorus, and potassium indices compared to reference plots [9, 10, 12, 13, 49].

Shifts in wildlife movement in response to human presence are context- and taxon- specific, driven by the cost-benefit of sharing space and resources [43]. Movement strategies are determined by animals' survival risk and availability of forage, mates, water, predation risk, and competition for resources [32, 50]. Similar to other African ungulates, elephants exhibit antipredator behaviour in response to humans [51]. In areas where there has been heavy poaching, elephants increase walking speed [52], move more at night and have lower tortuosity (increased path straightness) [52, 53]. Elephants can distinguish between ethnic groups recognising which humans cause a threat and which do not [54], thus if not perceived as a threat, the presence of certain human may not be avoided. Elephants exhibit high variability in resource selection and high plasticity in both herd and individual movement over-time [55] indicating a capacity to adjust movement in response to a changing environment. However, mechanisms driving the movement of elephants in a landscape dominated by nomadic pastoralists remains poorly understood, particularly on a large spatial scale.

This study aims to quantify the number and distribution of bomas over a large landscape in the Laikipia-Samburu ecosystem of northern Kenya and investigate its impact on elephant movement using satellite remote sensing techniques. Specifically, we seek to address the following two questions: 1) what are the changes in the distribution and density of bomas between 2011 and 2019, and 2) how do elephants' daily movement patterns relate to the presence of bomas across the landscape?

Materials and Methods

Study area

The analysis focuses on a pilot study area in the Laikipia-Samburu ecosystem delineated by the availability of concurrently collected adjacent Worldview-2 multispectral satellite images. Imagery covers 3377 km^2 clipped to an area where cloud cover is minimal in both 2011 and 2019 (Figure 1). The Laikipia-Samburu ecosystem is adjacent to the Rift Valley in north-central Kenya; it is a semi-arid system encompassing a wide range of habitats characterised by more mesic highlands in the south to hot, dry lowlands in the north [56]. The landscape is a mixture of national parks, commercial ranches, and areas supporting pastoral and/or sedentary subsistence production [57].

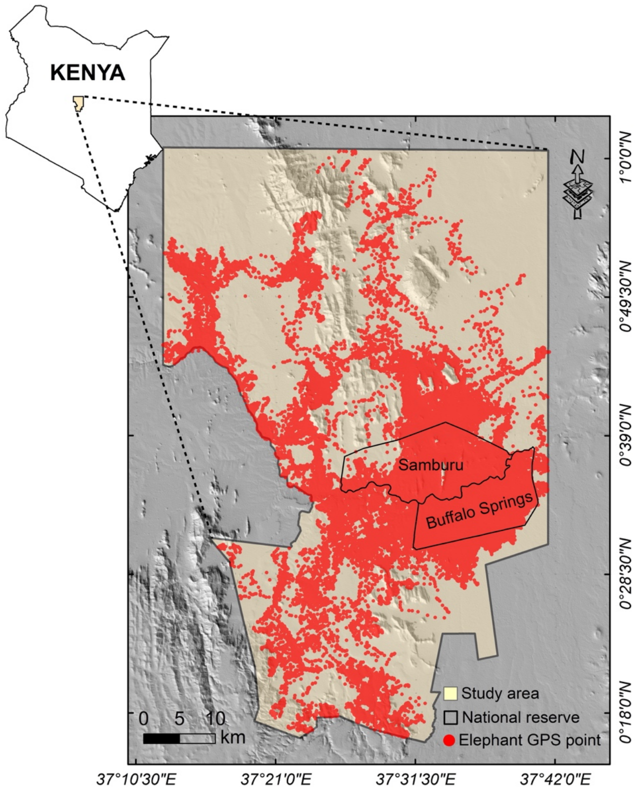

Figure 1: *Study area in the Laikipia-Samburu ecosystem of northern Kenya and the spatial distribution of elephant GPS tracking data (red dots, n = 4,722) representing 27 collared adult female elephants collected between 2018 and 2020. The location of two national reserves (Samburu and Buffalo Springs) in the study area are also highlighted.*

Digitising bomas from satellite imagery and change detection

The analysis relies on two sets of four adjacent images from the wet season acquired in 2011 (6th April & 9th May) and 2019 (11th May & 7th June). The spatial resolution varies between 48-54 cm and images are captured in the early morning between 08.03 - 08.17 local time. The dimensions of the human footprint (predominantly bomas) and water points were digitised in the imagery in ArcGIS Pro over a period of eight months. Active bomas are differentiated from inactive bomas based upon visibility and intactness of the fence line (Figure 2). All bomas labelled as inactive have a partial fence line that is visible but has largely decomposed. Other categories include permanent buildings and fenced agricultural areas and which often include bomas.

To understand changes in the number of bomas and distribution of other human-built structures between 2011 and 2019, a change detection analysis was implemented to compare the number and distribution of bomas. The study area was gridded using a grid size of 0.25 km^2 (500 x 500

m) and the density of bomas (defined as number of bomas and other human-built structures per pixel) and area covered by bomas was calculated for each year.

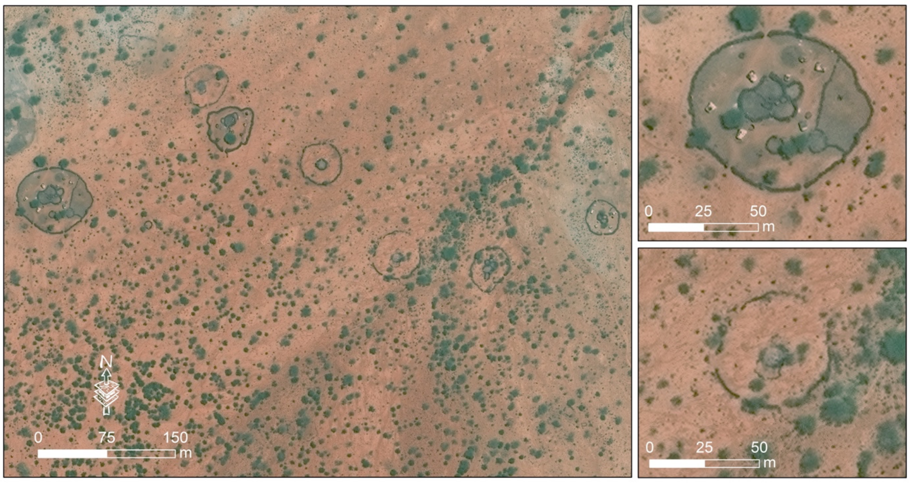

Figure 2*: Example of bomas visible in Worldview-2 imagery. On the left combination of active and inactive bomas; on the right example of active boma (top image) and inactive boma (bottom image). Satellite image (c) 2020 Maxar Technologies*

GPS tracking data and calculation of movement metrics of elephants

The wild elephant population in the Laikipia-Samburu ecosystem lives in close proximity to humans, primarily on communal and private land; less than 2% of the ecosystem is government-protected national parks [57]. It is the second largest elephant population in Kenya (approx. 8500 elephants) and is continuous and freely intermixing, with several distinct but overlapping subpopulations [58]. Elephants have a matriarchal herd structure, with GPS fixes from collared adult females representing approximate locations of 9-15 individuals [45]. Tracking data from 27 collared female elephants within the study area were analysed, one year prior to and after the 2019 image acquisition covering January 2018 - July 2020 (31 months). Single bull elephants were not included in our analyses because they disperse from the herd at maturity and have different resource requirements and different movement strategies from herds. GPS fixes representing biologically implausible movements were removed using a speed-filter of 9 km/h, consistent with previous approaches [55, 59, 60].

To describe the movements of elephants in response to the bomas on the landscape, two metrics were calculated: the daily travel distance and the night-day activity ratio (see below). The timescales for the movement metrics are selected with consideration of the spatial extent and resolution of data in the study area, considering the biological process of interest - negotiating human-modified landscapes. Daily movements within the home range are reflective of short-term space and resource requirements and provide an important indicator of how animals use the environment [61]. The two metrics used capture complementary aspects of elephant space use, the daily travel distance elucidates energetic budgets and the night-day activity ratio describes temporal activity patterns. Both parameters have strong theoretical links to accommodating human presence on the landscape.

There is the minimal variation in sunlight hours across the year at this equatorial site, so night and day are defined as being of equal duration starting at 18.00 and 06.00 h. Travel distance is defined as the sum of straight-line displacements (SLD) between sequential fixes over the course of 24 hours (beginning at 06.00 h) or each 12-hour period in the case of the night-day activity ratio. The night-day activity ratio is calculated as the total night travel distance/total day travel distance and is equivalent to the metric average speed used in previous studies [53]. Distances estimated from SLD represent the minimum necessary to explain the displacement between points, and are sensitive to the sampling schedule, therefore periods of higher frequency sampling (15- and 30-min fix rates) were resampled to the most common fix rate of hourly, and days missing more than two fixes were excluded. Although SLD is likely to underestimate true travel distance [62, 63], a consistent fix-rate and the exclusion of days with missing locations ensures comparability between collared matriarchs to allow examination of population-level variation. Only days where all GPS fixes fall within the study area were included, generating a final sample size of 4,722 elephant-days from 27 GPS-collared adult females.

Environmental variables

Several important spatial covariates that influence elephant movement are included in the movement models which are commonly use in movement studies of this nature. These include variables that represent ecological productivity, habitat types, availability of water, elevation, rainfall, and land-surface temperature. Habitat type and ecological productivity are represented by a land cover layer [64] and Normalised Difference Vegetation Index (NDVI) layer using Sentinel-2 satellite data from the European Space Agency, both at 20-metre resolution. The NDVI layer is from 2019 and the land cover data is from 2016 based on 1 year of Sentinel-2A observations from December 2015 to December 2016 [64]. Elevation is included via a 30 metre Digital Elevation Model (DEM) from the shuttle radar topography mission (SRTM) [65]. Rivers and seasonal water points were digitised from the Worldview-2 imagery (48-54 cm resolution) to describe availability of water. To quantify weather variables that may influence elephant movement, we used precipitation data (mm/month) from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) 0.05° spatial resolution
[32] and 2m air temperature from the ERA5-Land monthly average data at 0.01° resolution [66]. Averages of the covariates sampled under the 24 GPS points used in the movement metrics were used to create variables for the models. For a full summary of layers and processing steps, and how model variables were generated see Supplementary material 1.

Statistical analysis

To assess the relationships between bomas and elephant movement, two linear mixed-effects models were implemented—one for each of our movement metrics—using the *lme4* package [67] in R version 4.0.2 [68] with elephant ID included as a random intercept to account for baseline differences in the average response, and multiple observations per individual.

Our response variables for the two models, the daily travel distance and the night-day activity ratio, are modelled as a function of the spatial covariates described in Appendix S1: season, average distance to boma, elevation, average productivity, average distance to water, proportion of wooded savannah, forest, and average monthly temperature. Proportion of open savannah was excluded from the model as it was strongly related to wooded savannah (correlation coefficient -0.87, see Figure S1 in Appendix S1 for correlation matrix of all included covariates). The full model structures include all spatial covariates and an interaction term between distance to boma and season, to allow for potential variation in elephant response to humans because of surface water availability in different seasons. Support for the inclusion of terms in a final model was assessed via likelihood ratio tests comparing the full model with nested models via single term deletions. The final models were inspected for evidence of collinearity using the performance package [69] and model residuals were visually checked to identify any major violations of model assumptions.

Results

1. Changes in the distribution and density of boma and other human-built structures

There has been an increase in the number of human-built structures and the area of land occupied by humans in the savannah. Bomas are the most numerous structures in the landscape (Table 1) and are increasing at a faster rate than other structures. The ratio of bomas to permanent buildings increased by nearly 10% from 3.2:1 to 3.5:1 while the ratio of area coverage of bomas to buildings increased by 16.6%, from 8.1:1 to 9.4:1. Other human-built structures include permanent buildings and fenced agricultural areas which often include bomas. There was a more than 46% increase in the total number of human-built structures between 2011 and 2019, the majority of which are bomas. The average size of bomas increased from 36 m diameter in 2011 to 50 m in 2019. The area of land covered by structures has increased 13.53 km^2 representing a 21.8% increase in human-modified land, covering approximately an additional 0.8% of the landscape.

Table 1: *Number and total area of boma and human-built structures over the study area in 2011 and 2019*

Designation	Structures 2011	Structures 2019	Area km^2 2011	Area km^2 2019
Active bomas	4,521	7,359	12.74	18.72
Inactive bomas	5,473	7,678	12.5	15.71
Total bomas	**9,994**	**15,037**	**25.11**	**34.01**
Permanent building	3,054	4,202	3.1	3.6
Fenced agricultural area	940	1,194	33.82	42.94
Total structures	**13,988**	**20,433**	**62.03**	**75.56**

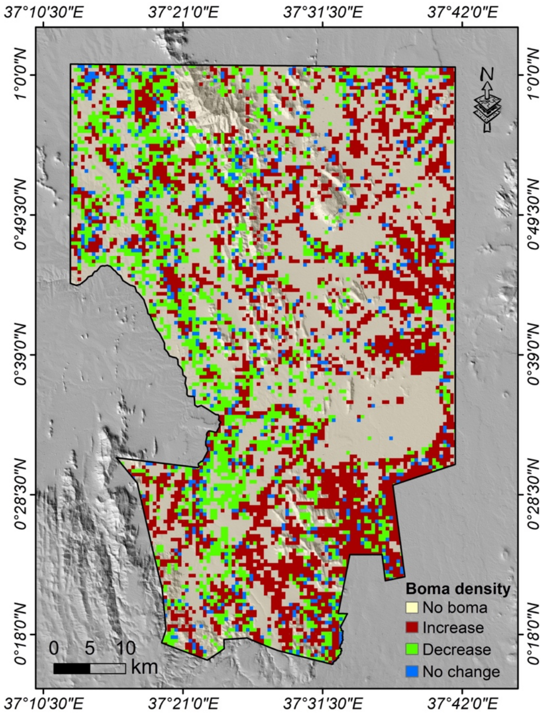

Figure 3. *Map showing changes in the density of bomas and other human-built structures (the majority of which are bomas) between 2011 and 2019. Grid size is 0.25 km² (500 x 500 m)*

Between 2011-2019, there has been a significant change in the locations of bomas. Few bomas remain active over the entire eight-year period. Of the 4,521 active bomas in 2011, less than a third are classed as active in 2019. Although they could have been re-occupied and abandoned in the intervening years, very few active bomas in 2011 have bomas re-established in an overlapping area in 2019 (598). The rate of disappearance of remotely sensed recently active bomas is high - only 24% of bomas labelled in the 2011 images are visible in 2019. While the number of bomas re-established on former sites in this eight-year period is small, the proximity of inactive to active bomas in 2019 is high; new bomas are built near former boma sites.

Table 2: *Change in the number of active and inactive bomas between 2011 and 2019 and the number not visible in 2011 but present in 2019*

2011	2019	Number
Active bomas	Still active	1,430
	Inactive	856
	No longer visible	2,235
Inactive bomas	Still inactive	889
	Active	598
	No longer visible	3,986

Not visible in 2011	Active	5,331
	Inactive	5,933

2. **Relationship between elephant movement and distance to bomas**

The model used for the night-day activity ratio includes season, elevation, distance to water, temperature, and distance to boma. Rainy season (vs dry) had a negative effect on predicted night-day activity ratio values i.e., animals became less nocturnal with increasing values, whereas elevation, distance to water and temperature had a positive effect i.e., animals were predicted to, on average, be more nocturnal with increasing values (see Appendix S1). There was support for the inclusion of an interaction term between season and distance to boma ($\chi2(1)=$ 10.56, p=0.0012). Female-led herds became more nocturnal on days when in closer proximity to bomas ($\chi2(1)=$ 81.57, p=< 0.0001; LRT statistic for main effect without interaction term), with this effect being more pronounced in the dry season (Figure 4, panel A).

The daily travel distance model includes season, elevation, average near difference vegetation index (measure of productivity), distance to water, proportion of time elephants spend in wooded savannah and forest, temperature, and distance to boma. Rainy season (vs dry), distance to water and proportion in forest had a positive effect on travel distance, while elevation, temperature, average productivity, and proportion in wooded savannah had a negative effect (Appendix S1). There was no evidence for substantial multicollinearity in either of our final models, with all terms producing VIF values <2, other than the terms involved in an interaction which still produced low values <5. Full model summaries, plots for each covariate and support for inclusion of terms from likelihood ratio tests are presented in Appendix S1.

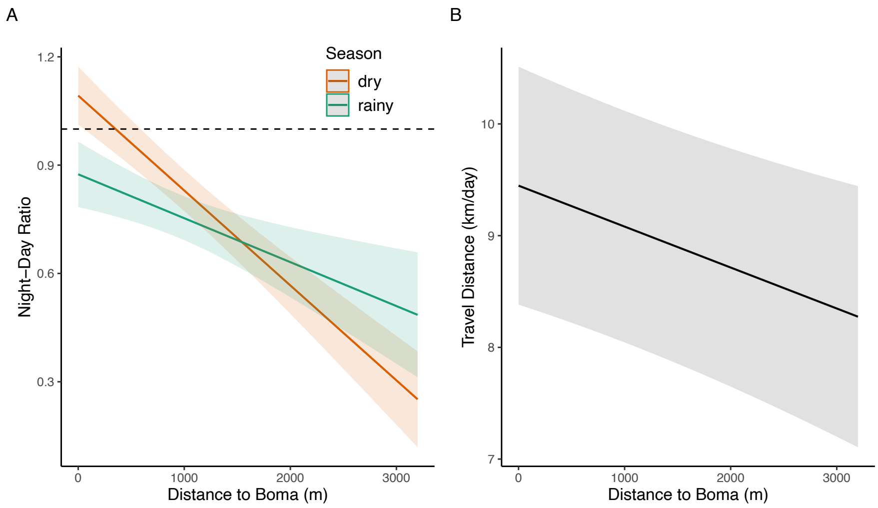

Figure 4: *Predicted values from two linear mixed-effects models describing female elephant movement metrics as a function of their average daily distance to bomas in the study area. (A) shows the ratio of nocturnal to diurnal travel distance, with increasing values representing greater distance travelled at night compared the day; (B) shows the total daily travel distance.*

The lines and associated confidence intervals were generated using the ggeffects package and represent predicted values for the response across the range of observed values for distance to boma holding the non-focal variables constant i.e., marginal effects.

Discussion

Spatial and temporal dynamics of bomas

This study is the first methodological proof of concept to demonstrate the application of using satellite remote sensing to monitor pastoralist movement at a landscape scale. The density, distribution, and relocation of bomas can be tracked using a two-phase approach. In our study site there has been a more than 46% increase in human-built structures, including bomas from 2011-19, covering an additional 13.53 km^2 of the landscape and representing a 21.9% increase in human-modified land. This finding reflects the broader global trend of an expanding human footprint and associated rise in livestock numbers [70].

Quantifying active vs. inactive bomas between 2011-19 shows that few bomas remain in the same location over an eight-year period. The dynamic movement of bomas mean positive influences from moderate grazing on plant productivity and plant diversity are spread across the landscape [71]. The last decade has been characterised by high climate variability, reduced and erratic rainfall and unpredictable availability of water and forage resources for pastoralists and livestock. Frequent movement can help to buffer livelihoods against these effects and mitigate the impact of increased environmental insecurity.

Most bomas digitised in 2011 were no longer visible in 2019. In contrast to permanent man-made structures, bomas are only temporarily visible, discernible by the intact or decomposing fence-line which leaves a short-term footprint on the landscape. While the ecological impacts from abandoned bomas are long-term, it takes time for the glade effect to become visible. Previous study from aerial photographs show that succession is slow and resettlement of sites occurs only after 20–25 years [10]. Less than a third of the bomas visible in 2011 were visible in 2019 and in the timescale of this study, few bomas are re-established in an overlapping area, although many were in close proximity. Pastoralists are becoming more numerous, and they shift bomas short distances to avoid manure pileup and build-up of parasite load which can lead to fungal infection in hoofs.

This study demonstrates the feasibility of monitoring bomas using satellite imagery, which can improve tracking of landscape change in African savannah environments. Current data layers showing human presence are limited by coarse spatial and temporal resolution. Human Footprint Index (HFI) is a commonly used metric to assess the impact of the human footprint in rural landscapes. This data layer was created in 2009. The metric combines eight variables derived from remote sensing and ground survey (including: population density, electric infrastructure, built environment, cropland, pastureland, roads, railways, and navigable waterways) to provide an index of human pressure in the landscape [16, 17]. The HFI index is often used to assess wildlife movement in relation to human presence [18-23] but it has a resolution of 1 km and is over a decade old. Many wild animals decide on foraging excursions at a smaller spatial scale than 1 km and the human population has increased in many landscapes since 2009 [72].

In the African savannah, the dominant human-built infrastructure is often temporary structures (i.e., bomas) rather than permanent buildings, as shown in this study. Thus, the use of HFI in these landscapes is limited, as bomas are not captured in the index. High spatial resolution imagery (<1m) required to identify such structures is only available from commercial providers. Access to this imagery is currently limited by high cost and narrow spatial coverage of the Earth surface compared to freely available imagery from state-run space programmes (e.g., Landsat from NASA and the Sentinels from the European Space Agency). However, as costs fall and new constellations come online (e.g., Worldview Legion & Pleiades Neo constellations launched in 2021) increased spatial and temporal image resolution will be available.

One limitation with this study is the reliability of differentiating between active and inactive bomas. From ground impressions, it is possible to see inactive bomas of varying ages, i.e., circles of shortgrass, but these cannot be reliably identified, and it is not clear how long-ago abandonment occurred so the focus of the study is on active and recently abandoned bomas – identified by the decomposition of the fence line (Figure 2). The rate of visible disappearance is also influenced by image quality and rainfall in the intervening years between image capture. Without significant ground-truthing, the magnitude of false positives and negatives in the dataset is unclear, but the large sample size (15,037 bomas in 2019) enables us to be confident in the observed trends.

Relationship between human-built structures and elephant movement

The results demonstrate that African elephants adapt their foraging excursions to the location of bomas, moving more nocturnally and traveling greater daily distances when in closer proximity to bomas. Spatial and temporal separation from humans is a risk-avoidance strategy of many animals [51, 52, 73]. Increased nocturnal activity when in closer proximity to bomas can be interpreted as a strategy that enables coexistence. As pastoralists and elephants rely on the same resources, in terms of forage and water, this time-sharing strategy may be optimal to ensure long-term access to required resources. For example, previous studies in the same ecosystem have shown that livestock and wild elephants use water points at different times of the day [74]. The response in night day activity ratio to human-structures was stronger in the dry season (as indicated by support for an interaction term between season and distance to boma). During the dry season there is higher competition for water, during this time elephants exhibit increased nocturnal movement which decreases the risk of conflict with pastoralists. In contrast, the response of elephant daily travel distance as a function of distance to nearest human structure was consistent between the seasons. The results from the daily travel distance model indicate that elephants travel significantly shorter distances in areas where there is higher average biomass productivity (Appendix 1, Figure S2, panel F), suggesting that at a daily scale distance travelled follows optimal foraging theory and is responsive to forage quality. Increased daily travel distance in relation to lower distance to bomas may be due to habitat fragmentation requiring greater travel distance to find suitable forage patches.

Elephants and other large mammals in semi-arid environments exhibit thermoregulatory behaviour linked to temperature and water availability [75]. Elephants increased their nocturnal movement in response to higher average temperature (Appendix 1, Figure S3) presumably to minimise heat load as it is cooler during the night. They also moved, on average, shorter daily distances when monthly temperatures were higher, and at higher elevation (Appendix 1, Figure S2, panels E &B) indicating energetic and thermal constraints. Elephants are highly water-dependent for hydration and evaporative cooling, and water access is a key limiting factor for elephants in this system [60]. When water availability is low there is reduced potential for evaporative cooling, and we would expect elephants to switch to more nocturnal movement which they do to a greater degree during the dry season and when further from the nearest water source (Appendix 1, Figure S3). Elephants in this ecosystem move greater daily distances during the rainy season, and when further from the nearest water source (Appendix 1, Figure S2, panels A & D). The former supports the fact that elephants are less restricted to permanent water during the rainy season [60] allowing greater daily travel distance, while the latter likely represents an increased travel distance cost to ensure access to sufficient water for daily requirements.

There is greater statistical support from the Likelihood Ratio Test (LRT) for the inclusion of average distance to nearest boma in the night day activity ratio model compared to daily travel distance and a greater magnitude of response. These findings suggest that the presence of human-build structures is more closely associated with elephant temporal activity patterns than daily travel distance. Across multiple taxa and study sites, human activity is found to have greater impact on animal space use (activity patterns will have a temporal impact captured in night day activity ratio) compared to habitat modification (impacting space use captured in daily travel distance) [28]. Understanding the underlying mechanisms of this is an interesting area of future research. The fixed-effects portion of the daily travel distance model explained more of the overall variance than the night day activity ratio model, indicating that there are other important variables that influence elephant temporal activity. There was strong support for consistent baseline differences between individual elephants in the daily travel distance model (see Appendix S1), while the variance components showed little support for consistent within individual differences for night-day activity ratio - consistent with previous findings [53]. Better understanding of the drivers that impact shifting temporal activity is an area of study that would benefit from further research.

Conclusion

This study shows the human footprint in our study site in terms of the number and distribution of bomas and other human-built structures has increased, and elephants readily adapt their foraging habits and itineraries in habitats shared with humans who are also nomadic in space and time. This paper is the first proof of concept that satellite remote sensing can be used to monitor pastoralists and elephants, showing how livestock and wildlife are coexisting. It also offers fine-scale insight into the movement strategies of elephants in a shared habitat. As the human population continues to expand, more bomas will be established. As conservation agencies work to conserve the elephant population in such landscapes, better understanding of how elephants are adapting to shifting human occupation can help in long-term landscape planning. Improved temporal and spatial resolution of satellites combined with better geolocation accuracy, coverage and falling costs of GPS tracking devices will enable more precise observation of human-wildlife movement in rural landscapes as demonstrated is possible in this study.

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Author contributions

I.D. conceived the idea of the paper and designed the methodology with oversight from T.W & D.W.M.; I.D. acquired, processed, and analysed the satellite data. FI & JW digitised the bomas in the image data; GF designed and implemented the analysis of the movement data in R Studio and contributed to the manuscript. S.L contributed comments on the manuscript. I.D. led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

Data availability

Given the sensitive nature of the location of elephants due to ongoing illegal killing, GPS data cannot be made public. Further information and requests for information and data related to the analysis should be directed to the corresponding author: Isla Duporge (Isla.duporge@zoo.ox.ac.uk)

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PART III: SYNTHESIS

The preceding chapters each contain their own discussion, in this section I briefly summarise the main results from each chapter, highlighting the key findings. I then briefly discuss future directions.

Chapter 1: Review on available quantitative data on the distribution of illegal hunting incidences

This chapter is an evidence map on the spatially explicit quantitative data available on illegal hunting incidences in sub-Saharan Africa.

Systematic searches were carried out across eight bibliographic databases and articles were screened against pre-defined criteria. Only wild terrestrial mammals listed as vulnerable, endangered or critically endangered by the International Union for Conservation of Nature (IUCN) whose geographical range falls in Sub-Saharan Africa and whose threat assessment includes hunting and trapping were included. Studies were required to include quantitative, spatially explicit data. In total 14,325 articles were screened at the level of title and abstract and 206 articles were screened at full text. Forty-seven of these articles met the pre-defined inclusion criteria.

Spatially explicit data - where the geographical illegal hunting location is identified was available for 29 species in 19 of the 46 countries that constitute Sub-Saharan Africa. The spatial biases in illegal hunting incidences, data collection method, geographical and species focus, and length of study were recorded. Data collection methods include GPS and radio tracking, bushmeat household and market surveys, data from anti-poaching patrols, hunting follows and first-hand monitoring of poaching signs via line transects, audio and aerial surveys.

There is a considerable lack of systematically collected quantitative data showing the distribution of illegal hunting incidences and few comparative studies between different land tenure areas. The majority of studies have been conducted in a single protected area looking at hunting on a gradient to surrounding village land. From the studies included in the map it is evident that spatial patterns do exist in relation to environmental and anthropogenic correlates.

For example, hunting increases in proximity to transport networks (roads and railway lines), to water sources, to the border of protected areas and to village land. There is a diverse range of methods in use to collect data on illicit hunting mainly drawing on pre-existing law enforcement data or researcher led surveys detecting signs of poaching. There are few longitudinal studies with most studies representing just one season of data collection and there is a geographical research bias toward Tanzania and a lack of studies in Central Africa.

Better understanding of spatial patterns in illegal hunting incidences can guide anti-poaching patrols and help to guide optimal positioning of wildlife ranger posts. If reliable and systematic data on the spatial distribution of illegal hunting incidences are collected (for example via the spatial Monitoring and Reporting Tool [https://smartconservationtools.org/]) then predictive models can be used to forecast the occurrence of future illegal hunting incidences. These can inform anti-poaching patrols and conservation policy.

Spatial data is particularly pertinent considering increased proximity of human settlement to wildlife and the rapid loss of species occurring in the sixth mass extinction [1]. The original focus of this work was to look at how land tenure relates to illegal hunting. However, there is not enough available data to answer this question as the majority of studies analyse a single protected area looking at illegal hunting intensity on a gradient to the border of the area and land tenure maps are not accurate or updated in many sub-Saharan African countries.

Future studies could look at whether the spatial biases found in this study hold in other regions outside sub-Saharan Africa. If the SMART datasets are made available to researchers, then cross comparison of patterns could be investigated across various sites. The findings from this study were presented during the Fourteenth United Nations Congress on Crime Prevention and Criminal Justice (7-12 March 2021) during a session titled 'Rethinking the 'boundary-arrangement' for an evidence-based approach in addressing wildlife and Forest crime.'

Chapter 2: A novel method to determine optimal flight altitude of UAV to minimise disturbance to wildlife

Anthropogenic noise obscures species auditory detection and communication, triggering behaviour that displaces time and energy from primary survival functions. UAVs are one new source of acoustic disturbance in the environment and the application of UAVs for wildlife research are numerous and continue to grow. Dealing with the issue of disturbance is necessary to support the use of this tool. UAVs, in many circumstances, provide a cheaper and less disruptive method to collect data than existing techniques (manned aircraft or vessels). Additionally, species can be monitored in locations that are impractical or unsafe to visit on foot. This chapter provides a method to understand UAV acoustic disturbance to wildlife.

Sound profiles of seven common UAV systems in the horizontal and vertical planes were recorded at 5-metre increments up to 120m. To understand how mammals perceive UAV sound, audiograms were used to calculate the loudness of each UAV for each species across the measured distances. These calculations filter the UAV noise based on the sensitivity of species' hearing over the relevant frequency spectrum. The method optimises the trade-off between image spatial resolution and flight altitude by calculating the lowest point at which either the UAV sound level decreases below an acceptable threshold or disturbance cannot be significantly further minimised by flying higher. Thus, noise is weighted according to species hearing sensitivity, rather than using a dB(A) weighting which is based on human hearing capabilities.

The aim is to promote ethical use of UAVs for wildlife monitoring. As sound pollution is on the rise globally in both terrestrial and marine habitats this method can be used and adapted to better understand disturbance from other sources of anthrophony. The results demonstrate that noise emitted by different UAV models vary in overall loudness and volume across the frequency spectrum. The difference in the acoustic profile of UAVs is of higher relevance when flown close to the target species, and the choice of UAV system is more relevant when flying over species such as elephants, whose hearing sensitivity is higher at very low frequencies. UAV sound levels converge in the upper frequencies; therefore, the choice of the system has less relevance when flying over species with greater high frequency sensitivity (e.g., Felidae and Carnivora). The choice of UAV system is especially important for species whose hearing sensitivity is highest between 1.5 and 6 kHz, as UAV sound is concentrated in this bandwidth. As shown in the audiograms, some species hear well across the entire frequency spectrum, while the hearing sensitivity of other species is concentrated at particular frequencies.

The research highlights the absence of audiograms available for most species. This lack of data prevents adequate understanding of how species perceive noise. Future research collecting audiograms for other species is highly recommended and developing techniques to do this outside of a laboratory setting in-situ.

Chapter 3: Counting African elephants from space with AI technology

Very few studies have used satellite imagery to monitor wildlife, of these; attempts to apply an automated detection technique have been applied in just three cases to detect albatross [2], whales [3, 4] and pack-ice seals [5]. To deal with the quantity of imagery generated from satellite surveys automatic detection is necessary.

This study investigates, for the first time, whether it is possible to detect the African Elephant from satellite imagery and whether it is possible to automate detection using a convolutional neural network. The focus is on the African Elephant but the methodological approach is transferrable to other large-bodied mammals. As the world's largest terrestrial mammal, elephants are an appropriate species to demonstrate this technique on, although they comprise only fifteen pixels using the highest resolution imagery currently available (Worldview 3 & 4). A large spatial and temporal satellite dataset covering multiple seasons and years (2009-2019) was used to generate more than a thousand elephant training labels that were fed into several Convolutional Neural Network (CNN) models to test automating detection. The results of the CNN detection are compared with human detection efficacy by sending the test dataset to 50 volunteers to label.

We were able to successfully use satellite imagery to count African Elephants and automate detection via a CNN with high comparable accuracy to human performance. The CNN in both homogeneous & heterogeneous areas received an F2 score of 0.75 while human detection was 0.78. However, the CNN performed better in heterogeneous areas with an F2 score of 0.778 compared to human performance of 0.766. Humans performed better in homogeneous areas with a score of 0.80 compared to 0.73.

To test whether the CNN could generalise to elephant herds outside of the training area we tested without further training on a known elephant population in the Maasai Mara in Kenya. The CNN managed to detect more than half the elephants in this image and the resulting F2 score was 0.57. This demonstrates that while the CNN needs additional training data representative of elephants in different locations to perform with high accuracy in other locations it still managed to learn the basic shape, structure and spectral composition of an elephant.

In the future, the temporal and spatial resolution of satellite imagery will improve, thus, more wildlife can be monitored from satellite with higher frequency and accuracy. Future research is encouraged to see which other mammals can be detected using this technique. Increased interdisciplinary collaboration between spatial ecologists and data scientists is encouraged to make best use of current capabilities as demonstrated in this study.

Chapter 4: A satellite perspective on the movement of African elephants in relation to nomadic pastoralists

Satellite data enables us to see large-scale change in the landscape in detail. When combined with biotelemetry data we can better understand movement in relation to landscape changes. Miniaturisation of GPS tags and additional on-board information (i.e., accelerometer, magnetometer, air pressure, and temperature and humidity loggers) enables an understanding of movement dynamics. Contemporary tags can measure change in heart rate, temperature, spatiotemporal position & orientation. This allows changes in velocity, fine-scale movement and body posture (via magnetometer) to be correlated with physiology and energy expenditure. Evolution in tracking capabilities (e.g. the deployment of Animal Research Using Space (ICARUS) on the International Space Station) has provided high accuracy global GPS cover for animal tags [6]. Very high-resolution satellites (less than 1 metre) have been online for the last two decades enabling species to be observed in-situ in relation to surrounding habitat. This study partners digitised satellite imagery and GPS tracking data to investigate how the human footprint in the rural savannah influences elephant movement. The composition of bomas in the savannah is ecologically significant; however, no large-scale remote sensing dataset exists to show the number or spatial or temporal shifts in these structures.

To assess changes in human presence we use a time-series approach between 2011 & 2019 covering an area of 3377km^2 in Northern Kenya. The study area is gridded and the density and area covered by bomas is calculated for each year. The study uses two complementary, spatial and temporal movement metrics at the daily scale to assess elephant movement in relation to bomas - daily travel distance, which relates to energetic requirements and night-day ratio, which relates to diurnal activity patterns.

This study shows that elephants exhibit plasticity in movement in a landscape shared with humans who are also highly mobile in space and time. The landcover change analysis shows bomas are the most numerous structures in the landscape and are increasing in number and area. There was a more than 50% increase in the total number of active and inactive bomas and the area of land covered by human-built structures increased 13.53km^2 representing a 21.8% increase in human modified land. The average size of bomas also increased from 36m diameter in 2011 to 50m in 2019, reflective of increasing cattle numbers. Few bomas remain occupied over the entire 8-year period and the rate of disappearance of remotely-sensed recently active bomas is high, only 24% of bomas labelled in the 2011 images are visible in 2019.

These findings reflect the broader global trend of an expanding human footprint and associated rise in livestock numbers. The dynamic movement of bomas mean the positive impacts from moderate grazing on plant productivity and diversity are spread across the landscape. The results demonstrate that African elephants adapt their movement in relation to bomas moving more nocturnally and traveling further daily distances when in closer proximity to bomas. Increased daily movement in relation to distance to bomas may be due to habitat fragmentation requiring greater travel distance to find suitable forage patches and the time-sharing strategy may be optimal to ensure long-term access to required resources.

Broader implications and future directions

Improving wildlife monitoring capabilities is important and necessary for several reasons. Irrespective of their wider value. Non-human animals are of significant scientific importance. They have evolved heighted sensory sensitivity in specific ways that in many cases exceed human capabilities. These heightened sensory capabilities of vision, olfaction, sound perception, detection of magnetic fields etc. enable animals to respond to stimuli, of which humans are unaware. For example, changes in elephant migration routes show that they are able to detect infrasound generated by distant thunderstorms up to 100 km away, days before the onset of rain [7]. Wildlife act as sentinels showing us the changing natural patterns of the world and provide insight into our evolutionary history [6, 8]. Movement patterns and breeding locations of animals can also be used to understand other events that impact human activities e.g., large gatherings of storks portend plagues of locusts and faint seismic activity triggering wildlife movement e.g., goats descending a volcano many hours before an eruption [9]. Wildlife are integral to healthy ecosystem function that we rely on for our survival. Losing species at the rate that is currently occurring in the sixth mass extinction means, to express only an anthropocentric perspective, humanity is losing valuable sources of knowledge. Human survival is closely intertwined with the life of other species as evidenced by zoonotic pandemics. Three-quarters of emerging infectious diseases in humans are zoonotic [10]. The Covid-19 pandemic triggered by the consumption of wild meat has caused the greatest shock to the global economy on record [11]. This event highlights the interconnectedness of humans and wildlife and the importance of studying wildlife not merely as an object of zoological enquiry but as an essential part of environmental, economic and global human security.

This thesis investigates different remote sensing applications to monitor wildlife and to understand movement in relation to the expanding human footprint. The focus is on the application of UAVs and high-resolution satellite imagery combined with machine learning and GPS tracking data. The case studies focus on Sub-Saharan Africa - as the continent faring worst in the sixth mass extinction and the species focus is the African elephant. Elephants are a species of global conservation concern categorised as Evolutionarily Distinct and Globally Endangered (EDGE) and are key ecological engineers in savannah landscapes.

The availability of remote sensing tools offer many advantages to zoological research enabling large-scale tracking and monitoring, while minimising disturbance through ground presence. Satellite resolution will continue to expand providing the opportunity to better understand landscape changes and monitor more species, more frequently. The first radio collar deployed on Grizzly bears in Yellowstone National Park was in the 1960s allowing the movement of the bears to be monitored up to 20 miles away [12]. Since then, the field of tracking has progressed rapidly and the future of wildlife monitoring will become increasingly sophisticated as remote sensing technologies further improve. It is important that methods of application using remote sensing tools keep pace with hardware development.

In terms of future directions, the ability to gather large amounts of remote sensing data does not necessarily lead to new knowledge if collected using a non-standardised approach. As technological capabilities expand, it is necessary that sampling protocols and standards are used and information on survey effort is recorded. Large verifiable data portals have been established for camera trap surveys (e.g., eMammal [https://emammal.si.edu/]) and GPS movement data (e.g., [https://www.movebank.org/] containing $>10^9$ data points on animal movement since 2007) [13].While these shared portals capture only a small amount of the remotely sensed wildlife data they are indicative of what the future holds. Large shared portals will likely come online in the future for wildlife data collected from UAVs and satellites. If combined with advances in machine learning, this will help to translate new large datasets into scientific knowledge through enhanced analytical capabilities so that we can better understand species occupancy, migration and movement strategies [14].

Agreements to track and conserve wildlife are in place at the global level. However, to ensure these agreements are met, up-to-date information on population numbers and movement dynamics is required. Advances in the application of remote sensing tools to collect this data is essential to help bolster such agreements. This research aims to contribute toward the global wildlife conservation effort by bolstering methods using remote sensing technology to gather data on wildlife.

The references listed here are for Introduction and Synthesis. The data chapters each contain their own reference lists.

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SUPPLEMENTARY MATERIAL

Chapter 1

** Inclusion Criteria and search terms: Additional File 1 & 2 in Chapter 1 & Protocol*

Inclusion Criteria

African Countries in Sub-Saharan Africa as defined by United Nations:

ANGOLA	MADAGASCAR
BENIN	MALAWI
BOTSWANA	MALI
BURKINA FASO	MAURITANIA
BURUNDI	MAURITIUS
CABO VERDE	MOZAMBIQUE
CAMEROON	NAMIBIA
CENTRAL AFRICAN REPUBLIC	NIGER
CHAD	NIGERIA
COMOROS	RWANDA
CONGO, DEM. REP.	SAO TOME AND PRINCIPE
CONGO, REP.	SENEGAL
COTE D'IVOIRE	SEYCHELLES
EQUATORIAL GUINEA	SIERRA LEONE
ERITREA	SOMALIA
ETHIOPIA	SOUTH AFRICA
GABON	SOUTH SUDAN
GAMBIA, THE	SUDAN
GHANA	SWAZILAND
GUINEA	TANZANIA
GUINEA-BISSAU	TOGO
KENYA	UGANDA
LESOTHO	ZAMBIA
LIBERIA	ZIMBABWE

IUCN Search Criteria:

Search by taxonomy:	MAMMALIA
Search by location:	Sub-Saharan Africa
Search by systems:	Terrestrial
Match habitat:	1. Forest, 2. Savanna, 3. Shrubland, 4. Grassland, 6. Rocky areas (eg. inland cliffs, mountain peaks), 8. Desert, 14. Artificial/Terrestrial, 16. Introduced vegetation, 17. Other, 18. Unknown
Search by threat:	5.1. Hunting & trapping terrestrial animals

Species listed for inclusion:

Acinonyx jubatus (Cheetah) Status: Vulnerable	VU
Addax nasomaculatus (Addax) Status: Critically Endangered	CR
Allocebus trichotis (Hairy-eared Dwarf Lemur) Status: Vulnerable	VU

Allochrocebus lhoesti (L'Hoest's Monkey) Status: Vulnerable	VU
Allochrocebus preussi (Preuss's Monkey) Status: Endangered	EN
Allochrocebus solatus (Sun-tailed Monkey) Status: Vulnerable	VU
Ammodorcas clarkei (Dibatag) Status: Vulnerable	VU
Ammotragus lervia (Aoudad) Status: Vulnerable	VU
Avahi laniger (Eastern Woolly Lemur) Status: Vulnerable	VU
Avahi mooreorum (Moore's Woolly Lemur) Status: Endangered	EN
Avahi occidentalis (Lorenz Von Liburnau's Woolly Lemur) Status: Endangered	EN
Avahi peyrierasi (Peyrieras' Woolly Lemur) Status: Vulnerable	VU
Avahi unicolor (Sambirano Woolly Lemur) Status: Endangered	EN
Beatragus hunteri (Hirola) Status: Critically Endangered	EN
Brachytarsomys villosa (Hairy-tailed Tree Rat) Status: Vulnerable	VU
Bunolagus monticularis (Riverine Rabbit) Status: Critically Endangered	CR
Canis simensis (Ethiopian Wolf) Status: Endangered	EN
Capra nubiana (Nubian Ibex) Status: Vulnerable	VU
Capra walie (Walia Ibex) Status: Endangered	EN
Caracal aurata (African Golden Cat) Status: Vulnerable	VU
Carpitalpa arendsi (Arend's Golden Mole) Status: Vulnerable	VU
Cephalophus adersi (Aders' Duiker) Status: Vulnerable	VU
Cephalophus jentinki (Jentink's Duiker) Status: Endangered	EN
Cephalophus spadix (Abbott's Duiker) Status: Endangered	EN
Cephalophus zebra (Zebra Duiker) Status: Vulnerable	VU
Cercocebus galeritus (Tana River Mangabey) Status: Endangered	EN
Cercocebus lunulatus (White-naped Mangabey) Status: Endangered	EN
Cercocebus sanjei (Sanje River Mangabey) Status: Endangered	EN
Cercocebus torquatus (Red-capped Mangabey) Status: Vulnerable	VU
Cercopithecus diana (Diana Monkey) Status: Vulnerable	VU
Cercopithecus dryas (Dryas Monkey) Status: Critically Endangered	EN

Cercopithecus erythrogaster (Red-bellied Monkey) Status: Vulnerable	VU
Cercopithecus erythrotis (Red-eared Monkey) Status: Vulnerable	VU
Cercopithecus hamlyni (Owl-faced Monkey) Status: Vulnerable	VU
Cercopithecus roloway (Roloway Monkey) Status: Endangered	EN
Cercopithecus sclateri (Sclater's Monkey) Status: Vulnerable	VU
Chlorotalpa duthieae (Duthie's Golden Mole) Status: Vulnerable	VU
Choeropsis liberiensis (Pygmy Hippopotamus) Status: Endangered	EN
Chrysospalax trevelyani (Giant Golden Mole) Status: Endangered	EN
Colobus polykomos (King Colobus) Status: Vulnerable	VU
Colobus satanas (Black Colobus) Status: Vulnerable	VU
Colobus vellerosus (White-thighed Colobus) Status: Vulnerable	VU
Cryptoprocta ferox (Fossa) Status: Vulnerable	VU
Daubentonia madagascariensis (Aye-aye) Status: Endangered	EN
Diceros bicornis (Black Rhinoceros) Status: Critically Endangered	CR
Dorcatragus megalotis (Beira) Status: Vulnerable	VU
Eidolon dupreanum (Madagascan Fruit Bat) Status: Vulnerable	VU
Equus africanus (African Wild Ass) Status: Critically Endangered	CR
Equus grevyi (Grevy's Zebra) Status: Endangered	EN
Equus zebra (Mountain Zebra) Status: Vulnerable	VU
Eudorcas rufifrons (Red-fronted Gazelle) Status: Vulnerable	VU
Eudorcas tilonura (Heuglin's Gazelle) Status: Endangered	EN
Eulemur albifrons (White-fronted Lemur) Status: Endangered	EN
small Eulemur cinereiceps (White-collared Lemur) Status: Critically Endangered	CR
Eulemur collaris (Collared Brown Lemur) Status: Endangered	EN
Eulemur coronatus (Crowned Lemur) Status: Endangered	EN
Eulemur flavifrons (Blue-eyed Black Lemur) Status: Critically Endangered	CR
Eulemur macaco (Black Lemur) Status: Vulnerable	VU
Eulemur mongoz (Mongoose Lemur) Status: Critically Endangered	CR

Eulemur rubriventer (Red-bellied Lemur) Status: Vulnerable	VU
Eulemur rufus (Red Brown Lemur) Status: Vulnerable	VU
Eulemur sanfordi (Sanford's Brown Lemur) Status: Endangered	EN
Eupleres goudotii (Eastern Falanouc) Status: Vulnerable	VU
Eupleres major (Western Falanouc) Status: Endangered	EN
Felis nigripes (Black-footed Cat) Status: Vulnerable	VU
Fossa fossana (Spotted Fanaloka) Status: Vulnerable	VU
Fukomys kafuensis Status: Vulnerable	VU
Galidictis grandidieri (Grandidier's Vontsira) Status: Endangered	EN
Gazella dorcas (Dorcas Gazelle) Status: Vulnerable	VU
Gazella spekei (Speke's Gazelle) Status: Endangered	EN
Genetta bourloni (Bourlon's Genet) Status: Vulnerable	VU
Genetta cristata (Crested Genet) Status: Vulnerable	VU
Giraffa camelopardalis (Giraffe) Status: Vulnerable	VU
Gorilla beringei (Eastern Gorilla) Status: Critically Endangered	CR
Gorilla gorilla (Western Gorilla) Status: Critically Endangered	CR
Hapalemur aureus (Golden Bamboo Lemur) Status: Critically Endangered	CR
Hapalemur griseus (Eastern Lesser Bamboo Lemur) Status: Vulnerable	VU
Hapalemur meridionalis (Rusty-gray Lesser Bamboo Lemur) Status: Vulnerable	VU
Hapalemur occidentalis (Sambirano Lesser Bamboo Lemur) Status: Vulnerable	VU
Hippopotamus amphibius (Hippopotamus) Status: Vulnerable	VU
Hipposideros lamottei (Lamotte's Roundleaf Bat) Status: Critically Endangered	CR
Hylomyscus baeri (Baer's Wood Mouse) Status: Endangered	EN
Hypogeomys antimena (Malagasy Giant Jumping Rat) Status: Endangered	EN
Indri indri (Indri) Status: Critically Endangered	CR
Kobus megaceros (Nile Lechwe) Status: Endangered	EN
Lemur catta (Ring-tailed Lemur) Status: Endangered	EN
Lepilemur ankaranensis (Ankarana Sportive Lemur) Status: Endangered	EN
Lepilemur betsileo (Betsileo Sportive Lemur) Status: Endangered	EN
Lepilemur dorsalis (Gray's Sportive Lemur) Status: Vulnerable	VU

Lepilemur edwardsi (Milne-Edwards's Sportive Lemur) Status: Endangered	EN
Lepilemur fleuretae (Fleurete's Sportive Lemur) Status: Critically Endangered	CR
Lepilemur grewcockorum (Grewcock's Sportive Lemur) Status: Endangered	EN
Lepilemur hollandorum (Holland's Sportive Lemur) Status: Endangered	EN
Lepilemur hubbardorum (Hubbard's Sportive Lemur) Status: Endangered	EN
Lepilemur jamesorum (James' Sportive Lemur) Status: Critically Endangered	CR
Lepilemur microdon (Small-toothed Sportive Lemur) Status: Endangered	EN
Lepilemur milanoii (Daraina Sportive Lemur) Status: Endangered	EN
Lepilemur mittermeieri (Mittermeier's Sportive Lemur) Status: Endangered	EN
Lepilemur ruficaudatus (Red-tailed Sportive Lemur) Status: Vulnerable	VU
Lepilemur sahamalazensis (Sahamalaza Peninsula Sportive Lemur) Status: Critically Endangered	CR
Lepilemur scottorum (Scott's Sportive Lemur) Status: Endangered	EN
Lepilemur seali (Seal's Sportive Lemur) Status: Vulnerable	VU
Lepilemur septentrionalis (Sahafary Sportive Lemur) Status: Critically Endangered	CR
Lepilemur tymerlachsoni (Nosy Be Sportive Lemur) Status: Critically Endangered	CR
Lepilemur wrightae (Wright's Sportive Lemur) Status: Endangered	EN
Liberiictis kuhni (Liberian Mongoose) Status: Vulnerable	VU
Loxodonta africana (African Elephant) Status: Vulnerable	VU
Lycaon pictus (African Wild Dog) Status: Endangered	EN
Mandrillus leucophaeus (Drill) Status: Endangered	EN
Mandrillus sphinx (Mandrill) Status: Vulnerable	VU
Microcebus arnholdi (Arnhold's Mouse Lemur) Status: Endangered	EN
Microcebus bongolavensis (Bongolava Mouse Lemur) Status: Endangered	EN
Microcebus danfossi (Danfoss' Mouse Lemur) Status: Endangered	EN
Microcebus gerpi (Gerp's Mouse Lemur) Status: Critically Endangered	CR
Microcebus jollyae (Jolly's Mouse Lemur) Status: Endangered	EN

Mirza coquereli (Coquerel's Giant Mouse Lemur) Status: Endangered	EN
Mungotictis decemlineata (Bokiboky) Status: Endangered	EN
Nanger dama (Dama Gazelle) Status: Critically Endangered	CR
Nanger soemmerringii (Soemmerring's Gazelle) Status: Vulnerable	VU
Neamblysomus gunningi (Gunning's Golden Mole) Status: Endangered	EN
Okapia johnstoni (Okapi) Status: Endangered	EN
Otomops harrisoni Status: Vulnerable	EN
Pan paniscus (Bonobo) Status: Endangered	EN
Pan troglodytes (Chimpanzee) Status: Endangered	EN
Panthera leo (Lion) Status: Vulnerable	VU
Panthera pardus (Leopard) Status: Vulnerable	VU
Paraxerus vincenti (Vincent's Bush Squirrel) Status: Endangered	EN
Phataginus tetradactyla (Black-bellied Pangolin) Status: Vulnerable	VU
Phataginus tricuspis (White-bellied Pangolin) Status: Vulnerable	VU
Piliocolobus badius (Upper Guinea Red Colobus) Status: Endangered	EN
Piliocolobus bouvieri (Bouvier’s Red Colobus) Status: Critically Endangered	EN
Piliocolobus epieni (Niger Delta Red Colobus) Status: Critically Endangered	EN
Piliocolobus gordonorum (Udzungwa Red Colobus) Status: Endangered	EN
Piliocolobus kirkii (Zanzibar Red Colobus) Status: Endangered	EN
Piliocolobus pennantii (Pennant's Red Colobus) Status: Endangered	EN
Piliocolobus preussi (Preuss’s Red Colobus) Status: Critically Endangered	EN
Piliocolobus rufomitratus (Tana River Red Colobus) Status: Endangered	EN
Piliocolobus temminckii (Temminck’s Red Colobus) Status: Endangered	EN
Piliocolobus tephrosceles (Ashy Red Colobus) Status: Endangered	EN
Piliocolobus waldronae (Miss Waldron’s Red Colobus) Status: Critically Endangered	CR
Poiana leightoni (West African Oyan) Status: Vulnerable	VU
Prolemur simus (Greater Bamboo Lemur) Status: Critically Endangered	CR
Propithecus candidus (Silky Sifaka) Status: Critically Endangered	EN

Propithecus coquereli (Coquerel's Sifaka) Status: Endangered	EN
Propithecus coronatus (Crowned Sifaka) Status: Endangered	EN
Propithecus diadema (Diademed Sifaka) Status: Critically Endangered	CR
Propithecus edwardsi (Milne-Edward's Sifaka) Status: Endangered	EN
Propithecus perrieri (Perrier’s Sifaka) Status: Critically Endangered	CR
Propithecus tattersalli (Golden-crowned Sifaka) Status: Critically Endangered	CR
Propithecus verreauxi (Verreaux's Sifaka) Status: Endangered	EN
Pteropus niger (Greater Mascarene Flying Fox) Status: Vulnerable	VU
Pteropus rodricensis (Rodrigues Flying Fox) Status: Endangered	EN
Pteropus rufus (Madagascan Flying Fox) Status: Vulnerable	VU
Pteropus voeltzkowi (Pemba Flying Fox) Status: Vulnerable	VU
Redunca fulvorufula (Mountain Reedbuck) Status: Endangered	EN
Rhinolophus cohenae (Cohen's Horseshoe Bat) Status: Vulnerable	VU
Rhinolophus guineensis (Guinean Horseshoe Bat) Status: Vulnerable	VU
Rhinolophus hilli (Hill's Horseshoe Bat) Status: Critically Endangered	CR
Rhinolophus maclaudi (Maclaud's Horseshoe Bat) Status: Endangered	EN
Rhinolophus ruwenzorii (Ruwenzori Horseshoe Bat) Status: Vulnerable	VU
Rhinolophus ziama (Ziama Horseshoe Bat) Status: Endangered	EN
Rhynchocyon chrysopygus (Golden-rumped Sengi) Status: Endangered	EN
Rhynchocyon udzungwensis (Grey-faced Sengi) Status: Vulnerable	VU
Rousettus obliviosus (Comoros Rousette) Status: Vulnerable	VU
Rungwecebus kipunji (Kipunji) Status: Critically Endangered	EN
Salanoia concolor (Brown-tailed Vontsira) Status: Vulnerable	VU
Smutsia gigantea (Giant Ground Pangolin) Status: Vulnerable	VU
Smutsia temminckii (Temminck's Ground Pangolin) Status: Vulnerable	VU

Tragelaphus buxtoni (Mountain Nyala) Status: Endangered	EN
Tragelaphus derbianus (Giant Eland) Status: Vulnerable	VU
Varecia rubra (Red Ruffed Lemur) Status: Critically Endangered	CR
Varecia variegata (Black-and-white Ruffed Lemur) Status: Critically Endangered	CR

Title of Articles Used for Benchmarking Search Strings:

1. Holmern, T., et al. (2007). "Local law enforcement and illegal bushmeat hunting outside the Serengeti National Park, Tanzania." Environmental Conservation 34(01): 55.
2. Ihwagi, F. W., et al. (2015). "Using Poaching Levels and Elephant Distribution to Assess the Conservation Efficacy of Private, Communal and Government Land in Northern Kenya." PLoS One 10(9): e0139079.
3. Sibanda, M., et al. (2015). "Understanding the spatial distribution of elephant (Loxodonta africana) poaching incidences in the mid-Zambezi Valley, Zimbabwe using Geographic Information Systems and remote sensing." Geocarto International 31(9): 1006-1018.
4. Watson, F., et al. (2013). "Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks." Biological Conservation 168: 1-9.

<table>
<tr><td>Agricola [http://agricola.nal.usda.gov]

via Endnote web search</td><td>Any field: Hunting and wildlife or poach*</td><td></td><td>1316</td><td>365</td></tr>
<tr><td>AGRIS [http://agris.fao.org/]</td><td>Hunting && (poach* || wildlife)</td><td></td><td>1805</td><td>1575</td></tr>
<tr><td>BIOSIS: Biological Abstracts [Accessed via Web of Science]

BIOSIS Citation Index-1969-Present

Articles Included in databases, 1,2,4</td><td>(TS=(((fauna OR wildlife) OR (tenure OR land) NEAR/2 (ownership OR right* OR holding* OR title OR administration OR management OR tenan* OR deed* OR pastoral OR private OR commun* OR customary OR state) OR ("natural resource") NEAR/2 (ownership OR pastoral OR private OR commun* OR customary OR state) OR ("property regime" OR area) NEAR/2 (communal OR protected OR communit* OR freehold OR "free leasehold" OR "Wildlife Management")) AND (hunting OR poaching OR bushmeat OR trapping OR snaring OR vulnerabl* OR endangered OR threatened OR risk OR "conservation dependent" OR extinct*)) AND TS=(GHANA* OR NIGERIA* OR TANZANIA* OR "SOUTH AFRICA*" OR MADAGASCA* OR ZAMBIA* OR UGANDA* OR BOTSWANA* OR MALAWI* OR KENYA* OR NAMIBIA* OR SENEGAL* OR ZIMBABW* OR ETHIOPIA*))</td><td>Refined by countries listed in Africa: COUNTRIES/REGIONS:

(GHANA* OR NIGERIA* OR TANZANIA* OR "SOUTH AFRICA*" OR MADAGASCA* OR ZAMBIA* OR UGANDA* OR BOTSWANA* OR MALAWI* OR KENYA* OR NAMIBIA* OR SENEGAL* OR ZIMBABW* OR ETHIOPIA*))</td><td>5022</td><td>4254</td></tr>
<tr><td>CAB Abstracts [Accessed via Ovid]</td><td>((((mammal* or fauna or wildlife or animal*) and (land adj2 (ownership or</td><td>1990-2018</td><td>1408</td><td>1308</td></tr>
</table>

1,2 included in database	right* or management or regim* or private or commun* or customary or state or protected or freehold or free leasehold))) or (ownership adj2 (pastoral or private or commun* or customary or state))) and (hunting or poaching or bushmeat or trapping or snaring or vulnerabl* or endangered or threatened or risk or extinct*)).af.			
PAIS Index [Accessed via ProQuest] **No articles included in database**	noft((mammal* OR fauna OR wildlife OR animal*) AND tenure OR land NEAR/2 (ownership OR right* OR holding* OR title OR administration OR management OR tenan* OR deed* OR pastoral OR private OR commun* OR customary OR state) OR "natural resource" NEAR/2 (ownership OR right* OR management OR regim* OR private OR commun* OR customary OR state) OR "property regime" OR area NEAR/2 (communal OR protected OR communit* OR freehold OR "free leasehold" OR "Wildlife Management") OR ownership NEAR/2 (pastoral OR private OR commun* OR customary OR state) AND (hunting OR poaching OR bushmen OR trapping OR snaring OR vulnerabl* OR endangered OR threatened OR risk OR extinct*))	South Africa OR Africa OR Ethiopia OR Ghana OR Uganda OR Kenya OR Tanzania OR Zimbabwe OR Sub-Saharan Africa OR Madagascar OR Mozambique OR East Africa OR Malawi OR Namibia OR Zambia OR Accra Ghana OR West Africa	279	204

SCOPUS [http://www.scopus.com] **All articles included in database**	TITLE-ABS (mammal* OR fauna OR wildlife OR animal*) AND tenure OR land AND n/2 (ownership OR right* OR holding* OR title OR administration OR management OR tenan* OR deed* OR pastoral OR private OR commun* OR customary OR state) OR resource AND n/2 (ownership OR right* OR management OR common OR regim OR private OR commun* OR customary OR state) OR property AND n/2 (right* OR regime OR system OR common) OR area AND n/2 (communal OR protected OR communit* OR "freehold" OR "free leasehold") OR ownership AND n/2 (pastoral OR private OR commun* OR customary OR state) AND ("hunting" OR "poaching" OR "bushmeat" OR "trapping" OR "vulnerabl*" OR "endangered" OR "threatened" OR "risk" OR "conservation dependent" OR "extinct*")	Limited to the Sub-Saharan Countries available: “South Africa" "Kenya" "Tanzania" "Zimbabwe” "Ethiopia” "Botswana" "Uganda” "Nigeria" "Namibia" "Zambia” "Ghana" "Madagascar” "Cameroon" "Congo" "Gabon" "Mauritius" "Mozambique", "Malawi” "Benin" "Burkina Faso” "Cote d'Ivoire" "Rwanda" “Swaziland" "Mali" "Niger" "Sierra Leone" "Sudan” "Democratic Republic Congo” "Gambia" "Seychelles" "Togo" "Liberia” "Angola" "Central African Republic "Undefined"	2,201	1702

Web of Science: Core Collection: Web of Science Core Collection: Citation Indexes Science Citation Index Expanded (SCI-EXPANDED) --1900-present Social Sciences Citation Index (SSCI) --1900-present Arts & Humanities Citation Index (A&HCI) --1975-present Conference Proceedings Citation Index- Science (CPCI-S) --1990-present Conference Proceedings Citation Index- Social Science & Humanities (CPCI-SSH) --1990-present Book Citation Index– Science (BKCI-S) --2005-present Book Citation Index– Social Sciences & Humanities (BKCI-SSH) --2005-present Emerging Sources Citation Index (ESCI) --2015-present Web of Science Core Collection: Chemical Indexes Current Chemical Reactions (CCR-EXPANDED) --1986-present *(Includes Institut National de la Propriete Industrielle structure data back to 1840)* Index Chemicus (IC) --1993-present	TS= ((mammal* OR fauna OR wildlife OR animal*) AND tenure OR land NEAR/2 (ownership OR right* OR holding* OR title OR administration OR management OR tenan* OR deed* OR pastoral OR private OR commun* OR customary OR state) OR “natural resource” NEAR/2 (ownership OR right* OR management OR regim* OR private OR commun* OR customary OR state) OR “property regime” OR area NEAR/2 (communal OR protected OR communit* OR freehold OR "free leasehold" OR “Wildlife Management”) OR ownership NEAR/2 (pastoral OR private OR commun* OR customary OR state) AND (hunting OR poaching OR bushmeat OR trapping OR snaring OR vulnerabl* OR endangered OR threatened OR risk OR “conservation dependent" OR extinct*))	Refined by: COUNTRIES/REGIONS: (TANZANIA OR NAMIBIA OR ETHIOPIA OR ZIMBABWE OR SOUTH AFRICA OR NIGERIA OR ZAMBIA OR UGANDA OR SENEGAL OR GHANA OR KENYA OR MALAWI OR BOTSWANA)	4091	4091
Zoological Record [Accessed via Web of Science] 1993-present **Articles Included in databases, 1,2,3**	TS= ((mammal* OR fauna OR wildlife OR animal*) AND tenure OR land NEAR/2 (ownership OR right* OR holding* OR title OR administration OR management OR tenan* OR deed* OR pastoral OR private OR commun* OR customary OR state) OR “natural resource” NEAR/2 (ownership OR right* OR management OR regim* OR private OR commun* OR customary OR	Broad Terms (BT)= Africa	1418	826

**Extraction form: Additional File 3 in Protocol*

Data extraction form/coding tool

No.	Category
0.	**General information**
0.1	Date article download & URL (for grey sources only)
0.2	Name of assessor primary extraction
1.	**Bibliographic information**
1.1	Publication type (if not research article)
1.2	Author (s)
1.3	Title
1.4	Journal or Publication title
1.5	Publication year
1.6	Volume/edition
1.7	Publication DOI in EndNote
2.	**Information on Study Context**
2.1	Type of land tenure sites included in study
2.2	Tenure site used as comparison if applicable
2.3	Country(s) of study
2.4	Region or district if mentioned
2.5	Number of study sites
2.6	Number of regions
2.7	Size of study area
2.8	Size of area surveyed
2.9	Specie (s) included in study (common name)
2.9.1	Is hunting permitted?
	Information on study design
3.1	Methods used for data collection
3.2	What is measured
3.3	Unit of analysis- largest to smallest
3.4	Sample Size Per Unit
3.5	Total sample size
3.6	Data collected over period
3.7	Methodology used
3.8	Hypotheses stated
3.9	Outcome
4	**Outcomes**
4.1	Tenure site that experienced highest level of hunting
4.3	Difference in level of illegal hunting (if quantified)
4.4	Most important confounding factors mentioned
4.5	Stated conclusion or finding of study
4.6	Research gap identified if explicity defined
5	**Context of study (evaluation)**
5.1	Organisation who funded the study (Other than University)
5.2	Type of organisation
5.3	Level of organisational operation
5.5	Are any of the authors based at an institution in the study area

Attribute table for Geocoded map

Country	District/Municipality

*Exclusion sheet: Additional file 3 in Chapter 1

This is the exclusion sheet lists the articles screened, the method used to gather data on illicit hunting (refer to Additional file 5), the focus of the study and the reason for exclusion.

Title	Number of method	Focus of study	Notes & Reason for exclusion
	1b	anti-predator behaviors as proxies for perceived pressure	No spatially explicit data on hunting locations
A Novel Approach to Assessing the Prevalence and Drivers of Illegal Bushmeat Hunting in the Serengeti	3A	Those living around PA consumed more bushmeat than elsewhere	No data on hunting
A survey of elephants (Loxodonta africana) in the Kahuzi-Biega National Park lowland sector and adjacent forest in eastern Zaire†	1a	Density study	No data on hunting collected.
A tale of three villages: choosing an effective method for assessing poaching levels in western Serengeti, Tanzania	3a/ 2	compares rates of poaching derived by self-assessment of poaching activities (based on household interviews), dietary recall of bushmeat consumption over a variety of time frames, and arrest records from anti-poaching units.	No spatially explicit data on hunting locations
An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa	1a	abundance survey- some data on hunting collected "However, we encountered extensive evidence of hunting across the study area (snares, gunshots, etc.), and village scouts often reported heavy harvest and sharp declines (e.g. of buffalo, giraffe and impala Aepyceros melampus) or extirpation (e.g. of zebra Equus quagga east of the Idodi-Pawaga WMA, Fig. 1) of some species"	No spatially explicit data on hunting locations
Assessing Africa-Wide Pangolin Exploitation by Scaling Local Data	3b	Synthesis of local-scale data on pangolin poaching from market surveys	While the markets are geo-located, the paper does not synthesize data from underlying surveys on location of hunting activities that supply the markets.
Assessing the Potential Threat Landscape of a Proposed Reintroduction Site for Carnivores	5b	A threat index was developed to establish which properties harboured the greatest threats to wild dogs.	No direct measure of hunting
Assessing the Potential Threat Landscape of a Proposed Reintroduction Site for Carnivores	4	Survey on peceptions of reintroducing African Wild dog across different land tenure areas	No spatially explict data, a threat index was calculated
Assessment and mitigation of human-lion conflict in West and Central Africa	4	Levels of human-widllife conflict	Focus is on depradation figures around a National Park
Assessment of wildlife populations trends in three protected areas in Tanzania from 1991 to 2012	1a	Density and distribution data	No measure on hunting
Bushmeat Consumption in the Tarangire-Manyara Ecosystem, Tanzania	3A	We tested how reported bushmeat availability during the past year was affected by distance to Kigongoni (a village reported to be a major marketplace for bushmeat) using a logistic regression. Previous studies have tested distance to protected areas as a possible correlate for bushmeat consumption, but this did not appear straightforward in our case because the dispersion of wild animals during the wet season, coupled with little law enforcement outside protected areas, makes illegal hunting more frequent in community areas than in protected areas [28]. Therefore, we hypothesized that bushmeat consumption may be related more to proximity of local bushmeat markets than to distance from protected areas.	394 interviews across villages in differeing proximity to Pas and Bushmeat markets- no spatially explicit data
Bushmeat consumption in western Tanzania: A comparative analysis from the same ecosystem	3a	Bushmeant consumption in two villages	hunting difference is not a variable
Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue	3c	Hunting follows in Madagascar	No spatially explicit data on hunting locations
Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income	3A	semistructured interviews to quantify annual rates of bushmeat harvest in 14 villages adjacent to the Makira Forest in north-eastern Madagascar.. Although the majority (75%) of those arrested in the National Park came from villages less than 16 km from the protected area boundary, hunters from villages up to 45 km from this boundary have been apprehended	No spatially explicit data on hunting locations
Bushmeat Hunting in Dwesa and Cwebe Nature Reserves, Eastern Cape, South Africa	1a/3d	Abundance study and monitoring poaching signs	No spatially explicit data on hunting locations
Bushmeat, wildlife-based economies, food security and conservation	4	Assessing earnings from bushmeat hunting and interviewing PA managers to ask about their thoughts on levels of sustainability	No spatially explicit data included
Can parks protect migratory ungulates? The case of the Serengeti wildebeest	1c	GPS collared wildbeest- tracked movement patterns	No data on poaching levels
Carnivore conservation under land use change: the status of Zimbabwe's cheetah population after land reform	1a	questionnaire survey and citizen science data to determine the population status and distribution of the cheetah 15 years after introduction of the FTLRP.	60 Districts: questions about cheetahs, cheetah occurrence, population trends and threats to cheetah survival- No spatially explicit data on hunting locations
Climate variability, human wildlife conflict and population dynamics of lions Panthera leo	1a	Lion mortality rates	Etosha National Park in Northern Namibia and surrounding area - No spatially explicit data on hunting locations
Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya	1a	density and demography of 13 wild and three domestic large herbivores between the Masai Mara National Reserve and the adjoining pastoral ranches using aerial surveys	No data on hunting collected.
Comparative Demography of an At-Risk African Elephant Population	1a/1c	Looked at MIKE data and demographic changes in elephants populations	Does not provide kill site data on where elephants were found
Conservation Value of Multiple-Use Areas in East Africa	1a	Abundance survey across multiple sites	no data on illicti hunting
Conserving biodiversity in a changing world: land use change and species richness in northern Tanzania	1a	species richness in relation to the degree to which they are exposed to human disturbance	Only collected data on abundance
Continent-wide survey reveals massive decline in African savannah elephants	1a	Aerial survey showing elephants numbers	No spatially explicit data on hunting locations
Cultural influences on attitudes about the causes and consequences of wildlife poaching	4	Perceptions on poaching-cultural norms	No measure on hunting level
Decline in hunter offtake of blue duikers in Bioko Island, Equatorial Guinea	1a	Off-take of blue duikers	Not a species of conservation concern
Demography and behaviour of African mammals subject to exploitation	1b	Looking at flight behaviour of species	No data on illegal hunting
Demography and behaviour of African mammals subject to exploitation	1b	Flight initatiation times in exploited and unexploited areas	No spatially explicit data
Densities of mammals in partially protected areas] the Katavi ecosystem of western Tanzania	1a	Density study	No data on illegal hunting
Devastating Decline of Forest Elephants in Central Africa	1a	Elephant prescence	No spatially explicit data
Differences between Pygmy and Non-Pygmy Hunting in Congo Basin Forests	3a	differences in offtake between pygmy and non pygmy groupos	No spatially explicit data on hunting locations

Hunting, food subsidies, and mesopredator release: the dynamics of crop-raiding baboons in a managed landscape	5b	Mathematical model of mesopredator release and hunting	No empirical data on illegal hunting
Identifying Conservation Opportunities among Malinké Bushmeat Hunters of Guinea, West Africa	3a	Social survey on reasons behind hunting and species hunted	No spatially explicit data on hunting locations
Identifying Source Populations and Genetic Structure for Savannah Elephants in Human-Dominated Landscapes and Protected Areas in the Kenya-Tanzania Borderlands	5a	Genetic difference in the metapopulation of elephants in rift valley	No data on illegal hunting
Illegal bushmeat hunting in the Okavango Delta, drivers impacts and potential solutions	3a	Analysis of hunting in Okavango Delta using household survey, occupancy surveys and a number of others datasets	GPS data on illegal hunting incidences was collected but not provided as "The latter two organizations also provided GPS coordinates of some hunting incidents; however, these data were too few and too spatially biased to allow for meaningful analysis."
Illegal Exploitation of Black Rhinoceros and Elephant Populations: Patterns of Decline, Law Enforcement and Patrol Effort in Luangwa Valley, Zambia	1a/2	Patrol effort and correlation with species abundace	There is some spatial data on hunting effort but only looked at in relation to patrol effort, it is all in one national park area and the distance to other areas is not quantified.
Illegal hunting and law enforcement during a period of economic decline in Zimbabwe: A case study of northern Gonarezhou National Park and adjacent areas	4	Perceptions on illegal hunting	No spatially explicit data on hunting locations
Illegal hunting and the bush-meat trade in Savanna Africa: drivers, impacts and solutions to address the problem	5d	Literature review on bushmeat hunting	No primary spatial data included
Illegal killing for ivory drives global decline in African elephants	5b	Modelling carcasses at national and international level	No spatially explicit data on hunting locations
Illegal resources extraction and preponderance distance of villages: A case study of four Nigerian national parks	2	Monitoring "illegal extraction" in different villages around national park	No data on the kind of illegal resources that are being extracted
Impact of Commercial Hunting on Monkey Populations in the Ta¨ı region, Cˆote d'Ivoire1	3b/1a	Impact of hunting on monkey species in the Ta¨ı National Park and adjacent forests in Cˆote d'Ivoire-	No spatially explicit data on hunting locations
Impact of Land Subdivision and Sedentarization on Wildlife in Kenya's Southern Rangelands	1a	Looking at envrionmental variation pre and post land subdivision in two rangeland areas in Kenya	No spatially explicit data on hunting locations- just measures of abundance
Impacts of Roads, Hunting, and Habitat Alteration on Nocturnal Mammals in African Rainforests	1a	impact of hunting on nocturnal species abundance in one rainforest	No spatial data on hunting and anaylsis conducted in just one site
Importance of Wild Meat in the Global South	3a	Economic Household Survey on the economic contribution and expenditure on meat	No data on hunting distriibution only on household economics and the relation with wildmeat expenditure and contribution to income
Insights for Integrated Conservation from Attitudes of People toward Protected Areas Near Hwange National Park, Zimbabwe	4	Assessment of local peoples perceptions of protected areas	No data on illegal hunting
Integrating research with management: the case of Katavi National Park, Tanzania	4	Same study as above	No data on illegal hunting
Interpreting long-term trends in bushmeat harvest in southeast Cameroon	3c	Village bushmeat hunting catches in Cameroon	27 species but none endangered
Large Mammal Distribution in a Transfrontier Landscape: Trade-offs Between Resource Availability and Human Disturbance	1a	Distribution study	No data on hunting. Anthropogenic variables used as a proxy to predict how they affect distributoin
Large-scale extinction of large carnivores (lion Panthera leo, cheetah Acinonyx jubatus and wild dog Lycaon pictus) in protected areas of West and Central Africa	1a	Data on lion extinctions across PAs in Africa	No spatially explicit data on hunting locations
Living on the edge: characteristics of human–wildlife conflict in a traditional livestock community in Botswana	4	Farmers peceptions on WMAs	No spatially explicit data on hunting locations
Local Hunting Strategies in Kwara State, Nigeria: Challenge for Wildlife Conservation policy enforcement	3c	Surveys on hunting strategies	No spatially explicit data
Local law enforcement and illegal bushmeat hunting outside the Serengeti National Park, Tanzania	2	analysis of patrolling effort and origin of hunters	No comparison of different land management areas and spatial distribution of hunting
Long-term monitoring of large rainforest mammals in the Biosphere Reserve of Ta¨ı National Park, Coˆte d'Ivoire	1a	Abundance and distribution data for range of species over time	No data on illegal hunting-They talk about a human population gradient across the park, which they suggest explains pattern of abundance of species due to implied hutning pressure, but offer no direct data on hunting level
Low leopard populations in protected areas of Maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator	1a	Leopard density and poaching risk	Distribution survey
Managers' perceptions of threats to the protected areas of Kenya: prioritization for effective management	5b	studied the relative severity of threats to Kenya's 50 protected areas and their relative vulnerability to such threats based on the perceptions of protected area managers.	No spatially explicit data on hunting locations
Mapping Hotspots of Threatened Species Traded in Bushmeat Markets in the Cross–Sanaga Rivers Region	3b	Dyanmics of bushmeat markets in terms of species sold, quantaties market price etc.	No spatially explicit data on hunting locations
Monitoring Great Ape and Elephant Abundance at Large Spatial Scales: Measuring Effectiveness of a Conservation Landscape	1a	Density and signs of human disturbance including poaching	Density survey
Monitoring law-enforcement performance in nine protected areas in Ghana	2	Comparing the efficacy of law enforcement in different protected areas	No spatially explicit data on hunting locations
Multi-faceted approaches to understanding changes in wildlife and livelihoods in a protected area: a conservation case study from the Central African Republic	1a,3b	Abundance survey and market survey	No comparison in spatial data of kills sites
Not rare, but threatened: the endemic Madagascar flying fox Pteropus rufus in a fragmented landscape	1a/3d	Mangoro valley of central eastern Madagascar monitored roost occupancy and abundance- Evidence of hunting was found at three roosts	No spatially explicit data on hunting locations- information- "Two roosts in Eucalyptus plantations and six in small isolated fragments of degraded, mid elevation dense humid forest."
On the merits and feasibility of wildlife monitoring for conservation: a case study from Katavi National Park, Tanzania	1a	Distribution and abundance survey	No data on illegal hunting
Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa	1a	abundance estimate	No data on illegal hunting
People and Wildlife Interactions around Serengeti National Park, Tanzania	3a	Overview of wildlife in serengeti and peoples relationship to it	No spatially explicit data on hunting locations
Primate and ungulate abundance in response to multi-use zoning and human extractive activities in a Central African Reserve	1a	Density data and recorded all indications of human activity on transects, including logging, gathering, snare and gun hunting	Hunting data not separated from other illegal activites
Property Rights and Natural Resource Conservation. A Bio-Economic Model with Numerical Illustrations from the Serengeti-Mara Ecosystem	1a	main point of the analysis is to find under what conditions community based management and property rights of the local people might result in a higher wildlife abundance compared to the no property rights scenario.	No data primary data collected on illegal hunting/poaching. This is an economic modelling study.
Protected Area Performance and Tourism in Ghana	1a/3d	Abundance survey using patrol data- data also collected on signs of poaching but not spatially explicit	No spatially explicit data on hunting locations
Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant	5a	Analysis on genetic connectivity of elephants	No data on illegal hunting
Quantity and significance ofwild meat off-take by a rural community in the Eastern Cape, South Africa	3a	quantified the magnitude of wildlife offtake per km2 in a rural area in South Africa-The study thus quantified off-take through (1) focus groups, (2) random household surveys and (3) hunter interviews. through surveying hunters directly	No spatially explicit data on hunting locations

Reductions in Primate Abundance and Diversity in a Multiuse Protected Area: Synergistic Impacts of Hunting and Logging in a Congo Basin Forest	1a	Abundance survey	No spatially explicit data on hunting locations
Relative densities of mammals in response to different levels of bushmeat hunting in the Udzungwa Mountains, Tanzania.	1a/3d	impact of hunting by comparing densities of mammalian species and recording hunting pressure	No spatially explicit data on hunting locations- information provided "little hunted West Kilombero Scarp Forest Reserve (WKSFR), the medium-hunted Udzungwa Scarp Forest Reserve (USFR) and the intensively hunted New Dabaga Ulongambi Forest Reserve (NDUFR)"
Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area, Tanzania	1a	the social dimensions of lion hunts	No spatially explicit data on hunting locations
Roadless Wilderness Area Determines Forest Elephant Movements in the Congo Basin	1a	Looks at Elephant movement patterns in relation to roads	No spatially explicit data on hunting locations
Roadless Wilderness Area Determines Forest Elephant Movements in the Congo Basin	1a	Assessing the impact roads has on movement patterns	No spatially explicit data on illegal hunting
Savanna elephant numbers are only a quarter of their expected values	1a	Elephant density and distribution	No spatially explicit data on hunting locations
Spatial and temporal variation in meat and fish consumption among people in the western Serengeti, Tanzania: the importance of migratory herbivores	3a	Consumption of Bushmeat	No spatially explicit data on hunting locations
Spatial distribution of snares in Ruma National Park, Kenya, with implications for management of the roan antelope Hippotragus equinus langheldi and other wildlife	3d	spatial snaring patterns in National Park	Species not of conservation concern - Hippotragus equinus langheldi
Spatial patterns ofillegal resource extraction in Kibale National Park, Uganda	3d	human entry trails, wood extraction, livestock grazing, and animal poaching signs were quantified	No diffrentiation between poaching and other signs
Spatio-temporal niche partitioning between the African lion (Panthera leo leo) and spotted hyena (Crocuta crocuta) in western African savannas	1a	Camera trap images of lions and hyenas in National Park and adjacent hunting areas	No data on illegal hunting
Subsistence hunting and bushmeat exploitation in central-western Tanzania	1a,3a	Study on bushmeat exploitation in Tanzania	No spatially explicit data on hunting locations
Subsistence Hunting in Arabuko-Sokoke Forest, Kenya, and Its Effects on Mammal Populations	1a	Level of hunting in a forest in Tanzania	None of the species in IUCN endangered categories
Supplies of bushmeat for livelihoods in logging towns in the Congo Basin	3a	Economic evaluation on the value of bushmeat hunting to local household economies	No spatially explicit data on hunting locations
Survey of gorillas (Gorilla gorilla gorilla) and chimpanzees (Pan troglodytes troglodytes) in Southwestern Cameroon	1a	Data on Gorilla density	Because there is only a density estimate which is used as a proxy for hunting level but not data on hunting frequency
Surveys of lions Panthera leo in protected areas in Zimbabwe yield disturbing results: what is driving the population collapse?	1a	Call-up technique to count lion numbers (broadcast noise of hurt wilderbeest and count how many lions arrive - sex and age)	No data on illegal hunting
Sustainability and Long Term-Tenure: Lion Trophy Hunting in Tanzania	5c	Focus on sustianability of trophy hunting blockes- High hunting offtake and the resultant offtake decline tended to be in blocks under short-termtenure. In contrast, lion hunting levels in blocks under long-termtenure matched more closely the recommended sustainable offtake of 0.92 lions per 1000 km2	No data on illegal hunting
Sustainability and Long Term-Tenure: Lion Trophy Hunting in Tanzania	1a	Offtake of lions in trophy hunting concession areas	Not illegally hunted
The First Survey of the Conservation Status of Primates in Southern Burkina Faso, West Africa	1a/2d	Abundance survey and monitoring signs of poaching across- five protected areas across the southern border of Burkina Faso as follows: Pama Partial Reserve, Kompienga province (36.45 km); Arly National Forest, Gourma province (50.37 km); Comoé-Léraba Partial Reserve, Comoé and Léraba provinces (55.21 km); Koulbi Protected Forest, Poni province (47.40 km); and Nazinga Game Ranch and Reserve, Nahouri province (48.30 km)	No data on species of conservation concern
The impact of buffer zone size and management on illegal extraction, park protection, and enforcement	5b	Modelling the optimal size of buffer zones	No quantative data on illegal hunting
The impact of land reform on the status of large carnivores in Zimbabwe	1a	Denisty of carnivores across land tenure sites	No quantative data on illegal hunting
The Importance of Hunting and Habitat in Determining the Abundance of Tropical Forest Species in Equatorial Guinea	1a	Hunting data only provided for one forest area	No spatial comparison
The Importance of Hunting and Habitat in Determining the Abundance of Tropical Forest Species in Equatorial Guinea	1a/3c	many habitat variables, such as agricultural disturbance, logging and rivers, can be confounded with hunting, and the relative importance of their hunting and habitat-mediated effects may vary between species. This necessitates an approach that isolates their independent effects, so that differences in abundance due to habitat factors are not wrongly attributed to hunting. We have shown that a combination ofcurrent hunting effort and habitat effects determine the abundance ofmammal species overall, but that the relative importance of hunting and habitat varies between species and species groups. For some species the effects of hunting and habitat are clear for others with wider range areas it is less clear e.g. Mandrills M. sphinx, despite being quite heavily hunted, showed no patterns in abundance, perhaps because their wide-ranging behavior over many thousands of hectares	No spatially explicit data on hunting locations
The influence of park access during drought on attitudes toward wildlife and lion killing behaviour in Maasailand, Kenya	5b	Analysis of livestock grazing rules- conclusion: PA policies should recognize that during times of severe droughts, when pasture and water is scarce elsewhere, permitting access to PAs could improve local attitudes toward lions and other wildlife. These findings are consistent with other studies of park-people conflict in the developing world, which found that flexible PA policies may improve local tolerance ofwildlife (Newmark&Leonard 1993; Fiallo & Jacobson 1995; Allendorfet al. 2006)	No spatial data on hunting locations
The influence of rainfall on zebra population dynamics: implications for management	1a	Simulation modelling analysis of the dynamics of a plains zebra population in Laikipia District, Kenya	No spatial data on hunting locations
The nature of hunting around the Western Corridor of Serengeti National Park, Tanzania	3c	in the household is a hunter, and if so, where does that person(s) hunt, and whether the informant knows about any hunters in the village. Furthermore, the informants were asked whether they think that the current level of hunting has any effect of herbivores and carnivores, what time of year is hunting (to their knowledge) most common, and whether they have used any wildlife products during the last year	No spatially explicit data on hunting locations
The Oil Industry as an Underlying Factor in the Bushmeat Crisis in Central Africa	3b	Exploring the effects of oil exploration on tropical ecosystems	No spatial data on illegal kill sites
The performance of African protected areas for lions and their prey	1a/4	Efficacy of Protected Areas to conserve Lions- all protected areas in Africa	No comparative data or spatial distribution data on poaching/illegal hunting
The plight of Malawi's wildlife: is trans-location of animals the solution?	1a	Looking at the impact of moving species	No spatial data on hunting locations
The presence of diurnal lemurs and human-lemur interactions in the buffer zone of the Ankarana National Park	1a	assess the presence of remaining lemur populations in the buffer zone surrounding the park, and use social survey techniques to understand how local communities interact with lemur populations. We observed no visual or auditory sign of lemurs on transects throughout the buffer zone, and recorded high rates of active lemur hunting within the buffer zone and the park.	No spatial comparison between sites hunted
The relative importance of trophy harvest and retaliatory killing of large carnivores: South African leopards as a case study	1a	evaluate the relative influences of retaliatory killing and trophy harvest on leopard population persistence, and to assess the sustainability of the current leopard trophy harvest in South Africa	No spatial data on hunting locations
The Social and Ecological Integration of Captive-Raised Adolescent Male African Elephants (Loxodonta africana) into a Wild Population	1a	How captive elephants fare in a wild population	No spatial data on hunting locations
Threat reduction assessment ofconventional and community-based conservation approaches to managing protected areas in Uganda	5b	Data collected using document reviews, interviews with government officials, and surveys ofPA wardens were compared with the threat reduction assessments including a measure of poaching	threat reduction assessment - No spatially explicit data on hunting locations
Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar	1a	Camera trapping survey	No spatial data on illegal hunting
Threats to wildlife and their utilizable products in the Cross River Rainforest, Nigeria	3a/3c	Household surveys on hunting	No spatially explicit data
Trapper profiles and strategies: insights into sustainability from hunter behaviour	3c	Profile of hunters and analysis of trapping methods and effort	Location of species hunted not disclosed so cannot gage spatial distribution
Trends in populations of elephant and other large herbivores in Gonarezhou National Park, Zimbabwe, as revealed by sample aerial surveys	1a	Aerial survey on elephant numbers	No spatial data on illegal hunting
UNDERSTANDING COMMUNITY PERCEPTIONS OF LAND USE CHANGES IN THE RANGELANDS, ZIMBABWE	4	Rangeland degradation	No spatially explicit data on hunting locations
Uneconomical game cropping in a community-based conservation project outside the Serengeti National Park, Tanzania	3a	Value of bushmeat to villages	No spatial data on hunting locations
Unravelling the Pangolin Bushmeat Commodity Chain and the Extent of Trade in Ghana	3b	We found that stakeholders closer to protected areas traded more pangolins compared to those further away. Our findings are consistent with those ofFa et al. (2006), who also found that the numbers ofanimals traded declined dramatically further away from the Korup (Cameroon) and Cross River (Nigeria) National Parks. Similar results have been observed in Côte d'Ivoire (Caspary 1999), Equatorial Guinea (Fa and Gracia Yuste 2001;Fa et al. 2005), Gabon (Foerster et al. 2012) and in Ghana (Schulte-Herbrüggen et al. 2013b). This hunting in close proximity to protected areas essentially reflects decreased time, effort and costs for hunters to find wildlife (Hofer et al. 2000). Looking at bushmeat market trade in various locations	No data on location of capture for bushmeat
Using spor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density	1a	abundance estimate	No data on illicit hunting
Wild meat consumption on S; Island, West Africa: implications for conservation and local livelihoods	3a	Using household surveys to ask about bushmeat consumption	No spatial data on illegal hunting
Wildlife Conservation on the Rangelands of Eastern and Southern Africa: Past, Present, and Future	5c	An analysis on land use and trophy hunting	No quantative data collected- an opinion piece
Wildlife Depletion in a West African Farm-Forest Mosaic and the Implications for Hunting Across the Landscape	1a	Abundance survey	No spatially explicit data on illegal hunting
Wildlife Depletion in a West African Farm-Forest Mosaic and the Implications for Hunting Across the Landscape	3a	Comparison of hunting across a forest/farmland mosaic	Hunting is legal
Wildlife hunting practices and bushmeat dynamics of the Banyangi and Mbo people of Southwestern Cameroon	3c	Hunting in one forest area- more hunting occurred in interior	Hunting is legal
Wildlife species richness and densities in wildlife corridors of Northern Tanzania	1a	Density study across two land use areas	No quantative data collected on level of hunting or poaching
Wildlife species richness and densities in wildlife corridors of Northern Tanzania	1A	Study on wildlife corridors showing they are still vital and harbor relatively high mammal species richness	No data on hunting
Wildlife use and the role of taboos in the conservation of wildlife around the Nkwende Hills Forest Reserve; South-west Cameroon	3a	Questionnaire survey for households on taboos related to wildlife	No quantative data collected on level of hunting or poaching

** Search Key: Additional File 5 in Chapter 1,*
(Additional File 4 is available online as a checklist - ROSES Form (https://environmentalevidencejournal.biomedcentral.com/articles/10.1186/s13750-018-0139-x#Sec24)

Methods used to monitor illegal hunting:

1- **Species as indicator**
1a) Abundance and distribution: Collecting population data to gage temporal and spatial changes in abundance and distribution which acts as a proxy for the level of illegal hunting. Methods used to collect this data include aerial surveys, line transects, camera trapping data, monitoring spoor and track counts or presence of species, collar data, call -ups
1b) Anti-predator behaviour Using species movement data to look at anti-predator behaviour and flight initiation time either via eye or accelerometer data this give an indication of species sense of threat and can act as a surrogate for level of anthropogenic risk in the environment
1c) GPS/Radio tracking: Monitoring species killed while being GPS tracked/radio collared or through capture, mark, recapture- often as study species or for monitoring success of species reintroductions or impact of industrial development e.g. roads

2- **Law enforcement data**
2a) Carcasses data collected by wildlife authorities/anti-poaching patrol via line transects, aerial surveys and during ranger patrols can include arrest records

3- **Consumption and offtake data**
3a) Household dietary recall: Household interviews/surveys on dietary recall and expense on bushmeat- price often used as proxy of supply
3b) Bushmeat market surveys to quantify offtake - price often used as proxy of supply
3c) Hunter survey/follow and surveys with hunters on their activities
3d) Research-led data on poaching signs e.g. carcasses, snares, cartridge shells, hunting camps line transects to

4- **Tolerance and Perception on human/wildlife conflict**

Studies on perception: to measure tolerance and gage level of human wildlife conflict of communities toward species to measure tolerance

5- **Other methods**
5a) Genetic analysis to find the source location of illegal wildlife seizures or of species to trace their movement patters
5b) Modelling pre-existing data: habitat variables in relation to wildlife, calculating a threat index or monitoring species interactions and contractions in range area
5c) Analysis of legal trophy hunts
5d) Literature review of bushmeat studies

**Inclusion Sheet: Additional File 6 in Chapter 1*

Title	Country	Species- may have been other species not mentioned, contacted authors when unclear	Reasearch Method	Finding	Land tenure area	Ranger posts- detection bias around ranger posts	Water bodies- whether this is detected will be depend on the season surveyed, also different species spend very different amount of time around water so will be highly species dependent	Season variation/Precipitation-whether this is detected will be depend on the season surveyed and also the affect rain has on the species of concern	Transport corridors: roads and railways- it is easier to sell bushmeat by roads and it is most villages are located close to road networks	Study length
A comparative study on bushmeat consumption patterns in ten tribes in Tanzania	Tanzania	Elephant/Hippopotamus/Abotts Duiker	3a	Hunting decreased with distance to National Park/Protected Area	Protected Area					1 year
Analysis of human activities in and around protected areas (PAs): Case of Kakum conservation area in Ghana	Ghana	Elephant only species mentioned	3a/3d	Hunting decreased with distance to National Park/Protected Area	Protected Area					2 months
Antipoaching standards in onshore hydrocarbon concessions drawn from a Central African case study	Gabon	Forest Elephant	3d	Increased hunting in oil concession. Small and large game poaching increased with distance from town, meaning poachers were willing or obliged to travel several kilometers to hunt. This is probably because target species avoid road edges and areas under direct human influence in the study area	Private Oil Concession	The number of ranger patrols substantially increased the probability that poaching-related threats disappear at a site if threats were originally present	Hotspots of large game hunting included a band along the ocean and 2 areas along major water bodies	Mean precipitation level during patrol months had a significantly negative median value for SGH, suggesting that more hunting signs were found in the dry season	Higher SGH occurence was found farther away from roads and in areas ofhigher NPP	3 years
Are ranger patrols effective in reducing poaching-related threats within protected areas?	Rwanda	Eastern chimpanzee (Pan troglodytes schweinfurthii)	2a	Higher hunting in the interior of PA- reduced closer to range posts- lower probability of threats closer to the park boundary- Although villages are located around the park, the majority of ranger posts are also located near the park boundary; thus, poachers would be more likely to be apprehended if engaged in illegal activities near the edge of the park.	Protected Area	the importance of ranger posts in deterring illegal poaching activity; the threat map can be used as a guide to identify locations where additional posts can be established to reduce poaching- related threats.			poaching-related threats was highest at lower elevations especially in areas that were close to roads and tourist trails;	10 years
Benefits and costs of illegal grazing and hunting in the Serengeti ecosystem	Tanzania	Giraffe only applicable species mentioned	3d	level of illegal hunting decreased as the distance hunters travelled on foot to hunting areas increased- Presence of ranger posts did not have expected impact	Protected Area					11 months
Bushmeat hunting in Serengeti, Tanzania: An important economic activity to local people	Tanzania	Elephant	3a	ethnic differences determined where hunting took place across PA, Game Reserve & village, numbers of meat meals are higher in the villages close to SNP boundaries	Protected Area, Game Reserve and Customary village land					1 year
Bushmeat trade in the Cross-Sanaga rivers region: Evidence for the importance of protected areas	Cameroon and Nigeria	Primate (Bale Monkey and others)	3b	Bushmeat of all three taxa examined was more expensive in markets farthest from a National Park- price decreased the closer to PA	Protected Area				Carcasses tended to be more expensive when traded closer to roads;	6 months
Cheetahs (Acinonyx jubatus) running the gauntlet: an evaluation of translocations into free-range environments in Namibia	Namibia	Cheetah	1c	Cheetahs hunted closer to game ranching areas- proof of human wildlife conflict. 8 dies outside PA, 6 inside.	Game ranching area and Protected Area					2.5years
Cocoa Farming and Primate Extirpation Inside Cote D'Ivoire's Protected Areas	Cote D'Ivoire	Multiple Primates- Cercopithecus roloway (Roloway Monkey)	3d	Impact of cocoa farming on species survival is mixed	Private Cocoa farm					3 years
Commercial bushmeat hunting in the Monte Mitra forests, Equatorial Guinea: extent and impact	Equatorial Guinea	Multiple: Leopard (Panthera Pardus), White-bellied Pangolin (Phataginus tricuspis), Giant Ground Pangolin (Smutsia gigantea), Primate (Colobus satanas (Black Colobus), Gorilla gorilla (Western Gorilla), Mandrillus sphinx (Mandrill) , Pan troglodytes (Chimpanzee)	3c	catch per unit price increased farther from villages, Hunting decreased with distance to area of human settlement "Equally, extraction rate was positively correlated with distance from the village since interference levels and hunting pressure decreases as distance from human habitation increases"	Protected Area, Customary land area					16 months
Conservation status of chimpanzees Pan troglodytes verus and other large mammals in Liberia: a nationwide survey	Liberia	Chimpanzee	3d	more snares in non-forested areas, more gun hunting in forested areas	State owned forest land, non-forest state land					5 months
Correlates of wildlife snaring patterns in Tsavo West National Park, Kenya	Kenya	Multiple species-Giraffe	3d	There was no significant difference in snare density as the distance increased from the park border- Snare density increased with distance from park border highest at 4km then zero at 10km- Low snare numbers near homestead in this study contrary to other studies suggests that snares may be placed in suboptimal areas depending on trade off between increasing snare success and reducing probability of being arrested by security patrol rangers	Protected Area		The past six years experience by de-snaring teams in Tsavo Park reveal that snare concentration is usually high around watering points		Areas of the park adjacent to highways, trans-national borders, ranches and town strata had high wildlife snaring pressure	3 months
Declining population of the Vulnerable common hippopotamus Hippopotamus amphibius in BÃ©nouÃ© National Park, Cameroon	Cameroon	Hippo	3d	hippo density lower and signs of hunting higher near golddiggers camp	Golddiggers camp- border of private industrial area					2 year survey/ data from 20 years
Deterring poaching in western Tanzania: The presence of wildlife researchers	Tanzania	Chimpanzee, Elephant	2D	Snare density lower closer to research base	Research base and Customary village area					4 years
Distinguishing ecological constraints from human activity in species range fragmentation: the case of Cross River gorillas	Nigeria/Cameroon	Western Gorilla	1a/3d	Increased hunting closed to PAs	Protected Area					21 years
Ecological and financial impacts of illegal bushmeat trade in Zimbabwe	Zimbabwe	Multiple species- Black Rhino, Cheetah, African Elephant, Lion, African Wild Dog	2a	Hunting was more frequent close to human settlements This implies that cells closer to the boundary had more illegal hunting incidents even taking into account variation in antipoaching effort. Areas worst affected by illegal hunting were ranches settled during land reform, those adjacent to resettled ranches and those close to urban centres outside the Conservancy. Of the 59 rhinoceroses poached in the Conservancy from 2000 to September 2010, 49 were killed on or close to resettled ranches. Dramatic loss of wildlife populations followed settlement of game ranches during land reform.	Game ranching area and Conservancy		poaching incidences closer to water sources			4 years
Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa	South africa	Leopard	1c	higher mortality near border of PA	Protected Area					5 years
Efficacy of Two Lion Conservation Programs in Maasailand, Kenya	Kenya	Lions	2A	Shows the reduction in the number of lions hunted after two conservation interventions- Lions are hunted less in areas where conservation programmes offer compensation to residents for loss of livestock- Despite the 2 spikes in killings, compensation was associated with reduced lion killing over time.	2 adjacent conservation areas one with compensation scheme, one without					8 years
Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population	Namibia	Lions	1a/1c	Sixty-two out of 82 known lion mortalities were caused by humans: lions were shot or poisoned on livestock farms bordering the ENP, ies consisted of subadult males and adult females (Table 2). Subadult males formed the highest proportion of lions shot or poisoned on farmland bordering the ENP	Livestock Farms					17 years
Evidence for post-depletion sustainability in a mature bushmeat market	Ghana	Multiple species- Cercocebus torquatus (Red-capped Mangabey)	3B	No correlation between offtake and distance to city	Village lands and urban area					2 months
Explanatory factors for household involvement in illegal bushmeat hunting around Serengeti, Tanzania	Tanzania	Author contacted: Hippo, elephant, giraffe	3A	More hunting occurs in villages closer to national park- The closer to a PA, the higher was the overall bushmeat consumption (r = 0.43, p < 0.001, n = 192), and the stronger law enforcement was perceived to be, the lower was the overall bushmeat consumption	Protected Area					10 months
Forest elephant crisis in the Congo Basin.	Congo	Forest Elephant	3d	Consistent with MIKE survey data, the probability of human presence on the Megatransect decreased significantly with increasing distance from the nearest road in contrast to the probability of elephant occurrence, and was consistently lower inside protected areas compared to outside for all distances from the nearest road	2 national parks and buffer zones				We found that the probability of human presence decreased with increasing distance from the nearest road, in contrast to the probability of elephant occurrence. The probability of elephant presence increased with distance to roads, whereas that of human signs declined. no poached carcasses were found beyond 45 km of a road.	2 years and 1 year
Getting to grips with the magnitude of exploitation: Bushmeat in the Cross–Sanaga rivers region, Nigeria and Cameroon	Nigeria and Cameroon	Multiple: Panthera pardus (Leopard	3B	Distance to the main national park was significantly inversely correlated with bushmeat carcasses per inhabitant (r = 0.57, p = 0.043) or biomass per inhabitant (r = 0.74, p = 0.021). The relationship varied across species with a large proportion of species (50% in the Nigeria sample and >40% in Cameroon) showing a strong negative relationship	Protected Area and bufferzone					5 months

Hotspot elephant-poaching areas in the Eastern Selous Game Reserve, Tanzania	Tanzania	Elephants	2A	Incidences of poaching are higher on the edges of the ESGR. most poaching incidents in ESGR between 2010 and 2013 occured along the edges of the reserve because poaching mostly occurs during the rainy season lasting from MidNovember to May, the edges of the reserve were easily accessed by the poachers, who usually travel on foot. Additionally, the edges of the reserve are less risky to poachers in the same season because the reserve is bordered by open areas	Game Reserve	It tends to be difficult to transport rangers for patrol to distant and remote areas during the wet season		Poaching takes place throughout the year, but the incidences of poaching were significantly higher during the wet season than during the dry season, supporting our second hypothesis. This finding was observed because large areas of the reserve cannot be easily accessed by vehicles, as most of the roads are seasonal and cut off by flooding rivers in the rainy season. It tends to be difficult to transport rangers for patrol to distant and remote areas during the wet season. Therefore, as only a small number of easily accessible areas of the reserve are frequently patrolled, there is more room for poachers to roam around in the reserve (Nahonyo, 2005). Another important factor is that high levels of poaching during the rainy season were attributed to the closing of tourist operations such as tourist hunting, which may allow the poachers to enter the reserve without being noticed easily (EIA, 2010). The effort to combat poaching during the wet season was also undermined by poor visibility due to thick vegetation, which may make the ability to observe poachers in the wild more difficult		5 years
Hunting for Livelihood in Northeast Gabon: Patterns, Evolution, and Sustainability.	Gabon	Multiple species: Leopard	3c	Hunting with guns <5km from village, snares = <2KM from villages	Customary village land		Hunting increases in the dry		The poor state of roads in the study area was clearly a	1 year
Hunting for the Benefits of Joint Forest Management in the Eastern Afromontane Biodiversity Hotspot: Effects on Bushmeat Hunters and Wildlife in the Udzungwa Mountains	Tanzania	Abbott's duiker	3c/3d	Introduction of joint-forest management saw reduced hunting	Joint Forest Area					7 year
Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot	Botswana	Multiple Species: Felis nigripes (Black-footed Cat) Status: Vulnerable, Giraffa camelopardalis (Giraffe) Status: Vulnerable, Hippopotamus amphibius (Hippopotamus) Status: Vulnerable	3A/3c	Interviews revealed that most hunting occurs outside of protected areas between the veterinary fences that encompass the delta WMAs and the roads that encircle the delta 10–30 km from the WMA boundaries. Twenty-one percent of hunters, however, acknowledged hunting inside protected areas	Wildlife Mangement Areas					8 months
Illegal hunting and law enforcement during a period of economic decline in Zimbabwe: A case study of northern Gonarezhou National Park and adjacent areas.	Zimbabwe	African elephant (Loxodonta africana), hippopotamus (Hippopotamus amphibius), giraffe (Giraffa camelopardalis), African lion (Panthera leo)	2a/3A	Hunting decreased in PA due to increased enforcement despite economic collaphse and varied in line with law enforcement efforts.	Wildlife Management Area and Protected Area					10 years
Illegal wildlife use and protected area management in Ghana	Ghana	Elephant	2a	Commerical ivory hunting spatially more sensitive to elephant density and enforcement while subsistence is more sensitive to human population density	Customary land area					2 years
Local perspectives on factors influencing the extent of wildlife poaching for bushmeat in a game reserve, western Tanzania	Tanzania	Multiple Species: Hippopotamus, Elephant, Giraffe	3A	Hunting increases closer to reserve	Reserve			Most poaching activities were carried out in the rainy seasons	In the Mara-Serengeti region, most of the patrol roads become hardly passable during the rain seasons, hence hampering antipoaching patrols [43]. In Ugalla Game Reserve, the wet season is the most difficult time of the year for game rangers to access the reserve as many roads become muddy and impassable [44]. It is this time of the year when poachers devastate wildlife populations, taking advantage of the patrol teams' infrequent visits and poor coverage of their operations within the reserve	6 months
Pattern and sustainability of the bushmeat trade in the Haut Niger National Park, Republic of Guinea	Guinea	Colobus polykomos (King Colobus), Colobus polykomos (King Colobus) Status: Vulnerable	3B	No significant correlation between the mean number of carcasses per market and the distance between villages and the park's core area/Overall, the mean number of carcasses per market in villages located along the roads that mark the limit of buffer zone (12.6 ± 8.2 SD, n = 4) did not differ significantly from that of villages located off roads	Protected Area and Customary Village Land			In the HNNP, the bushmeat trade is the highest during the mid dry season (greatest number of carcasses and largest biomass). This is the favoured hunting period because annual grasses (mainly from the Gramineae family) that grow during the rainy season and reach their maximum height in October are burnt (by both hunters and cattle herders) at the onset of the dry season, thus allowing good visibility for hunting. In addition, men are fully available for hunting activity because no farming is carried out during this period (first field work begins at the onset of the rainy season). Unlike ungulates and rodents, primates are mainly traded from the mid to late rainy season. However, primates are considered crop pests and are actively shot when they try to raid crops during the rainy season. A similar pattern has been documented in other places	The number of carcasses counted in villages bordering a heavily trafficked road was significantly higher than in more rural villages, thus highlighting the stimulating effect of roads on the bushmeat trade. Villages located along the roads that mark the limit of the buffer zone tend to be more populated than those off roads. Although there are few forest people inhabiting the Haut Niger region, Faranah (which is located along a highly trafficked paved road) is an important stopover where bushmeat is purchased by people from the forest region when travelling from (or returning to) their native region. This emphasizes the key role that large roads play in the bushmeat trade. Trafficked roads stimulate commercial hunting because of the opportunity created to sell large volumes of bushmeat (Wilkie et al., 2000; Eddeni & Dame, 2006). The large number of game carcasses traded in the four villages of sector B in the HNNP is best explained by the fact that these villages are located along the sole paved road that connects the central part of Guinea to the eastern part and to neighbouring countries (Mali, Ivory Coast) with which an intense commercial trade exists.	1 year
Poaching risks in community-based natural resource management.	Namibia	Multiple species: Hippopotamus, Leopard, Lion	3d/3a	Hunting increased with increased proximity to national park/protected area, areas with documented poaching events did not correspond to those areas perceived by stakeholders to have high poaching risks.	Protected Area and Customary Village Land				The perceived livelihood risk was highest near residential areas and along roads and trails- this proved to be true	7 years
Predictors of elephant poaching in a wildlife crime hotspot: The Ruvuma landscape of southern Tanzania and northern Mozambique	Mozambique and Tanzania	Elephant	2a (aerial survey)	In Mozambique, the number of elephant carcasses is positively associated with State-managed protected areas. In Tanzania, elephant carcasses are positively correlated with community-managed sites. Community-managed protected sites (WMA) in Tanzania have a strong positive relation to the number of elephant carcasses. Implementation of these reserves has been considered top-down, reducing community support for conservation actions	community-managed site and protected area			warmest sites with lowest rainfall is where carcass numbers were highest- lowest elevation areas- hese predictors are also good proxies of the detectability of poaching, and our results show fewer elephant carcasses in forested areas. Carcasses are more difficult observed in forested areas by aerial censuses and poachers presumably have as well greater freedom of action without been detected		2 months
Preliminary assessment of the impacts of human activities on gorillas Gorilla gorilla gorilla and other wildlife at Dzanga-Sangha Reserve, Central African Republic	Central African Republic	Gorilla	3d	the use of illegal snares in the hunting zone closest to the population centre appeared to be more intense than in the remote hunting zone	Customary village land and Reserve		hunting heavier around water bodies			1 month
Rates and causes of mortality in Endangered African wild dogs Lycaon pictus: lessons for management and monitoring	SA, Zambia, Zimbabwe, Ken	African Wild Dog	1C	Highest death caused by anthropogenic causes outside National Park, most natural deaths inside PA	Protected Area				Deaths higher near roads- roadkill	15 years
Spatial analysis of aerial survey data reveals correlates of elephant carcasses within a heavily poached ecosystem	Tanzania	Elephant	2a (aerial survey)	Poaching unaffected by proximity to ranger posts.	Protected Area	Our analysis provides evidence that different ranger posts show different correlations with carcass distribution. In essence, our evidence suggests that whilst most ranger posts have no discernible impact on the distribution of carcasses, a small number such as the Ruaha National Park headquarters at Msembe are associated with fewer elephant carcasses in their immediate vicinity, whilst others seem associated with higher occurrence of carcasses. Variation in the numbers of carcasses in the areas around ranger posts could reflect both different resource allocation between posts and other activities associated with ranger posts	poachers operate near waterholes where elephant activity is likely high and during the wet season when ranger patrols activity is minimal.			3 years

Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks	Zambia	African wild Dog, Elephant, Leopard, Lion, Hippo, Giraffe	2a	Huting higher on the border of protected area in the buffer zone, decresed toward interior	Protected Area and neighbouring community GMA	snaring occurred in close proximity to tourism camps, ranger outposts, and other potential poaching deterrents.	Snaring largely occurred within 10 km of water and also closer to crops which corresponds with water			1 year 3 months
The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk	Zimbabwe	Lions	1C/2D	Illegal conflict related deaths highest in communal lands but snares hihgest in other land types i.e. PA, Game Reserves and trophy hunting areas. snaring bycatch was lower in communal lands than in other land use types, and that it decreased as distance to a household increased	PA, Game Reserves and trophy hunting areas		Regarding lion habitat selection, both sexes avoided communal lands compared to other land use types and selected areas close to waterholes, snaring decreased as distance to water increased		distance to the railway line with mortality decreasing as the distance to the railway line increas	3 years
The pattern of poaching signs in Ugalla Game Reserve, western Tanzania	Tanzania	African elephant Loxodonta africana	2D	The rate of encountering wire snares was the lowest in the reserve.	Game Reserve and surrounding area				Mentioned in another study- For example, it has been reported that in rainy seasons, remote places suffer from poaching as antipoaching patrols are constrained by muddy and hardly passable roads (WD, 1998; FCF, 2008)	4 months
The role of bushmeat in a West African agricultural landscape	Ghana	Multiple species: White bellied pangolin and elephant	3A/3C	Households closer to urban centre still hunt but less than those in rural locations. A household's access to fresh bushmeat, especially in the more rural villages, depended upon their own hunting activities or a close relationship with a hunter where households closer to urban centre reported rarely obtaining bushmeat from hunters but instead from urban markets, which sourced bushmeat from a wide area.	Urban settlement and Rural Customary Land area			These hunters were responding to economic signals and the seasonally changing profitability of different activities. In Jachie and Kwaman firearm hunters tended to rely on hunting income mainly during times of low agricultural activity. Hunting thereby potentially served as a safety net. Previous studies (SchulteHerbrüggen, 2010, in Ghana; Solly, 2004, in Cameroon; de Merode et al., 2004, in Democratic Republic of Congo) found similar evidence that bushmeat hunting secured a small but reliable income during the lean agricultural season.		2 months
The role of incentive mechanisms in wildlife management: A case study of Moyowosi Game Reserve and Serengeti National park, Tanzania	Tanzania	Elephant	2a	Elephant poaching higher in game reserve than in national park- due to having two different bodies that manage these protected areas, government market failure was identified in Moyowosi game reserve than Serengeti national park.	game reserve and national park					
The status of anthropogenic threat at the people-park interface of Bwindi Impenetrable National Park, Uganda.	Uganda	Mountain Gorilla, chimpanzee (Pan troglodytes), elephant, African golden cat	3d	Hunting increased toward interior of park- not seen within 150metre of park boundary	Protected Area					3 years
Unravelling the Pangolin Bushmeat Commodity Chain and the Extent of Trade in Ghana	Ghana	Pangolins	3A/3B	Hunting increased with proximity to PA and more pangolins for sale closer to PA	Protected Area				direct sales to consumers, often located on busy roadside verges,	5 months
Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon.	Gabon	Multiple species: Mandrillus sphinx (Mandrill), Gorilla gorilla (Western Gorilla), Pan troglodytes (Chimpanzee)	3d	Hunting increased closer to human settlement	Customary village land		The clustering of most villages along roads and rivers may buffer remote forest from the effects of small-scale hunting. We expected that species richness would asymptote at some distance from the nearest village. Instead, species richness increased linearly with distance.		60 small villages located along three main roads, two active logging concessions	1 year
Wildlife hunting practices and bushmeat dynamics of the Banyangi and Mbo people of Southwestern Cameroon	Cameroon	Multiple Species: Mandrill (Mandrillus leucophaeus) and chimpanzee (Pan troglodytes), Cross-River Gorialla (Gorilla gorilla diehli), Black-bellied Pangolin, White-bellied Pangolin, Cercopithecus erythrotis (Red-eared Monkey), Elephant, Cercocebus torquatus (Red-capped Mangabey	3c	Hunting in one wildlife sanctuary- more hunting occurred in interior	Wildlife sanctuary				No such road and bridge network ever reached the Mbo lands and the only means of transport to Mbo communities is a strenuous 6–10 h hike through thick forest. This in turn dissuades Ministry of Agriculture and Ministry of Environment and Forests extension officers posted to Mbo	11 months
Wildlife snaring - an indicator of community response to a community-based conservation project.	Zambia	Multiple species: Lion, Elephant	3d/3a	Hunting increased with proximity to PA- On average, respondents set snares 1.6 km (SE 2.0) away from their village. 28 per cent admitted snaring in the national park.	Protected Area		84% of respondants to interviews said they set snares along the Lusangazi River, which borders South Luangwa National Park, Most of its 750 people live along the Lusangazi River, where there are fertile alluvial soils for growing maize, sorghum, groundnuts and other food crops.	the dry season was preferred for snaring. The main reason given was that animals were easier to catch due to the high concentrations of wildlife at water sources and known feeding sites.		4 months
Spatiotemporal trends of illegal activities from ranger-collected data in a Ugandan national park	Uganda	Multiple species	3d	Hunting decreased with distance to human settlement, more hunting closer to refugee camp	Refugee camp and Customary village land					

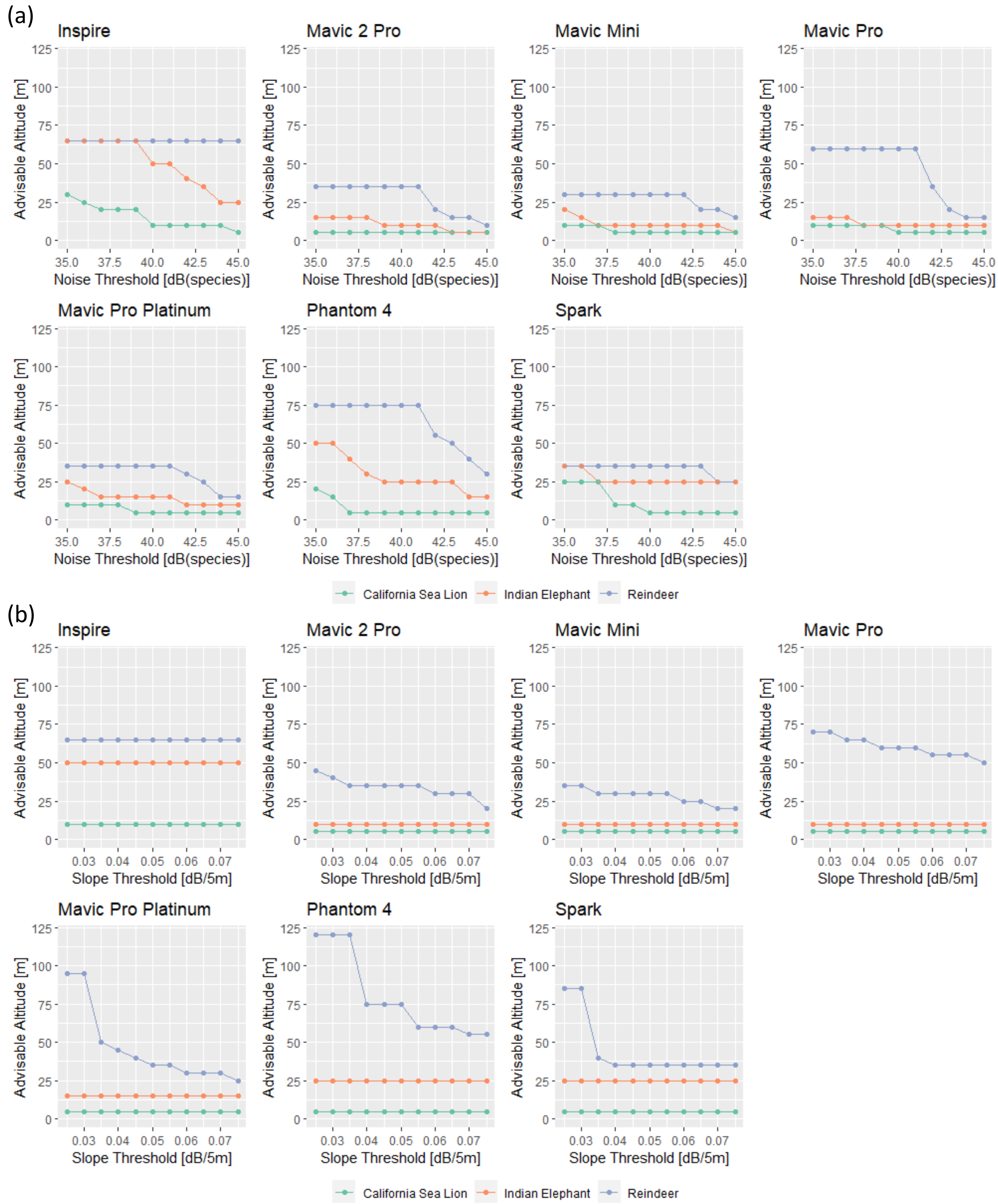


Figure S1. Sensitivity of advisable altitude to the choice of noise threshold (a) and slope threshold (b). The thresholds chosen for the final analysis in this study were 40 dB(species) and 0.05 dB/5m.

		UAV SYSTEM						
Target Species		**Inspire**	**Mavic 2 Pro**	**Mavic Mini**	**Mavic Pro**	**Mavic Pro Platinum**	**Spark**	**Phantom 4**
Common name and species	**Classification**	**Upper rows: Advisable altitude to fly (metres)** Lower rows: dB(*species*) at the advisable altitude						
Common harbor seal (*Phoca vitulina)*	Carnivora Pinnipedia Phocidae	**90**	**50**	**35**	**65**	**65**	**35**	**75**
		27	23.7	23.6	23.9	23.2	24.2	23.9
California sea lion (*Zalophus californianus)*	Carnivora Pinnipedia Otariidae	**90**	**40**	**30**	**60**	**50**	**35**	**75**
		28.2	25.4	25.8	25.4	25.2	25.7	25.3
Northern fur seal (*Callorhinus ursinus)*	Carnivora Pinnipedia Otariidae	**65**	**30**	**25**	**35**	**35**	**35**	**55**
		34.6	33.3	33.5	32.3	32.4	32.2	32.7
Harp seal (*Pagophilus groenlandicus)*	Carnivora Pinnipedia Phocidae	**90**	**55**	**45**	**85**	**100**	**115**	**120**
		16.7	11.6	11.2	11.6	10.8	11	12.1
Spotted seal (*Phoca largha*)	Carnivora Pinnipedia Phocidae	**90**	**65**	**45**	**105**	**80**	**85**	**120**
		54.2	50	49.4	49.3	49.2	49.6	50.4
Sea Otter (*Enhydra lutris*)	Carnivora Mustelidae	**65**	**35**	**30**	**35**	**35**	**35**	**60**
		45.6	43.1	43.1	43.1	43.1	43.1	42.9
Rhesus macaque (*Macaca mulatta)*	Primates Cercopithecidae	**65**	**45**	**30**	**70**	**55**	**35**	**75**
		42.4	39.5	39.5	38.9	38.8	39.3	39.3
Japanese macaque (*Macaca fuscata)*	Primates Cercopithecidae	**65**	**80**	**45**	**105**	**100**	**85**	**120**
		47	42.9	42.3	42.7	42.3	42.5	43.5
Vervet monkey (*Chlorocebus pygerythrus)*	Primates Cercopithecidae	**65**	**75**	**60**	**85**	**100**	**115**	**120**
		47.7	42.4	40.6	42	40.6	40.7	42.1
De Brazza's monkey(*Cercopithecus neglectus)*	Primates Cercopithecidae	**65**	**50**	**35**	**70**	**95**	**85**	**120**
		43.7	40.1	40.2	40.6	39.7	39.8	40
Yellow baboon (*Papio cynocephalus)*	Primates Cercopithecidae	**65**	**50**	**35**	**70**	**95**	**85**	**120**
		47.3	43.9	44.5	44	43.4	43.4	43.9
	Primates	**65**	**55**	**35**	**80**	**95**	**115**	**120**

Chimpanzee (*Pan troglodytes*)	Homininae	43.4	38.9	39.3	39.3	38.4	38.2	39.1
Reindeer *(Rangifer*	Cetartiodactyla	**65**	**35**	**30**	**60**	**35**	**35**	**75**
tarandus)	Cervidae	43.8	41.4	41.4	41.4	41.4	41.4	41
White-tailed deer	Cetartiodactyla	**65**	**35**	**30**	**60**	**35**	**35**	**75**
(*Odocoileus virginianus)*	Cervidae	46.9	44.5	44.6	44.2	44.4	44.5	44.1
Domestic goat	Cetartiodactyla	**90**	**75**	**55**	**105**	**95**	**110**	**120**
(*Capra hircus)*	Bovidae	55.6	50.9	49.9	49.9	49.6	49.8	50.9
Domestic cattle	Cetartiodactyla	**65**	**35**	**30**	**50**	**35**	**35**	**75**
(*Bos Taurus)*	Bovidae	54.8	52.3	52.4	52.2	52.2	52.4	51.9
Alpaca	Cetartiodactyla	**65**	**40**	**30**	**65**	**40**	**35**	**75**
(*Vicugna pacos)*	Camelidae	45.1	42.7	42.6	42.4	42.1	42.6	42.3
Indian elephant	Proboscidea	**65**	**80**	**90**	**80**	**100**	**115**	**120**
(*Elephas maximus)*	Elephantidae	35.9	28.5	26	30.1	27.1	27.1	29.9
Domestic horse	Perissodactyla	**65**	**75**	**45**	**85**	**95**	**85**	**120**
(*Equus caballus)*	Equidae	40.6	36.4	35.3	35.9	35.2	35.5	36
Unweighted		**60**	**105**	**45**	**105**	**80**	**75**	**45**
		57.5	47.3	46.4	47.3	47.2	46.6	57.6

Table S1. Advisable flight altitude (metres, white background) and corresponding sound level (dB(species), grey background) based on drone recordings and species audiograms computed only based on the point where sound level no longer significantly declines with higher altitude (i.e. without an acceptable SPL threshold).

Appendix 1. Image list

Table 1: Images from the training site

Note:

- Due to slicing with overlapping the total number of elephants for the whole image may be less than the total number of elephants from subimages of this image as some elephants can be counted more than once if they appear in several subimages

Date	Time (UTC)	Satellite	Resolution	Cloud cover	Off-Nadir	Sun-Elevation	Number of elephants	Image ID
01_12_2014	08.12	WV3	36cm	6%	22.4°	62.59°	Training: 187 Validation:52 Test: 10	10400100048A0A00
03_04_2017	08.37	WV3	33.44 cm	0	16.2°	44.14°	Training: 26 Validation: 19 Test: 5	104001002A937D00
29_01_2016	08.27	WV3	31.92 cm	0	9.2°	60.68°	Training:178 Validation:9 Test:11	104001001715F800
10_02_2016	08.38	WV3	37cm	0	24.4°	56.2°	Training:259 Validation: 19 Test: 32	104001001874C700
08_10_2018	08.34	WV4	34.07 cm	0	17.14°	55.36°	Training:119 Validation:1 Test: 59	825a438a-4704-46b9-b4e3-9a6d750d42f3-inv
27_03_2018	08.27	WV4	33cm	0	13.4°	44.83°	Training:236 Validation:16 Test:24	c1f56965-3f5d-42d8-abeb-2db75b747848-inv
20_01_2019	08.42	WV3	32.92 cm	0	13.8°	63.11°	Training only:22	1040010045D30C00
22_11_2017	08.24	WV4	32.86 cm	18%	12.06°	64.62°	Training only:10	761e95c2-e4fd-497c-813a-100f53ea17f3-inv
11_01_2018	08.33	WV4	35cm	0	20.9°	62.95°	Training:117	8f9b42bd-0988-4072-984a-

Appendix 2. Comparison of human and machine results on individual images

Here additional analysis comparing human and CNN performances on the test sub images are shown. These examples expand on Section 3.1 of the main paper.

Figure 1 shows the results on individual sub images. This confirms overall competitive performance between machines and humans. The figure indicates the diversity of human results. For half of the sub images the human performance ranges from 0 to 1. One can also notice that some of the sub images were difficult for humans and easier for the CNN models and vice versa. We further investigate four of such sub images below.

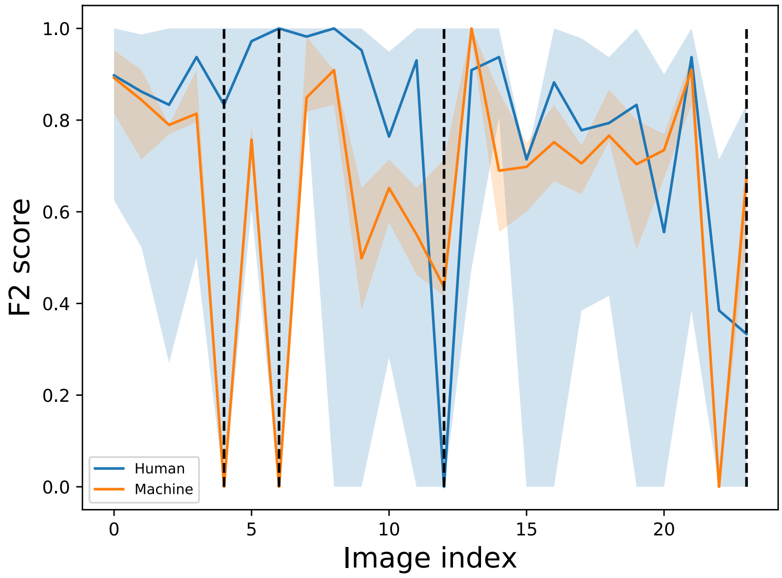


Figure 1 F2 score obtained by human and machine on individual sub images. Solid lines show the median performances and shaded areas represent the range between the minimum and the maximum F2 score. Vertical dashed black lines indicate sub images investigated further.

To analyse the difference in difficulty between the humans and CNN models we show detections on four test sub images. These show a significant difference between human and CNN performance. For each of the sub images we find a median human and CNN model performance and visualise these.

Figure 2 presents detections in sub images where human detection outperforms the CNN models. Although in general the CNN models show better results in the heterogeneous environment, they failed to detect an elephant in the forest area in sub image 4. Sub image 6 is the only test sub image without elephants. Most humans correctly identify the absence of elephants, whereas the CNN produces several false positives detections. This may be the results of hyperparameter tuning to increase overall F2 score, i.e. false positives are punished less than false negatives.

Figure 2 Sample showing human and CNN detections where the humans outperform CNN models. CNN detections are (green boxes) and ground truth labels (red boxes) and human labels (magenta circles). Raw images on left, detections on right. Satellite image (c) 2020 Maxar Technologies

Figure 3 provides detections in sub images where the CNN models outperform humans. Despite the fact that in general the CNN models performed worse in the homogeneous environments, in sub image 12 they manage to detect elephants in the open grassland while the majority of the humans did not identify these elephants. The CNN models also detected more elephants in the forest area in sub image 23 than an average human did.

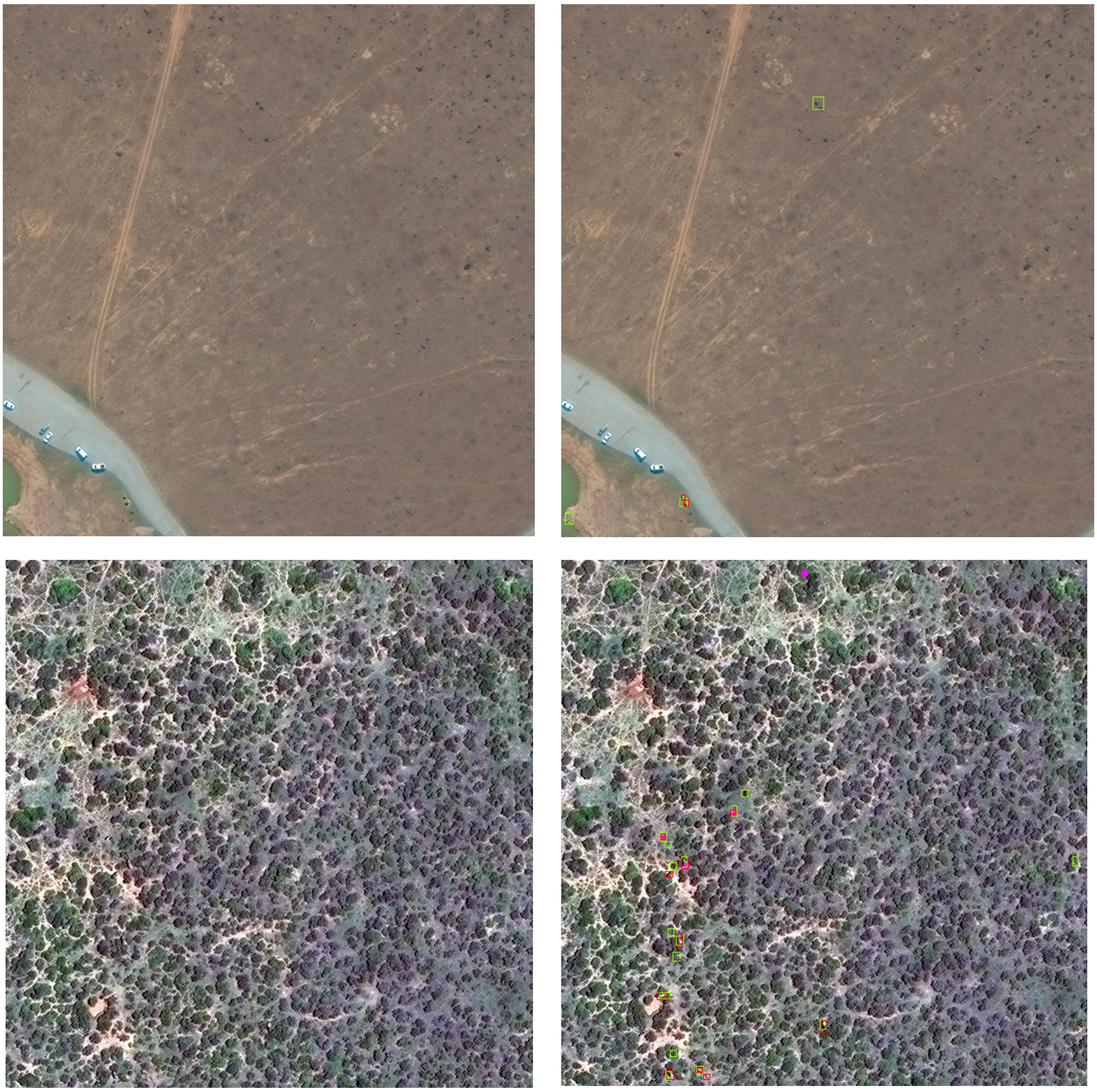


Figure 3 Image with CNN detections (green boxes) and ground truth labels (red boxes) and human labels (magenta circles) Sample human and CNN detections where the CNN models outperform humans. Raw images on left, detections on right. Satellite image (c) 2020 Maxar Technologies

Chapter 4

Supplementary Material

Spatial covariates included in movement model

Table S1: Sources for spatial covariates and the biological variables they represent in the context of elephant biology.

Biological Variable	Input Data	Source
Habitat Type	Land Cover (20m resolution)	Sentinal-2 satellite data from the European Space Agency
Habitat Productivity	Normalised Difference Vegetation Index (20m resolution)	
Availability of Water	Digitised rivers and seasonal water points (48-54 cm resolution)	Worldview-2 imagery
Elevation	Digital Elevation Model (30m resolution)	Shuttle radar topography mission
Rainfall	Precipitation in mm/month (0.05 deg resolution)	Climate Hazards Group InfraRed Precipitation with Stations Data
Land Surface Temperature	Air temperature at altitude 2m (0.01 deg resolution)	ERA5-Land monthly average data

The eleven classes from the land cover layer are reclassified into four broad groups – forest (i.e., tree cover areas, sparse vegetation), wooded savannah (i.e., shrubs cover areas), open savannah (i.e., grassland), and other types (i.e. cropland, bare areas, built-up areas, open water vegetation aquatic or regularly flooded) to reflect habitat categories relevant to elephant ecology. The proportion of points per day that fell in each of the first three categories is obtained by sampling the habitat categories under the observed movement points to derive a proxy of time spent in different habitat types over the course of the day. This created three variables: proportion of points in forest, wooded savannah and open savannah, respectively. To describe habitat productivity, the mean NDVI value for each pixel over 2019 was calculated. To create the variable average productivity, the values from the annual mean NDVI layer were sampled under observed points and summarised as the mean per day.

Availability of water across the study area was calculated as the distance to nearest digitised river and seasonal water points for each point, and summarised to give a daily average distance to water. The availability of water at both rivers and man-made waterpoints is seasonal throughout the study area. During the dry season, human herders dig waterholes on the banks of the river to enable their livestock to drink, which elephants and other wild animals then utilize. The presence of human footprint across the landscape was described similarly by calculating the distance to nearest digitised human feature and again summarised as the mean value per day, with high values representing days on average further from bomas, and low values the converse.

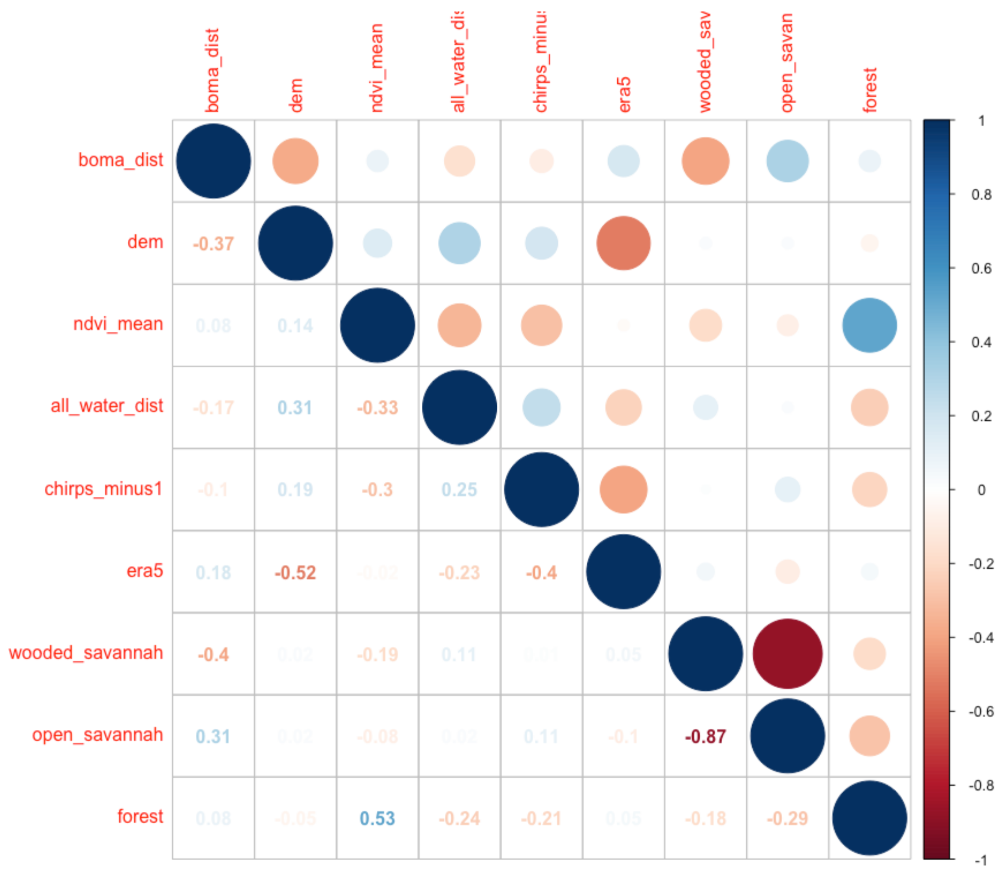
For our three physical/climatic variables (elevation, temperature, and precipitation), there was no further processing of the input layers and the values under observed points were sampled directly off the input rasters. For temperature and precipitation, the data is provided at a monthly temporal resolution, and the time stamp for the location data was used to match this to the closest month. The temperature and elevation data was summarised to give mean daily elevation and temperature. The CHIRPS data was used to assign each day to either “wet” or “dry” season based on a threshold of 50 mm/month in the month prior to the observed point. This threshold was selected based on a visual inspection of the annual distribution of rainfall over the study period. By assigning wet or dry per day using the spatially explicit precipitation layer, we account for spatial and temporal variation in the onset of rain across the study area. Air temperature at an altitude of 2m is used from the ERA5-Land monthly average data at a 0.1 deg resolution. Prior to sampling, both the GPS locations and environmental layers were projected to WGS 84/UTM Zone 37N (using bilinear interpolation for continuous rasters, and nearest neighbour for categorical).

Tracking data

The tracking data is collected via hourly GPS fixes from elephant collars. These collars come from five different companies (Africa Wildlife Tracking, Savannah Tracking, Lotek, Followit, Vectronic-aerospace), different models are deployed on different individuals at various times and are removed or replaced as necessary due to loss of battery life, mortality, connection error, or damage.

Explanatory variables

Figure S1: Correlation plot of our daily summarised explanatory variables generated using the function *corrplot()* from the eponymous R package. Note the strong negative correlation between the proportion of points in wooded savannah (wooded_savannah) and open savannah (open_savannah).



Linear-mixed effects model outputs

Table S2: Full output from the final models for Daily Travel Distance (travel_dist_km) and Night Day Ratio (DNR). The p values shown below are a simple approximation, based on the t-statistics and using the normal distribution function, for the drop-p value from likelihood ratio tests (LRTs) see further below. The marginal R-squared considers only the variance of the fixed effects, while the conditional R-squared takes both the fixed and the random effects into account (based on Nakagawa et al. 2017). For season, our reference category (the intercept) relates to dry season.

	travel_dist_km			DNR		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	93.1206	61.6374 – 124.6038	**<0.001**	-23.8989	-30.2014 – -17.5964	**<0.001**
season_alt [rainy]	1.2981	1.0487 – 1.5475	**<0.001**	-0.2180	-0.3130 – -0.1230	**<0.001**
dem	-0.0095	-0.0109 – -0.0081	**<0.001**	0.0005	0.0003 – 0.0008	**<0.001**
ndvi_mean	-13.4033	-15.6710 – -11.1355	**<0.001**			
all_water_dist	0.0003	0.0002 – 0.0004	**<0.001**	0.0000	0.0000 – 0.0001	**0.005**
boma_dist	-0.0004	-0.0006 – -0.0001	**0.003**	-0.0003	-0.0003 – -0.0002	**<0.001**
wooded_savannah	-1.0723	-1.5153 – -0.6294	**<0.001**			
forest	4.2807	3.3383 – 5.2231	**<0.001**			
era5	-0.2405	-0.3447 – -0.1363	**<0.001**	0.0824	0.0616 – 0.1033	**<0.001**
season_alt [rainy] * boma_dist				0.0001	0.0001 – 0.0002	**0.001**
Random Effects						
σ^2	12.30			0.51		
τ_{00}	6.83 $_{name}$			0.01 $_{name}$		
ICC	0.36			0.02		
N	27 $_{name}$			27 $_{name}$		
Observations	4722			4722		
Marginal R^2 / Conditional R^2	0.114 / 0.430			0.049 / 0.070		

Likelihood Ratio Tests: Daily Travel Distance

There was no support for the inclusion of an interaction term between distance to boma and season from the LRT statistic using single term deletions from the full model.

```
Single term deletions

Model:
travel_dist_km ~ season_alt + dem + ndvi_mean + all_water_dist +
    boma_dist + wooded_savannah + forest + era5 + boma_dist:season_alt +
    (1 | name)
                     npar   AIC     LRT   Pr(Chi)
<none>                    25364
dem                     1 25530 167.819 < 2.2e-16 ***
ndvi_mean               1 25495 132.552 < 2.2e-16 ***
all_water_dist          1 25382  19.817 8.523e-06 ***
wooded_savannah         1 25384  21.997 2.731e-06 ***
forest                  1 25441  78.938 < 2.2e-16 ***
era5                    1 25382  20.131 7.232e-06 ***
season_alt:boma_dist    1 25363   0.352    0.5528
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

After removal of the higher-level interaction term, all variables were statistically significant at the 0.05 level.

```
Single term deletions

Model:
travel_dist_km ~ season_alt + dem + ndvi_mean + all_water_dist +
    boma_dist + wooded_savannah + forest + era5 + (1 | name)
                npar   AIC     LRT   Pr(Chi)
<none>               25363
season_alt         1 25463 102.620 < 2.2e-16 ***
dem                1 25530 169.230 < 2.2e-16 ***
ndvi_mean          1 25493 132.449 < 2.2e-16 ***
all_water_dist     1 25380  19.545 9.823e-06 ***
boma_dist          1 25369   8.601   0.00336 **
wooded_savannah    1 25383  22.499 2.103e-06 ***
forest             1 25439  78.739 < 2.2e-16 ***
era5               1 25381  20.466 6.070e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Likelihood Ratio Tests: Night Day Ratio

There was support for the inclusion of an interaction term between distance to boma and season from the LRT statistic using single term deletions from the full model. The variables average productivity (ndvi_mean), proportion of points in wooded savannah (wooded_savannah), and forest (forest), were excluded from the final models based on lack of support from LRT statistic.

```
Single term deletions

Model:
DNR ~ season_alt + dem + ndvi_mean + all_water_dist + boma_dist +
    wooded_savannah + forest + era5 + boma_dist:season_alt +
    (1 | name)
                     npar   AIC    LRT   Pr(Chi)
<none>                    10262
dem                     1 10275 14.525 0.0001383 ***
ndvi_mean               1 10260  0.054 0.8165954
all_water_dist          1 10268  7.466 0.0062880 **
wooded_savannah         1 10262  1.369 0.2420224
forest                  1 10262  1.450 0.2284988
era5                    1 10320 59.056 1.533e-14 ***
season_alt:boma_dist    1 10272 11.056 0.0008839 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Marginal Effect Plots: Daily Travel Distance

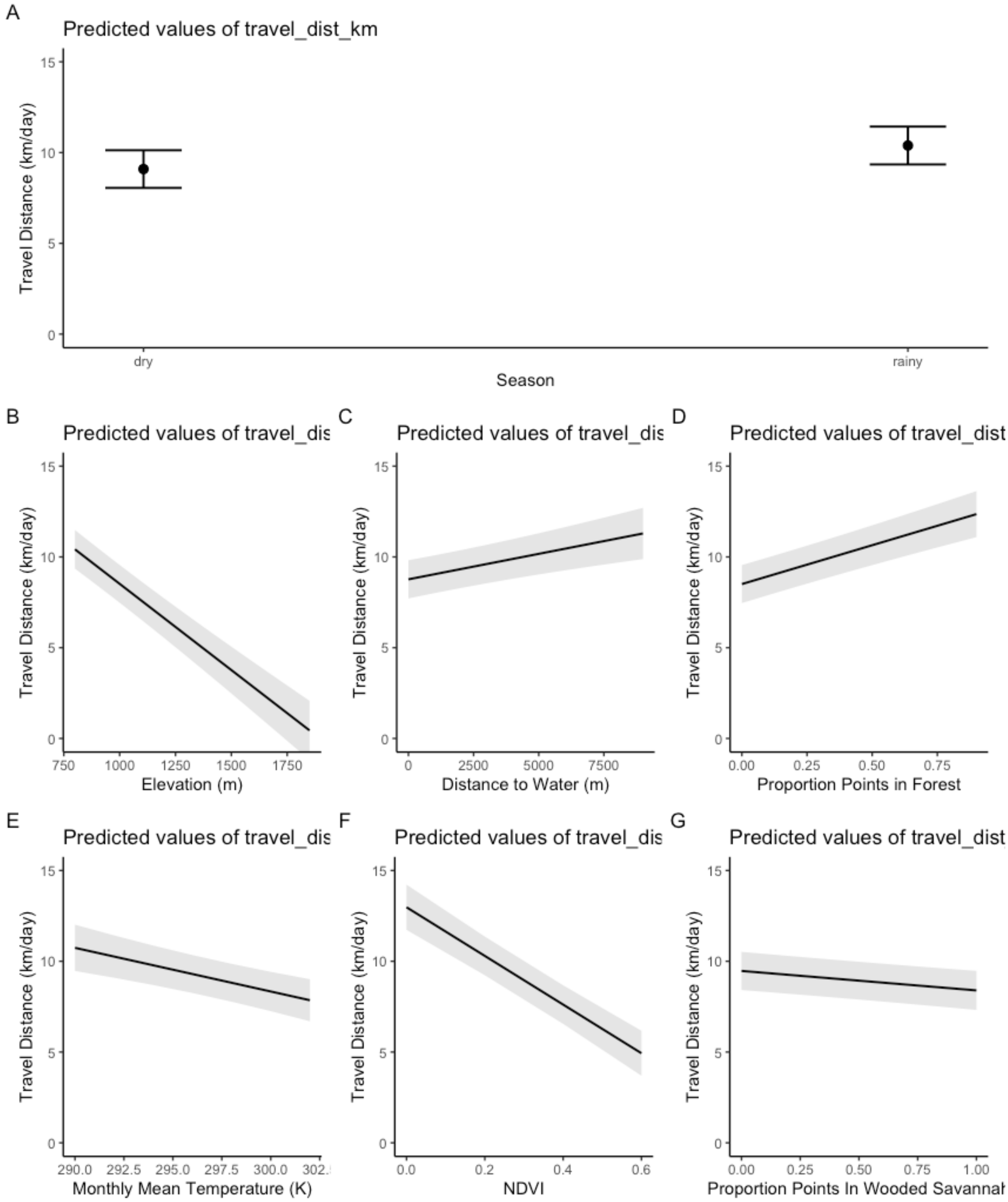


Figure S2: Predicted values of response for each focal explanatory variable generated the same way as Figure 3 in the main text.

Marginal Effect Plots: Night Day Ratio

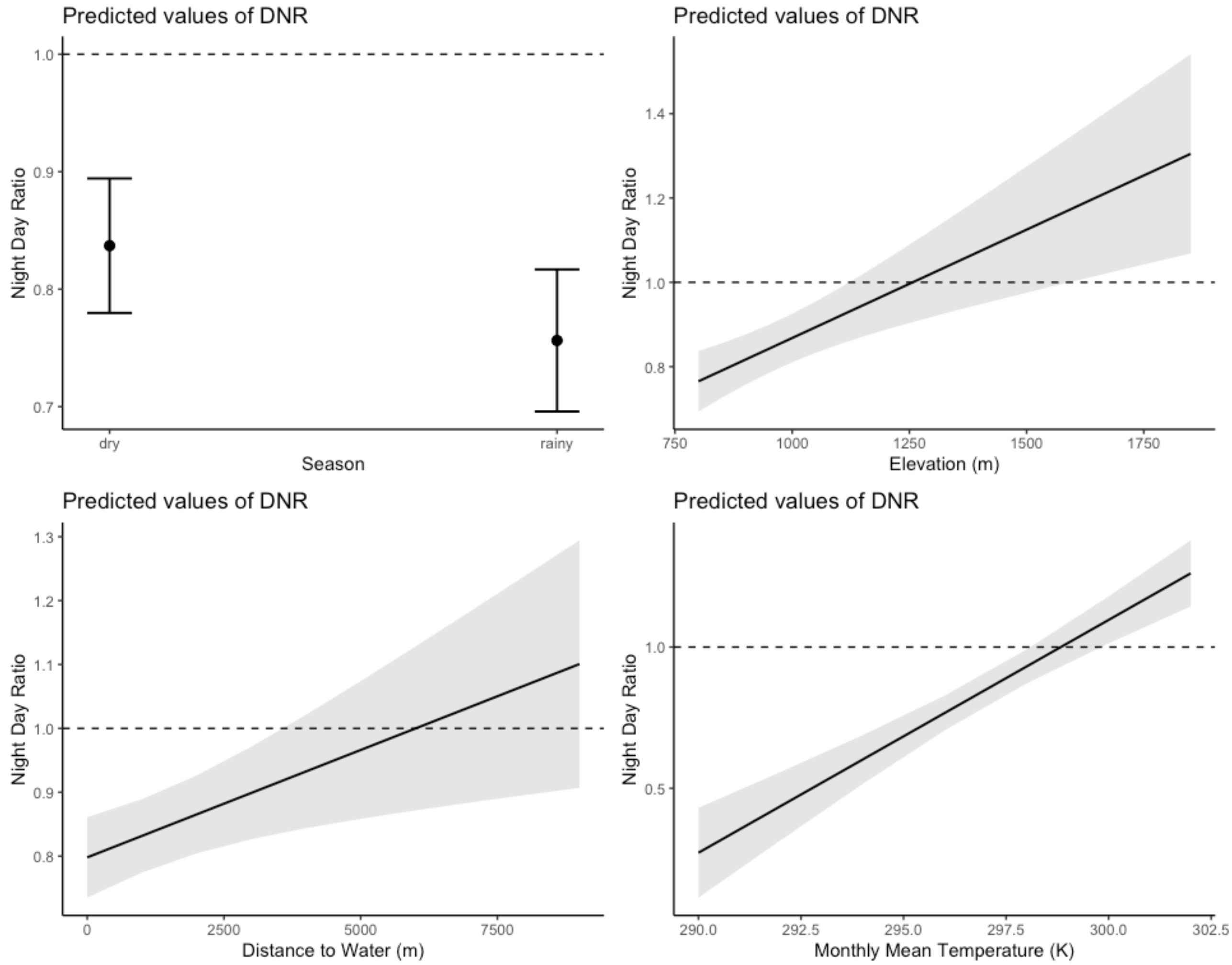


Figure S3: Predicted values of response for each focal explanatory variable generated the same way as Figure 3 in the main text. Dashed horizontal line at 1 represents equal travel during the night and the day periods.

References

Nakagawa S, Johnson P, Schielzeth H (2017) *The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisted and expanded.* J. R. Soc. Interface 14. doi: 10.1098/rsif.2017.0213