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Quantifying the exploitation of terrestrial wildlife in Africa

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SUMMARY

The overexploitation of wild animals is one of the greatest threats to biodiversity and to millions of people depending on wild meat for food and livelihoods, yet broad-scale data to evaluate species' declines are limited. The aim of my thesis is to create a database of the exploitation of terrestrial animals (hereafter 'wildlife') in Africa and, using this database as a tool, explore questions relating to the exploitation of wildlife in Africa.

Following the introduction in Chapter 1, Chapter 2 provides the methods used to develop and populate the database, and collate studies on the exploitation of wildlife in Africa. Descriptive statistics are then presented that highlight different aspects of the collated data.

Using a database of wildlife harvests across Central Africa, I compared three non-spatial and one spatial method of quantifying the total annual biomass of harvested wildlife in Chapter 3. Furthermore, I investigated the socioeconomic and environmental drivers of exploitation, and used this information to spatially map harvested wildlife.

In Chapter 4 I proposed two novel indicators for harvested terrestrial species: the mean body mass indicator assessing whether hunters are relying increasingly on smaller species over time; and the offtake pressure indicator as a measure of harvesting pressure on wild animals within a region.

In Chapter 5, I further developed the indicators of exploitation and investigated trends in taxonomic composition and mean body mass of harvested individuals, in relation to accessibility to urban centres and over time.

Using African pangolins as a case study, I demonstrate that collating local-scale data can provide crucial information on regional trends in exploitation of threatened species to inform conservation actions and policy (Chapter 6) by analysing trends in the number and price of pangolins harvested and sold over time.

The final chapter (Chapter 7) of this thesis contains the discussion of the overall findings from the thesis, and my overall conclusions.

Declaration

The thesis conforms to an 'article format' in which the middle chapters consist of discrete articles written in a style that is appropriate for publication in peer-reviewed journals in the field. The first and final chapters present a synthetic overview and overall discussion of the field and the research undertaken respectively, while chapter 2 is a general methods section describing data collation and storage.

Chapter 3 is written in the style of an article appropriate for *Conservation Biology* as:

Ingram, D. J., Coad, L. and Scharlemann, J. P. W. 2017. Quantifying the harvest of wildlife in Central Africa. *Conservation Biology.*

The author contributions are as follows: DJI collated all data, conducted all data curation, formal analyses, visualization, and wrote the manuscript; LC and JPWS provided supervision, and reviewed and edited the manuscript; JPWS acquired the funding; DJI, LC and JPWS conceptualised the research.

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The author contributions are as follows: DJI collated all data, conducted all data curation, formal analyses, visualization, and wrote the first draft of the manuscript; LC and JPWS provided supervision, and wrote, reviewed and edited the manuscript; JPWS acquired the funding; BC contributed to the methodology for one of the indicators; NFK, TB, JEF, DJCG, FM, JS, EJS and GT provided data; DJI, LC and JPWS conceptualised the research.

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The author contributions are as follows: DJI collated all data, conducted all data curation, formal analyses, visualization, and wrote the manuscript; LC and JPWS provided supervision, and reviewed and edited the manuscript; KAA, FM, EJS, KSB, TB, EG, AG, EG, TH, TOWK, AMNO, JRP, JS, MRN, HS, CLV, MW, CELW and DSW provided data; JPWS acquired funding; DJI, LC and JPWS conceptualised the research.

I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

Signature:……………………………………….

Date:…………………………………………...

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"*We must not let a forest full of trees fool us into believing all is well*"

Kent H. Redford, 1992

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1 Introduction

1.1 Biodiversity decline

The world is experiencing widespread human-induced species extinctions. Species' extinction rates now vastly exceed the natural average background rates (Ceballos et al. 2015). Anthropogenic processes are the main drivers of global declines of biodiversity and extinctions (biodiversity here defined as "diversity within species, between species and of ecosystems" [Secretariat of the Convention on Biological Diversity 2005]), largely through habitat loss and degradation, overexploitation, climate change, invasive species, and pollution (Maxwell et al. 2016). Recently, overexploitation (the removal of individuals from the wild faster than populations can recover) was identified as the main pressure driving species declines (Maxwell et al. 2016). However, indicators to monitor species exploitation across a large scale are lacking (Joppa et al. 2016). For example, indicators have been produced that monitor the state of biodiversity, the pressures on biodiversity, the responses to address biodiversity loss, and the benefits that humans derive from biodiversity (Tittensor et al. 2014). However, these indicators provide little information on the extent or magnitude of the exploitation of terrestrial wildlife. Aggregated population trends of utilised species (Tierney et al. 2014), and indicators to track the extinction risk of internationally traded species and those used for food and medicine have been developed (Butchart et al. 2010).

For some anthropogenic processes, maps of the spatial extent and magnitude have been produced (Pereira et al. 2012; Tulloch et al. 2015), for example land-use change (Jetz et al. 2007), fishing pressure (Worm et al. 2009), climate change and ozone air pollution (Tai et al. 2014), deforestation (Hansen et al. 2013), and roads (Ibisch et al. 2016). However, limited examples of threat mapping are available for the exploitation of terrestrial wildlife. A recent map of the cumulative global human footprint does not include the effects of the exploitation of terrestrial wildlife (Venter et al. 2016). Moran & Kanemoto (2017) recently produced a global map of species threat hotspots based on the consumption of commodities in the United States. However, maps were built by linking extent-of-occurrence maps for threatened species with global supply chains, and therefore consider only threats that can be linked to industries and do not quantify the number of animals killed from hunting (hereafter "harvests"). Maps of the exploitation of terrestrial wildlife in Central Africa exist (Ziegler et al. 2016), but are based on extrapolations from few data points. Given that overexploitation is one of the greatest pressures on wildlife, quantifying and mapping exploitation is greatly needed as a first step towards understanding the full suite of pressures exerted by humans.

1.2 The global exploitation of wildlife

Humans have exploited wildlife for millennia (Barton et al. 2012), and nowadays it is still a vital source of nutrition for more than one billion people worldwide, and supports the livelihoods of approximately 15% of the global population (Brashares et al. 2004, 2014; Abernethy et al. 2013; Weinbaum et al. 2013). Wildlife is also used in a variety of traditional and cultural practices, such as for medicine (e.g. pangolins, Boakye et al. 2014), festivals (Sirén 2012), fetish and magic (e.g. vultures, Buij et al. 2016), and can be regulated by cultural taboos (Colding & Folke 2001). Furthermore, wildlife is hunted for sport (e.g. trophy hunting [Packer et al. 2011]), as pets (e.g. lorisiforms, Svensson et al. 2016), and for the international trade (e.g. Nijman 2010). The harvest of wildlife globally is estimated to be worth more than US$400 billion annually (Brashares et al. 2014), and the illegal trade of wildlife US$50-150 billion annually (UNEP 2014).

In cases where hunting is unsustainable, overexploitation occurs and leads to defaunation, which refers to “the global extinction of faunal species and populations, and the decline in abundance of individuals within populations” (Young et al. 2016). Humans have been described as “unsustainable super-predators” (Darimont et al. 2015), and hunting is thought to have led to the extinction of a number of species including the Atlas Bear (*Ursus arctos crowtheri,* Calvignac et al. 2008) and the Great Auk (Serjeantson 2001). The heaviest vertebrates are often most threatened by hunting, which are preferentially targeted first by hunters, and are harvested down a size gradient (Dirzo et al. 2014; Ripple et al. 2017). Defaunation has consequences for community composition, ecological interactions and behaviour, ecosystem services and functions, and evolution (Young et al. 2016). Heavily defaunated areas typically exhibit biotic homogenization (Hughes et al. 2007), and reduced phylogenetic and functional diversity. Wildlife declines, and illegal hunting, have also been linked to conflict, exploitative labour practices, organized crime and vigilante governance (Brashares et al. 2014), endangering both people and wildlife.

1.3 The exploitation of wildlife in the tropics

Despite only accounting for less than 30% of the Earth's surface, the terrestrial realm accounts for a greater proportion of global biodiversity than the marine realm (Gaston 2000). Terrestrial tropical regions in particular house over half of the world's biodiversity (Corlett & Primack 2010), where species are more likely to be more numerous, endemic, and range-restricted (Stevens 1989; Gaston et al. 1998). Furthermore, tropical species have a greater risk of extinction than temperate species, and tropical regions are thought to be the epicentre of current and future extinctions (Brook et al. 2008). Yet, it is in this region that people rely on wildlife the most (Brashares et al. 2014).

In the tropics, hunting for subsistence is common by both indigenous peoples and other rural populations across the tropics, where wildlife provides important sources of protein (Brashares et al. 2014), fats (Sirén & Machoa 2008), and micronutrients (Fa et al. 2015b). Hunting wildlife can contribute substantially to livelihoods, and communities nearer to markets sell a higher proportion of the wildlife that they catch (Brashares et al. 2011). As access to markets increases through building roads and technological advancements, people are increasingly hunting for commercial purposes (Abernethy et al. 2013). The hunting of some species can be driven by international demand, as a source of livelihood. For example, the international trade of wildlife from Asia was identified as one of the main challenges impeding biodiversity conservation in the region (McNeely et al. 2009). Between 1998 and 2007, more than 35 million animals were exported from Asian nations, of which 30 million animals from approximately 300 species were wild-caught (Nijman 2010).

A recent pan-tropical analysis shows that mammal and bird populations were reduced by approximately 80% and 60% respectively in hunted areas (Benítez-López et al. 2017), presenting a sustainability issue in the poorest and most biodiverse region on Earth. Hunting pressure is thought to be most intense near human settlements, radiating out from settlements, where community composition of vertebrates has been shown to decline along a defaunation gradient (as shown in Gabon by Koerner et al. 2016). Hunted areas have been shown to have different plant seedling recruitment in comparison to unhunted areas (Effiom et al. 2013), and reduced recruitment of large tree species, which may have implications for carbon storage (Peres et al. 2016). In addition, Galetti et al. (2015) found that declines in large seed predators resulted in dietary shifts of rodents in the Atlantic forest, Brazil. Defaunation has also resulted in cascading effects, for example the loss of large predators caused the increase, or 'release', of mesopredators (Ritchie & Johnson 2009). Wildlife provides and facilitates key ecosystem services and functions, and research shows that these processes are disrupted in defaunated areas, e.g. decline in water quality (Rantala et al. 2015).

In the rural tropics, wildlife provides vital provisioning services such as food and medicinal resources, and serves as an important source of cultural services and livelihoods for millions of people (Brashares et al. 2004; Weinbaum et al. 2013). Therefore, defaunation also presents a major threat to the people who rely on wildlife. Research in Madagascar shows that removing access to wildlife, and thus access to wild meat, resulted in a 29% increase in childhood anaemia (Golden et al. 2011), while in Central Africa wild meat availability was correlated with stunting in children (Fa et al. 2015b). When terrestrial wildlife has been depleted by overexploitation, the consumption of fish has been shown to increase in some places (Brashares et al. 2004; Ordaz-Németh et al. 2017). In East Africa, landscape-level prevalence of rodent-borne zoonoses increased following declines of large mammals (Young et al. 2014).

1.4 Understanding exploitation in Africa

Exploitation of wildlife differs among the three tropical continents. It is thought that exploitation pressure increases from Latin America, Africa, to Asia. Bennett & Rao (2002) predict that the high levels of biodiversity decline in Asia are a glimpse of the future for Africa, given its predicted increases in human population and industrial development. Furthermore, declines of wildlife in Asia, has led in some cases, to increases in the international trade in wildlife from other continents to meet demands. For example, declines in Asian pangolins (Family: Manidae) are thought to have led to increases in the international trade of African pangolins to Asia (Challender & Hywood 2012; Gomez et al. 2016).

Africa is one of the most biodiverse continents in the world, containing a number of biodiversity hotspots, and in Central Africa one of the world's remaining areas of wilderness (Mittermeier et al. 1998). Extant terrestrial megafauna (carnivores > 15kg and herbivores > 100kg) are most diverse in Africa, and the numbers of declining megafauna is also the highest (Ripple et al. 2016b). Many hunted African species are experiencing declines in wildlife due to hunting (Jimoh et al. 2013; Benítez-López et al. 2017), with at least 91 species of mammal threatened by hunting alone (Ripple et al. 2016a). Further to current pressures, it is predicted that Africa will experience a dramatic increase in total human population up to 2100 (Figure 1.1), where half of all global human population growth is projected to occur up to 2050 (UN DESA 2017). With many countries in Africa developing rapidly, it is particularly important to understand wildlife harvest and use to target appropriate conservation actions and policies to both safeguard wildlife and food security.

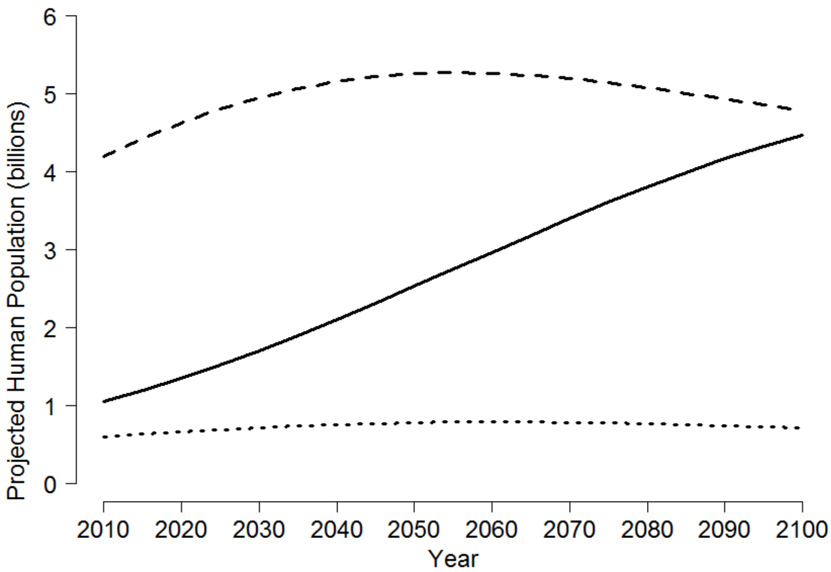

Figure 1.1. Projected human populations for Africa (solid line), Asia (dashed line), and South America (dotted line) between 2010 and 2100. Data from UN DESA (2017).

Increasing human population, industry, and infrastructure will likely allow increased accessibility to remote areas, which in turn facilitate hunting and other extractive activities (Watson et al. 2016; Kleinschroth & Healey 2017). African countries, particularly those in Central Africa, house large mineral deposits of gold, diamond, manganese and cobalt (Edwards et al. 2014), which together with the discovery of oil, has dramatically changed the economies of countries such as Cameroon and Equatorial Guinea (Abernethy et al. 2016). In addition, many areas are now under pressure from the recent expansion of the palm-oil industry. While the palm-oil industry is relatively small in Africa compared to that in Southeast Asia, the environmental conditions in the humid parts of West and Central Africa make it suitable for expansion (Fitzherbert et al. 2008). Recent evidence shows that palm oil companies are acquiring land and expanding in West and Central Africa (Sayer et al. 2012; Penikett & Park 2013). Not only do extractive industries such as logging and mining have consequences in terms of land-use change (Figure 1.2), but they also have secondary impacts such as wildlife exploitation. For example, in the Democratic Republic of Congo miners actively hunt and consume wildlife due to lack of alternatives (Spira et al. 2017). Extractive industry workers are also implicated in wildlife trade; for example, a study in Gabon revealed that Asian industry workers request pangolins from hunters more than any other species (Mambeya et al. *2018*).

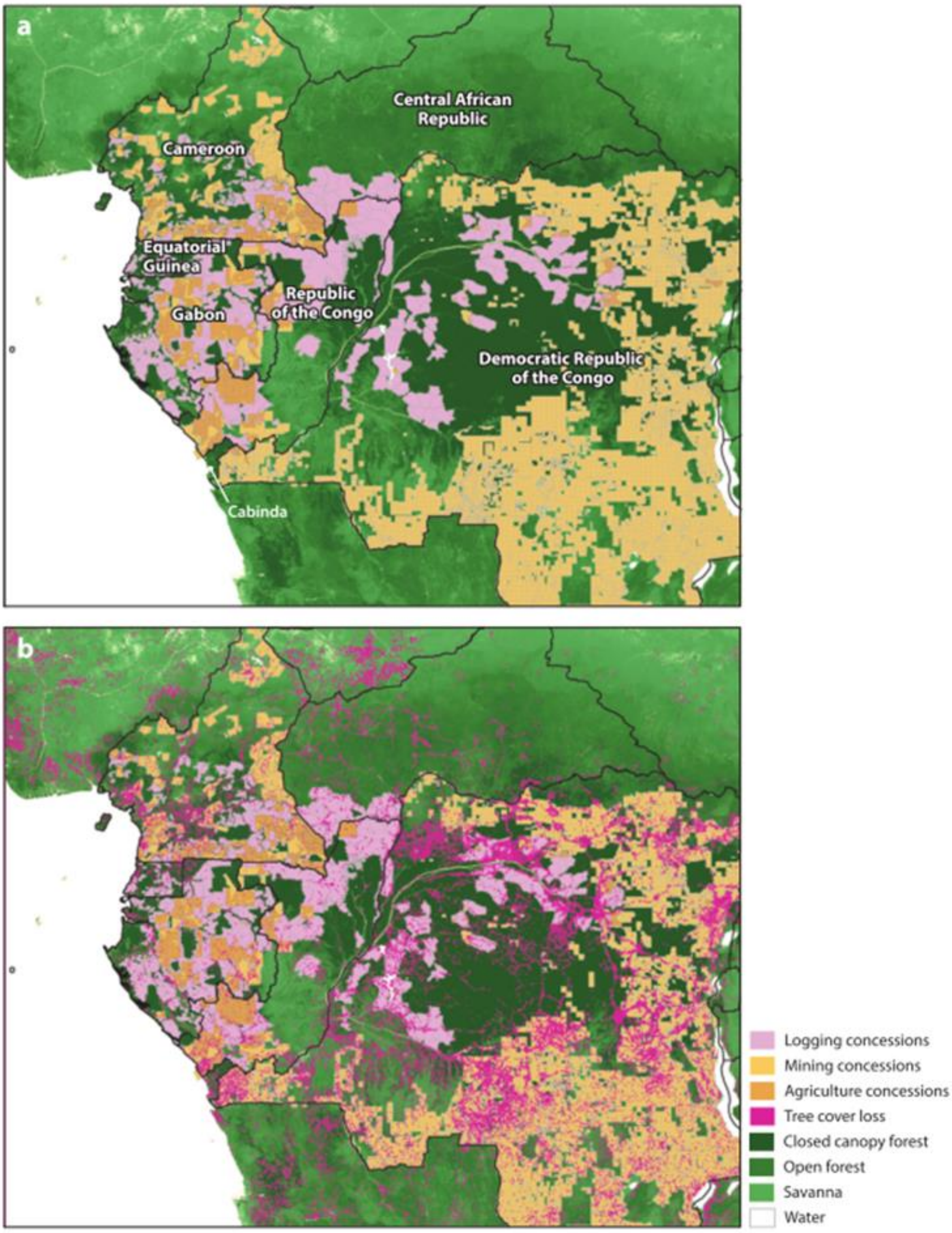

Figure 1.2. Map of the extent of a) extractive industries and b) tree cover loss in Central Africa between 2000 and 2015. Reproduced from Abernethy et al. (2016).

1.5 Monitoring the exploitation of wildlife

To fulfil global commitments to halt biodiversity loss, robust data are needed to inform a diverse range of indicators that monitor and track the state of biodiversity, a number of which are already available (e.g. Living Planet Index; Loh et al. 2005). Accurate estimates of wildlife harvests are needed to contribute towards indicators that track exploitation, and could inform international initiatives, such as the Convention on Biological Diversity (CBD) Aichi biodiversity targets, the UN Sustainable Development Goals (SDGs), and the FAO Food Security Indicators. To ensure that indicators are robust and reliable, three main efforts are recommended: 1) elimination of spatial (and taxonomic) biases of studies, 2) improvement of data collection efforts, and 3) investigation of the ways in which indicators respond to policy changes (Jones et al. 2011). Unlike many other pressures, the exploitation of wildlife cannot be readily quantified by satellite remote sensing. For example, while some forests may appear structurally undisturbed from above, hunting-induced wildlife declines are invisible from satellites, and so effectively 'empty' forests appear intact (Wilkie et al. 2011). Investigating wildlife exploitation at its source provides a vastly more detailed understanding of wildlife harvests, and enables reporting to international commitments (e.g. United Nations Sustainable Development Goals), and mechanisms to track food security.

In the marine realm, systems to investigate and track the exploitation of wildlife have been developed. For example, the Sea Around Us project provides time series fisheries catch data globally from 1950 onwards (Pauly 2007). Furthermore, the FAO Fisheries and Aquaculture Department maintains a database of global fisheries catches, trade, and production (FAO 2017). Detailed and long-term data such as these can be used to track catches over time, and together with population data can be used to assess the sustainability of catches. Whilst global estimates of the magnitude and distribution of fish catches are available (Worm et al. 2009), limited progress has been made in the development of appropriate monitoring systems of terrestrial wildlife harvest, despite international agreements towards such endeavours (e.g. Decision XI/25, CBD 2012).

In the terrestrial realm, monitoring wildlife harvesting where it occurs is particularly challenging, and doing so over large spatial extents and time periods is more difficult still. One of the main differences with fisheries catches is that the majority of catches are sold and there are few routes to market, therefore catch information can be collected by monitoring arrivals at ports. When attempting to monitor terrestrial wildlife harvests, difficulties arise because the commodity chain is complex as wildlife is consumed at many points along the chain, and there are many routes to market, and so collecting data for terrestrial wildlife on such a scale would involve substantial infrastructure and finance. The FAOSTAT Food Balance Sheets (FAO 2017) have been used to derive estimates of wild meat (referred to in Africa as 'bushmeat') consumption, however these estimates are not based on exact quantities of bushmeat consumed, instead consumption is estimated as "the difference between the amount of non-bushmeat protein available and the product of the number of inhabitants, times the daily protein supply per person" (Ziegler 2010). Studies are needed that quantify exact numbers of animals harvested, and provide detailed data over time to track changes over time, and that aid in the monitoring and evaluation of harvests, and effectiveness of interventions.

The flow of wildlife from harvest to use can be complex, and depending on where monitoring takes place, the information obtained can differ (Figure 1.3). Wildlife is harvested by a hunter, and may be immediately consumed whilst on a hunting trip. Alternatively, wildlife may be taken to their settlement for local consumption (hunter, family, or gifted within the settlement) or for sale, or wildlife may be sold directly to an intermediary dealer. Intermediaries may buy wild meat from a rural market, and then sell to urban markets likely for a higher price. After sale, wildlife may be consumed by urban consumers or sold on to international consumers.

Various different approaches have been adopted to investigate the exploitation of terrestrial wildlife at a local scale, and these approaches typically fall into three categories of studies: hunting, consumption, and market studies. Additionally, some approaches investigate exploitation through seizures of illegally traded species, however seizures can occur at any point of the chain depending on where law enforcement is active. Each approach may be used to collect data at a different part of the wild meat commodity chain (Figure 1.3), can be used to answer different questions about exploitation, and has advantages and disadvantages as outlined below.

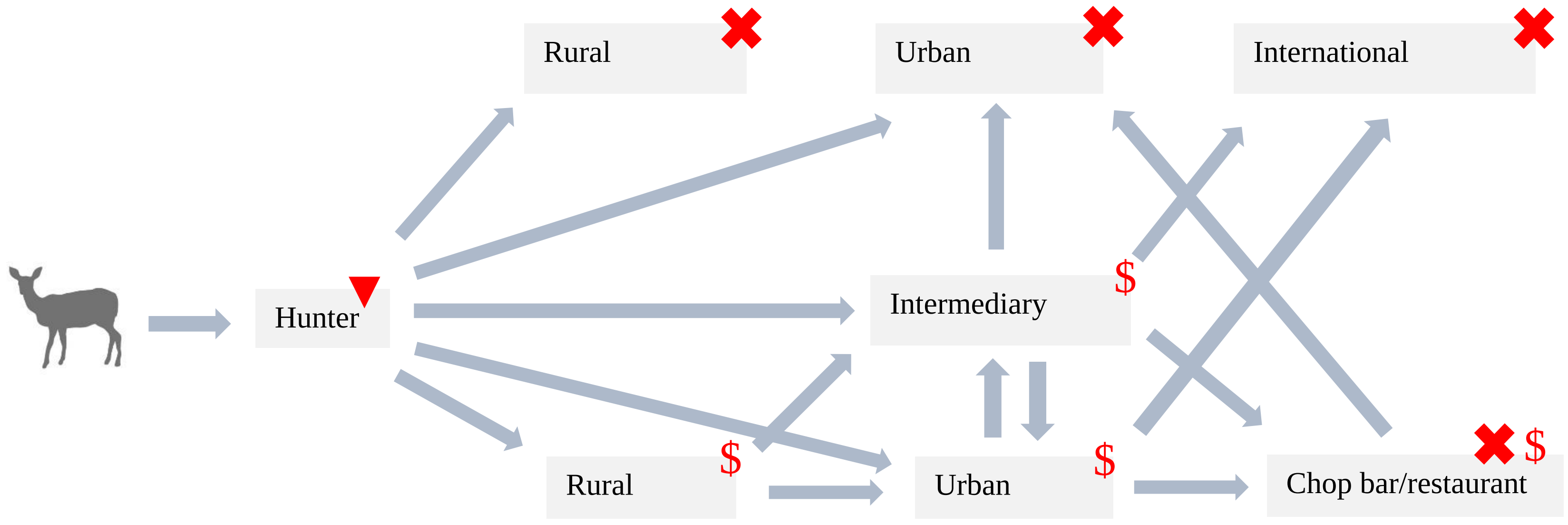

Figure 1.3. Schematic of the flow of wildlife (arrows) in the commodity chain. Symbols illustrate the locations in the chain where market ($), consumption (X), and hunting studies (▼) can take place. Seizures of illegally traded species can be made at any point across the chain.

The most direct approach of quantifying wildlife harvests is by documenting all of the animals harvested by hunters at a settlement, hereafter ‘hunting studies’. Studies may do this by counting the carcasses that enter the village upon the hunters’ return (Coad et al. 2013), by following the hunters on their hunting trips (Kümpel 2006), or by using questionnaires where hunters recall the animals captured (Fusari & Carpaneto 2006). Hunting studies are a way of quantifying the numbers and identities of species that were hunted, and are particularly useful because they can provide information on the exact locations where animals were harvested. Other detailed information often provided by these studies includes the hunting method (e.g. guns, snares), the number of hunters involved, and the area over which animals were hunted, which can be useful to quantify hunting effort, investigate the sustainability of harvests, or conduct spatial analyses. However, conducting hunting studies requires finding a community willing to be studied, disclose hunting practices, and building a relationship with them over time. Hunters may be unwilling to disclose information on their hunting practices, especially if they are hunting species protected by wildlife legislation, for fear of the repercussions of law enforcement.

Studies that quantify the consumption of wildlife by people, hereafter ‘consumption studies’, have been conducted in Eastern (Rentsch & Damon 2013; Ceppi & Nielsen 2014; Kiffner et al. 2015), Central (de Merode et al. 2004; Starkey 2004; Poulsen et al. 2009) and Western Africa (Dei 1991; Brashares et al. 2011). One example is Matsuura and Moussavou (2015), who provided four families from two villages in Gabon with scales, with which they recorded and weighed all sources of food that were consumed. In another study, Nyahongo et al. (2009) used questionnaires to record the number of meals per week that contained meat or fish. Consumption studies are particularly useful for understanding the contribution of wild-sourced foods to nutrition intake and diets. However, consumption studies are likely to underestimate the total mortality of wildlife, because animals may also be sold, or used for purposes other than consumption. For example, Peres (1991) showed that the harvest of some species may be twice the number estimated from consumption alone.

Another approach of investigating the exploitation of wildlife is to count the number of animals offered for sale on wild meat markets, hereafter ‘market studies’, and have been conducted across the African continent (Fa et al. 2006; Whiting et al. 2011; Bergin &

Nijman 2014; Akani et al. 2015), but few studies exist in Eastern Africa where wildlife regulations are typically enforced more strictly (but see Nielsen et al. 2014). Typically, market studies are a way of investigating the assemblages of animals offered for sale and volumes of animals traded. Price data from market studies can also be used as an indicator of demand. However, species that are illegal to hunt and trade, for example gorillas (*Gorilla gorilla*), are unlikely to be displayed on markets for fear of law enforcement. In addition, species that have little market value, or are not worth the transport and sale costs, may also not appear on markets e.g. squirrels (Family: *Sciuridae*). Furthermore, it is difficult to investigate the sustainability of wildlife harvests from market data, because often one cannot discern the location or populations from which the animals were caught, although this may be possible from small local village data.

Generally, most studies that have investigated the exploitation of wildlife were conducted over relatively short periods of time, providing a ‘snapshot’ of the wildlife harvested at the time. At a local, or site-level, many studies have monitored the harvest or trade (sale at wild meat markets) of wildlife at known locations and periods of time. Currently, no mechanisms exist to track terrestrial wildlife harvests over large spatial and temporal scales. However, combining site-level datasets could provide a valuable approach to enable large-scale (e.g. regional) assessments of exploitation and thus provide an overview that can inform conservation policy and action.

1.6 Thesis outline

Overexploitation is one of the greatest threats to biodiversity and to the millions of people depending on wild meat for food and livelihoods, yet broad-scale data to evaluate species’ declines are limited. Without first quantifying and understanding exploitation levels across regions, conservation policies and actions cannot be effectively targeted. Quantifying the exploitation of terrestrial wildlife is challenging, and methods to obtain broad-scale estimates of exploitation are lacking. The overarching aims of my thesis are to quantify the harvest of wildlife in Africa, investigate the potential drivers of wildlife harvests, and explore overall trends, enabled by creating a database of the exploitation of terrestrial wildlife in Africa.

To enable analyses of the exploitation of wildlife in Africa over a large spatial scale, available data were collated from the literature and stored in a way that allow analyses. Chapter 2 provides details of the overall methods used to collate studies and store data on the harvest of wildlife in Africa in a purpose-built database. Descriptive statistics are presented that highlight different aspects of the collated data such as the taxonomic breadth of harvested wildlife, and biases in the data, e.g. caused by research effort, or taxonomic and geographic biases. The data collated in Chapter 2 are used in analyses in the following chapters.

Estimates of the total terrestrial wildlife harvest in Africa are lacking, and methods to produce estimates and identify hotspots of harvest remain largely unexplored. In Chapter 3, I explore three different methods of quantifying the exploitation of wildlife: extrapolating by number of hunters, by the rural population, or by area. By using a mixed-effects modelling framework, I investigate the socioeconomic and environmental drivers (accessibility to humans, habitat type, distance to road, and distance to protected area) of the annual biomass of wildlife harvested per hunter. Furthermore, I demonstrate a method to spatially extrapolate and predict exploitation across Central Africa based on the drivers previously identified.

Having calculated static estimates of total wildlife harvests, in Chapter 4 I investigate methods to track harvests. Harvest data have been collected in different locations, with different environmental conditions, and over different periods of time. By analysing these data together, it may be possible to produce indicators that can track wildlife harvests over time. In Chapter 4, I take inspiration from the fisheries and wildlife population trends literature, and propose two indicators to track changes in terrestrial wildlife harvest. The first indicator evaluates change in the average size of mammals and birds harvested over time, while the second indicator combines time-series studies in an index to track the number of mammals and birds harvested over time.

Previous studies have shown that the availability of wildlife in a given area is reflected in the composition of the animals harvested, which suggests that hunting studies could be used to infer depletion. Furthermore, research has indicated that some species respond differently to hunting pressure. Building upon the indicators proposed in Chapter 4, I investigate how the composition of harvested wildlife, and the mean body mass of mammals and birds changes over time and across a gradient of human accessibility, defined as the travel time to the nearest major settlement and used as a proxy for hunting pressure, as a potential indicator of wildlife depletion (Chapter 5).

Many threatened species are under pressure from hunting, including species that have received little in the way of research attention. Hunting and market studies could provide crucial information on these species, that would otherwise be difficult to obtain. In Chapter 6, I present the first comprehensive assessment of pangolin exploitation in Africa, by investigating the number of pangolins harvested, temporal trends in pangolin harvests, and whether the price of pangolins has changed at rural and/or urban markets over time, as an indicator of demand.

Chapter 7 is the concluding chapter in this thesis, where I discuss the overall findings.

2 Materials and Methods

2.1 Introduction

Hunting is a dynamic system, which is spatially and temporally heterogenous, and can be influenced by a combination of complex and changing factors such as availability and access to alternative foods (Nasi et al. 2011), alternative livelihood opportunities (Kumpel et al. 2010), access to markets (Brashares et al. 2011), hunting technology (Dounias 2016), prices and wealth (Wilkie et al. 2005), and governance (Siren 2015) among others. Hunting of a given species can be considered sustainable if harvest levels allow the species to regenerate itself (Weinbaum et al. 2013). Sustainable hunting has been suggested as a way of fulfilling human needs whilst avoiding species extinctions (Bodmer and Lozano 2001), although methods to assess sustainability need further work (Milner-Gulland & Akcakaya 2001; Weinbaum et al. 2013).

Conservation decision-makers need information on the sustainability of the harvest of wild animals to make effective and appropriate decisions on whether actions are required to ensure that overexploitation can be addressed. Decisions on conservation actions and policies are made at multiple levels, from parties to international conventions, national governments, non-governmental organisations (NGOs), to academics. At the international and national level, decisions need to be made on conventions (e.g. Convention on International Trade in Endangered Species of Wild Fauna and Flora, CITES), laws and targets (e.g. Aichi Targets 1-4) to ensure that harvest levels are not detrimental to populations of wild animals. Furthermore, national governments, NGOs, and academics need to know where and when to target resources to monitor exploitation and address overexploitation. To inform decisions, several questions need to be answered: Specifically, when and where is the harvest of wildlife sustainable? Which species are harvested unsustainably? What are the environmental and socio-economic drivers that determine patterns in the harvest of wildlife? To what extent does wildlife contribute to local livelihoods?

As discussed by Weinbaum et al. (2013), there are multiple types of data that are needed to understand the sustainability of hunting, including: abundance / population estimates (i.e. the current state of wildlife), life history traits (e.g. reproductive rates), and the quantity of wildlife harvested over a given area and time (i.e. the pressure). Several initiatives quantify the abundance of wild animals and collate information on changes in abundance over time at specific locations (e.g. Living Planet Index; Collen et al. 2009). For several hunted mammals in Africa, we know some life history traits, although further data is needed to cover a wider range of habitats, circumstances, and species (van Vliet and Nasi, 2018). Quantitative information on hunting is currently available to decision-makers from local-scale studies, or inferred from widely distributed questionnaires (e.g. Ziegler 2010). However, broad-scale information on wildlife harvests, population sizes, and life history traits are currently not available, and is a major gap in knowledge that impedes progress towards understanding the sustainability of hunting.

The overarching aim of this chapter is to fill one of the major gaps in knowledge, namely harmonised information on harvests of terrestrial wildlife. I do this by collating data from disparate studies into a purpose-built database, providing a means to inform conservation decision-making. Similar methods (collating and analysing disparate datasets) have been successfully used in other initiatives to understand the response of biodiversity to land-use (Hudson et al. 2017), and fragmentation (Pfeifer et al. 2017). Advances in statistical methods now allow disparate studies to be compared, whilst accounting for differences between studies and biases that may affect trends and patterns that emerge from the data. For example, using a mixed-effects modelling framework allow differences to be included as random effects in a model (e.g. studies conducted by the same author), whilst investigating the environmental and socio-economic drivers of harvests using fixed effects.

Specifically, I will collate information on the harvest of wildlife by hunters in Africa. Throughout, I define a ‘hunter’ as an individual who harvests wildlife for subsistence, cultural or livelihood purposes, thus excluding hunting exclusively for trophies. Trophy hunting was excluded because both the hunting and wildlife is typically managed, and the system is governed by a different set of drivers. Given that the main objective is to provide information on total wildlife harvests, I focus my efforts on hunting and market data particularly (as opposed to consumption data). Hunting data provides the most accurate information on where and when animals were harvested, whilst market data can provide information on prices and overall quantities offered for sale. Collating these datasets will allow several pertinent questions to be answered, but I acknowledge the limits of the questions that can be answered (Table 2.1).

Table 2.1. Example questions that could and could not be answered using a database on wild meat harvests alone.

Question	Data requirements	Can it be answered using this database?
Has the price of a wildlife product (carcass, piece, derivative) changed over time?	Price records, time	Yes
Which species are harvested?	Harvest records	Yes
How many individuals are harvested in a given area?	Harvest records, effort, area	Yes
How does the harvest change over time?	Harvest records, effort, time	Yes
How does the harvest change over space?	Harvest records, effort, area	Yes
What are the drivers of wildlife harvests?	Harvest records, socio-economic and environmental variables	Yes
Has the price of a wildlife product (carcass, piece, derivative) changed over time?	Price records, time	Yes
Which species are sold at market?	Market counts	Yes
What quantity of wildlife is consumed?	Consumption records	Not currently, but additional module can be added to the database
Effect of different quantities of harvest on the abundance of wildlife?	Harvest records, abundance	No
Are certain species (e.g. larger or smaller ones, taxonomic groups) affected more by hunting?	Abundance, body mass	No
Is hunting sustainable?	Abundance, harvest records, life history traits	No

This chapter describes and outlines the development of a database, which is used throughout this thesis, and contains quantitative information on the hunting and sale of terrestrial wildlife in Africa. This database was ultimately created to act as a tool for decision-makers, to address questions relating to the magnitude and spatial extent of wildlife harvesting (see Chapters 3 - 6) and the contribution of harvested wildlife to local livelihoods. In this chapter, I will 1) describe the methods used to design and populate a database on the hunting and sale of wildlife, 2) investigate the spatial, temporal, and taxonomic differences between studies, and 3) compare this database to previous efforts aimed at documenting wildlife harvests.

2.2 Methods

2.2.1 Terminology

Here, I use the term 'wildlife' to encompass all wild terrestrial vertebrate and invertebrate animal species. Throughout, I refer to 'sources' which may be published literature, grey literature (e.g. reports from non-governmental organisations), or BSc/MSc/PhD theses. Sources contain data on the number of individuals per species harvested, hereafter 'harvest' data, and/or contain data on the number of individuals offered for sale at a market, 'market' data. Harvest or market data are collected at a particular location, hereafter 'site', which includes, but is not restricted to, villages, towns, logging camps, and national parks.

2.2.2 Data inclusion criteria

Sources were included, and data extracted, if sources: a) were published, in press, or were collected using a published methodology; b) included harvest or market data, recorded as the number of individual animals or total biomass per taxonomic group; c) provided the geographical coordinates of the sites or contained a map whereby the coordinates could be acquired by identifying the sites on Google Earth (2017) by referencing against the map in the source, and; and d) provided some measure of sampling effort (e.g. the number of days sampled, number of hunters followed), and the dates over which sites were sampled regardless of sampling length.

Although information on consumption was not included in this version of the database, the database has been specifically designed to be modular and thus a consumption module can easily be added.

2.2.3 Literature searches

I employed a variety of methods to search for sources that collected data on harvest or sale of wildlife over a known time period in any continental African country (i.e. not including Madagascar). Firstly, I identified studies from the West and Central African bushmeat database (Taylor et al. 2015). Then, I conducted searches between September 2013 and March 2017 for further sources that contained information on the hunting or sale of wildlife. I searched for sources using academic search engines and bibliographic databases (Table 2.2) using search terms in English, French, and Spanish with Boolean operators (Table 2.3). I employed a snowball sampling technique, whereby I obtained information on potential sources from the contacts and reference lists of others (Noy 2008). The reference lists of sources identified above were searched for other potential sources. In addition, I contacted researchers by email from the United Kingdom Bushmeat Working Group to provide information on unpublished studies and contacts that were not previously identified.

Table 2.2. Websites, libraries and databases in which I searched for sources.

Type	Name	Location
Website	Google Scholar	www.scholar.google.co.uk
	Bushmeat Crisis Task Force	www.bushmeat.org
	Interdisciplinary Centre for Conservation Science Thesis Archive	www.iccs.org.uk/content/thesis-archive
	ISI Web of Knowledge (All Databases)	www.wok.mimas.ac.uk
Database	West and Central African Bushmeat Database	Taylor et al. (2015)
Libraries	University of Sussex	Falmer, UK
	CIRAD	Baillarguet, France

Table 2.3. Key terms used in literature searches.

Language	Terms
English	Africa; bushmeat; Central Africa; Congo Basin; consumption; defaunation; East Africa; harvest; hunt; market; offtake; pressure; subsistence; sustainability; trade; West Africa; Southern Africa; wildlife; wild meat
French	Afrique; afrique centrale; afrique de l'Est; afrique de l'Ouest; afrique du Sud; Bassin du Congo; chasse; consommation; la viande sauvage; marché; viande de brousse
Spanish	África; África Austral; África Central; África del Norte; África Occidental; África Oriental; consumo; caza; fauna; cuenca del Congo; defaunación; carne de monte; carne de animals silvestres; mercado; sostenibilidad

2.2.4 Data preparation

The taxonomic identity of wildlife was extracted from the sources where given. If the taxonomic identity of animals was not reported as the Latin binomial (scientific name), or I was unsure of the species, then authors were contacted for clarification. For animals which had not been identified to species level, I recorded them at the most resolved taxonomic level possible (e.g. 'pangolin' would be recorded as Family: Manidae). Species identities were checked against the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2017).

Sources were separated into 'studies' where each study represents the data at a particular site and separated by whether the data is harvest or market data, which I refer to specifically as 'hunting studies' or 'market studies' respectively. If a study collected data for one year, I separated this data into monthly 'samples'. If the data could not be separated into monthly samples, then the sample is the same as the study information (Figure 2.1). Monthly samples were chosen because it allows for the investigation of seasonal changes in the harvest of wildlife (e.g. Kumpel et al. 2006; Coad et al. 2007). Where a study did not include the harvest data in the paper, I contacted the authors for the raw data.

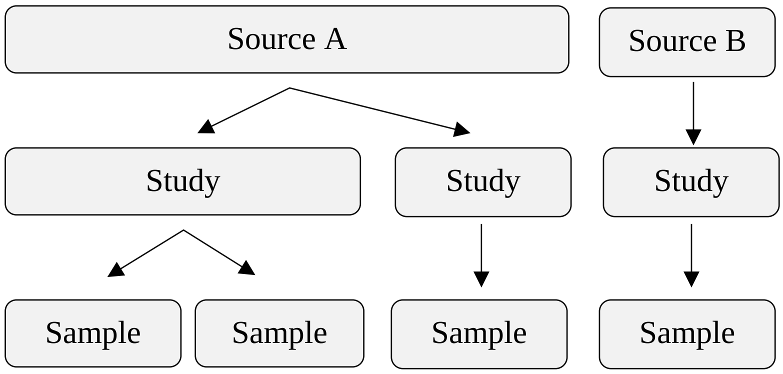

Figure 2.1. Schematic of the relationship between Sources, Studies, and Samples. Source A is an example of a Source that contained Studies at multiple sites, and where data could be separated into monthly Samples. Source B contained one Study, and the data could not be separated into monthly Samples.

Further information was extracted from sources to enable comparison and identify differences between sources, where available. For hunting studies: The area over which animals were harvested by hunters (hereafter 'hunter territory') was collated, to enable estimates of wildlife harvested per unit area to be calculated. Information on whether the source collected data in a specific hunting season (peak or not) was recorded, where possible, if the source identified that the site had hunting seasonality. The method by which animals were harvested (e.g. snare, trap, and gun) and the use of the animals harvested (consumed, sold or gifted) were also collated. For hunting and market studies: survey method (e.g. questionnaire, log book), site type (village, town, city, game reserve, logging concessions, national parks or protected areas) and site characteristics (whether or not a site is located inside a protected area, and the site human population) were collated. Categories within each of the aforementioned data types were taken from the sources. I contacted the corresponding authors of sources in circumstances when a) summarised data were provided, but more detail was needed (i.e. the raw data), and b) to ask for the further information described above.

2.2.5 Database structure

Information extracted, listed in the inclusion criteria, from sources or provided by authors was stored in a relational database implemented in Microsoft Access (2013) that I developed for this project. The structure of the database contains six main tables (Figure 2.2):

Source table contains information on the author(s) who collected the data, the year and title of publication (if published), and the type of source (journal article, thesis, non-governmental report).

Site table contains information on the name, geographic coordinates, coordinate accuracy, and country of the site(s) in which a sample took place.

Study table contains information on the type of study (hunting / market), the start and end dates of data collection, whether the study collected data on the full composition of wildlife harvested / offered for sale, the hunter territory size (in km^2). If the study was a hunting study, I also recorded information on the number of hunters surveyed, and the total number of hunters at a site.

Sample table contains information on a subset of a study, if the data could be temporally disaggregated. In addition, this table includes the start and end dates of the sample, the number of days sampled (the 'sample cover days'), the human population at the site at the time of the sample, and the hunting season.

Species table houses information on the taxonomic classification and conservation status of exploited wildlife, which I extracted from the International Union for Conservation of Nature (IUCN, 2017).

Data table contains information on the quantity of wildlife harvested / offered for sale and the units the quantity was reported in, and the sample and species to which it relates.

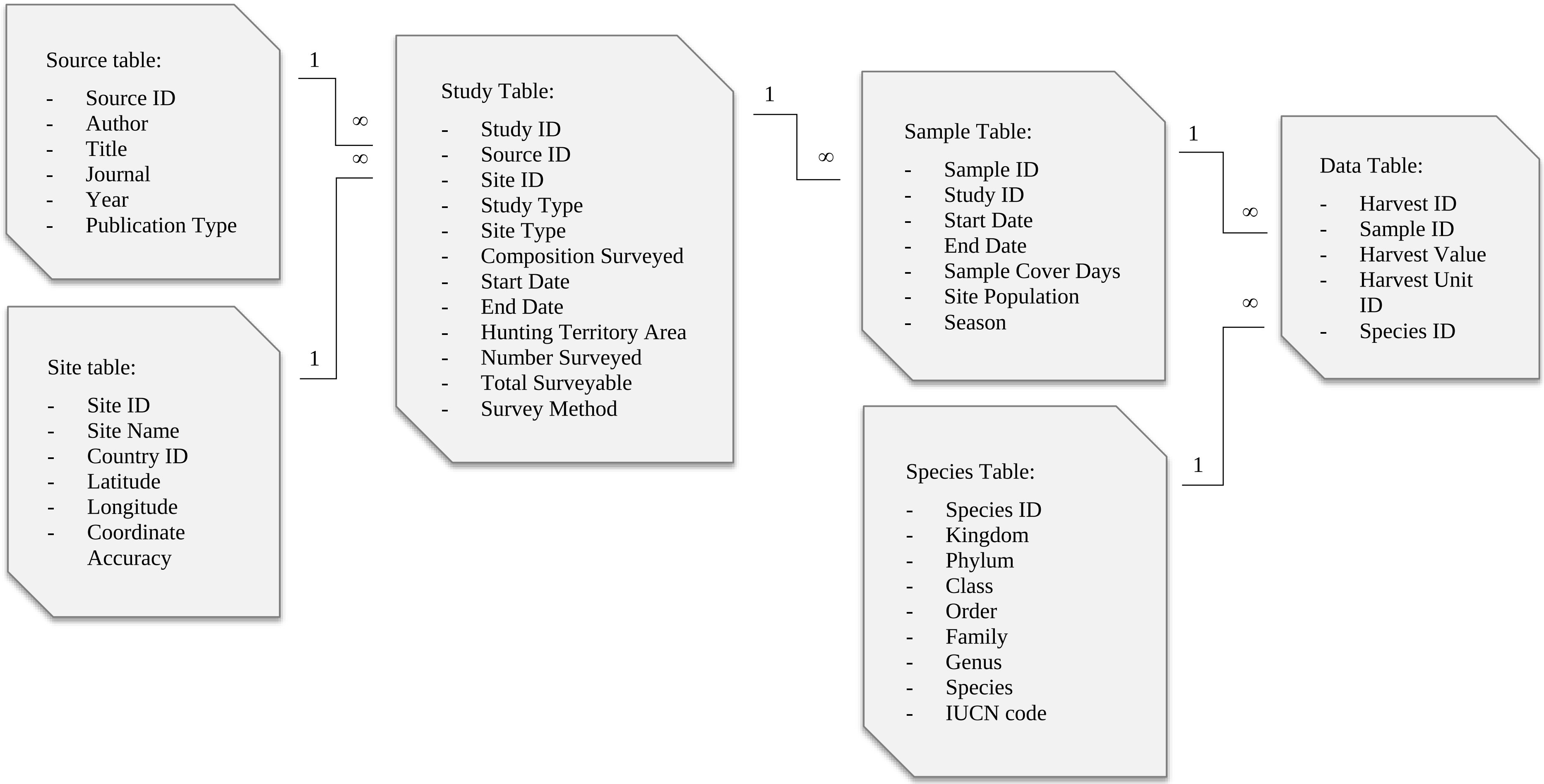

Figure 2.2. Schematic of the relational database. Boxes represent tables in the database, and bulleted lists within each box represent variables contained in a given table. Tables are linked by ID fields, with the symbols 1 and ∞ representing a one-to-many relationship.

2.3 Results

2.3.1 Data

I found a total of 137 sources that matched my inclusion criteria, which comprised 67 published journal articles, 31 reports, 16 PhD theses, 10 master’s theses, 7 raw datasets, 5 book chapters, and 1 bachelor’s thesis. Sources were separated into 354 studies, of which 250 were hunting studies, and 104 were market studies. Studies were conducted between 1974 and 2016 (Figure 2.3A) at 316 sites. Hunting studies spanned the years 1976-2016, with the majority clustered between 1998 and 2015, while market studies spanned 1974-2015 are were mostly conducted between 2003 and 2015. Hunting studies were sampled for 149 days (median, 56 – 365 days interquartile range, Figure 2.3B), while market studies were sampled for 27 days (median, 1.5 - 212 days IQR). Studies that collected time-series across multiple years were available at 14 sites for hunting studies, and at 1 market.

Studies included information on 1,282,440 individual animals, 242,789 from hunting studies and 1,039,651 from markets. A further biomass of 414,046 kg that cannot readily be converted to number of individuals was reported from three market studies and is included in the database. For hunting studies, 98 (39% of hunting studies) provided information on hunter territory size or the area over which wildlife harvests were recorded (e.g. if it was a reserve), and was a mean of 541 km^2 (± 270 km^2 standard error), and a median of 108 km^2 (50 - 278 km^2 IQR). 131 hunting studies (52% of hunting studies) provided information on the number of hunters surveyed and 95 (38%) provided information on the total number of hunters at a site, with a median of 43% (15 – 94% IQR) of hunters were surveyed.

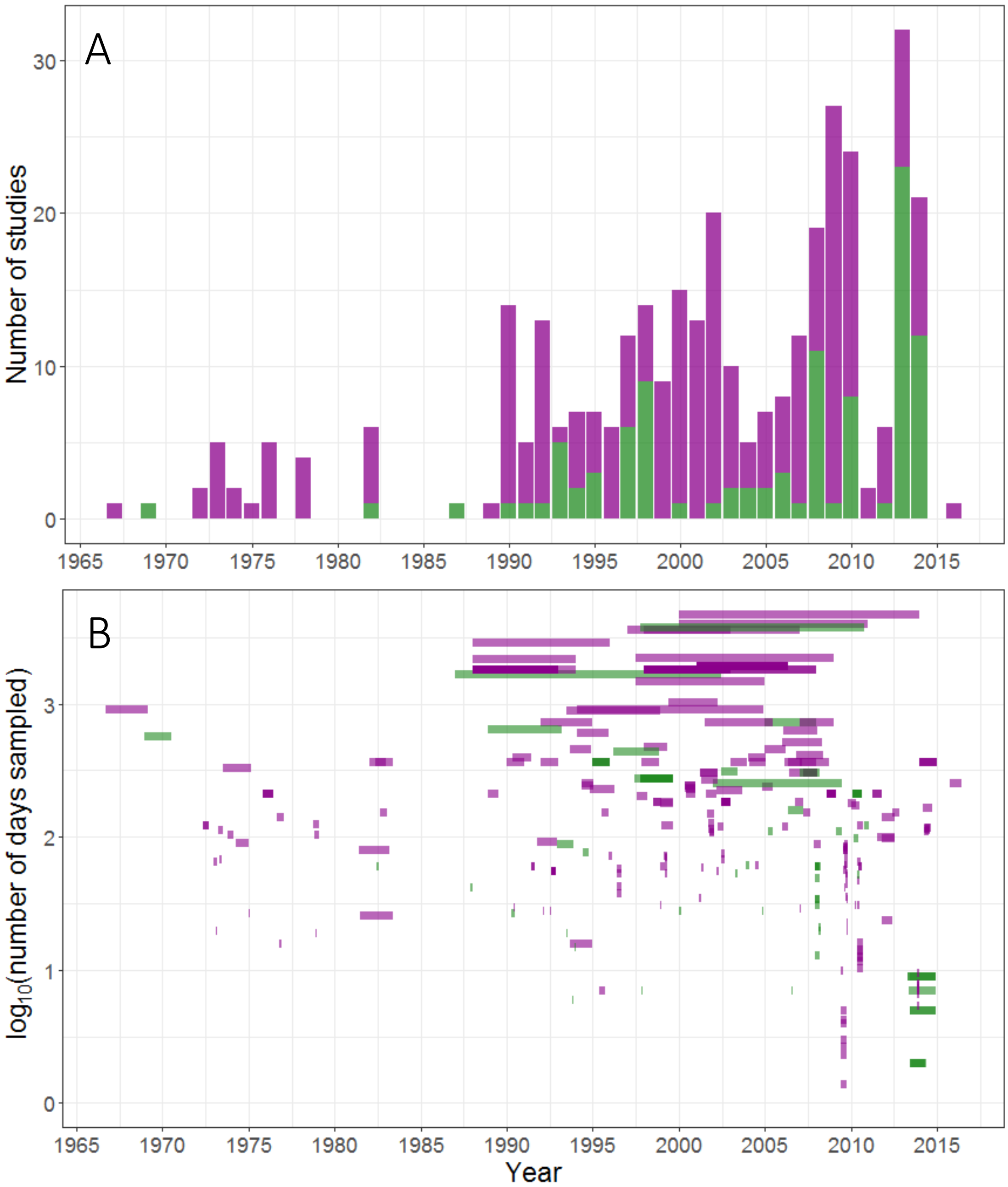

Figure 2.3. Hunting (purple) and market (green) studies conducted over time, plotted as A) number of studies by mid-year of study, and B) log10 transformed number of days sampled, where the length of bars represent the start and end dates of the study. In B, bars are translucent to show overlapping bars. Three studies were excluded in B where the exact number of days sampled between the start and end date were not provided.

2.3.2 Geographic coverage

I found studies conducted in 25 of 54 countries in Africa (Figure 2.4). Hunting studies were conducted in 20 countries, while market studies were available from 15 countries. Hunting studies were most frequently conducted in Cameroon (n = 63 studies), Democratic Republic of Congo (40), and Tanzania (50), while market studies were most frequently conducted in Democratic Republic of Congo (22) and Morocco (20). I found few studies that had taken place in southern African countries, and studies in northern African (Morocco) were conducted by one research group.

Studies fell within 8/9 biomes (Figure 2.5), located in 40/111 ecoregions in Africa (Figure 2.6, Olson et al. 2001). Studies were also found in areas that have been identified for their irreplaceability and/or vulnerability. Studies fell within 4/8 biodiversity hot spots (Mittermeier et al. 2005), 1/2 megadiversity countries (Democratic Republic of Congo, Mittermeier et al. 1997), and both high-biodiversity wilderness areas in Africa (Congo Forest and Miombo-Mopane, Mittermeier et al. 2003). Studies fall within other conservation priority areas such as the frontier forests (Bryant et al. 1997), centres of plant diversity (WWF & IUCN 1997), crisis ecoregions (Hoekstra et al. 2005), endemic bird areas (Stattersfield et al. 1998), and last of the wild regions (Sanderson et al. 2002).Thus, information from this study may be useful for conservation activities in these areas.

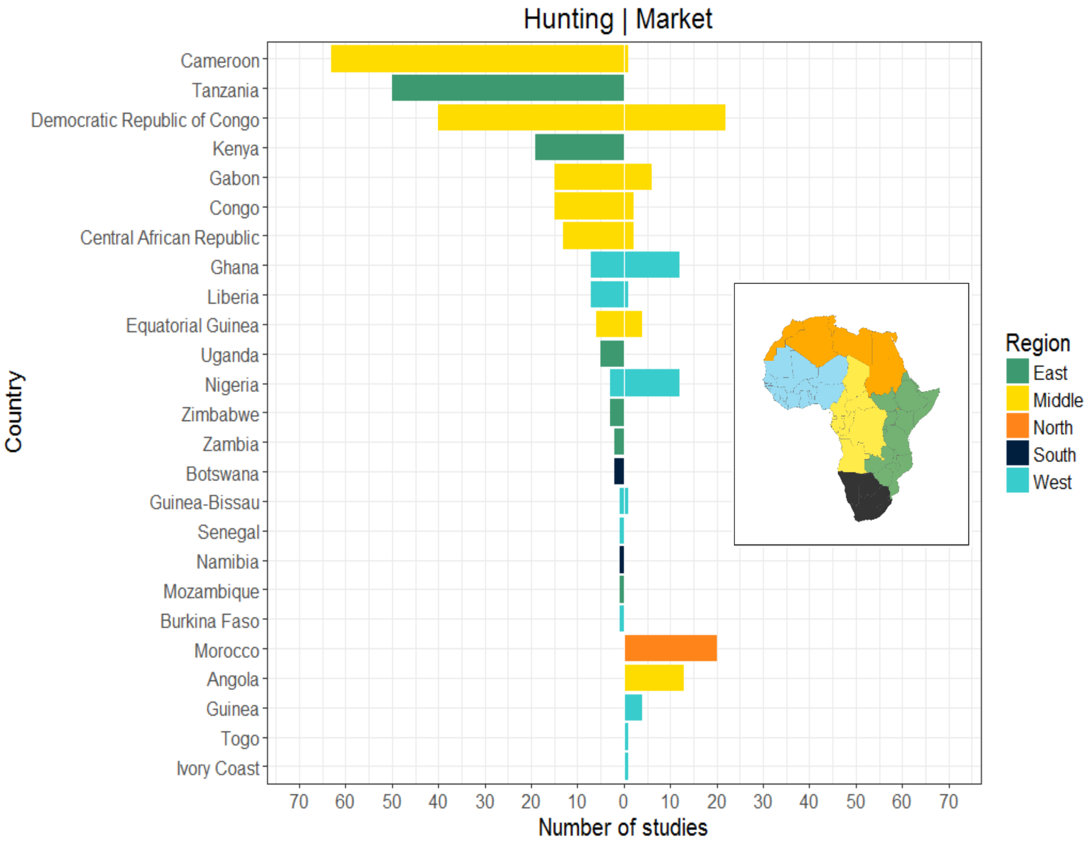

Figure 2.4. The number of studies per country in the OFFTAKE database, ordered from most to least number of studies per country in the hunting studies. Bars are coloured by the UN Subregion the country falls within (see inset).

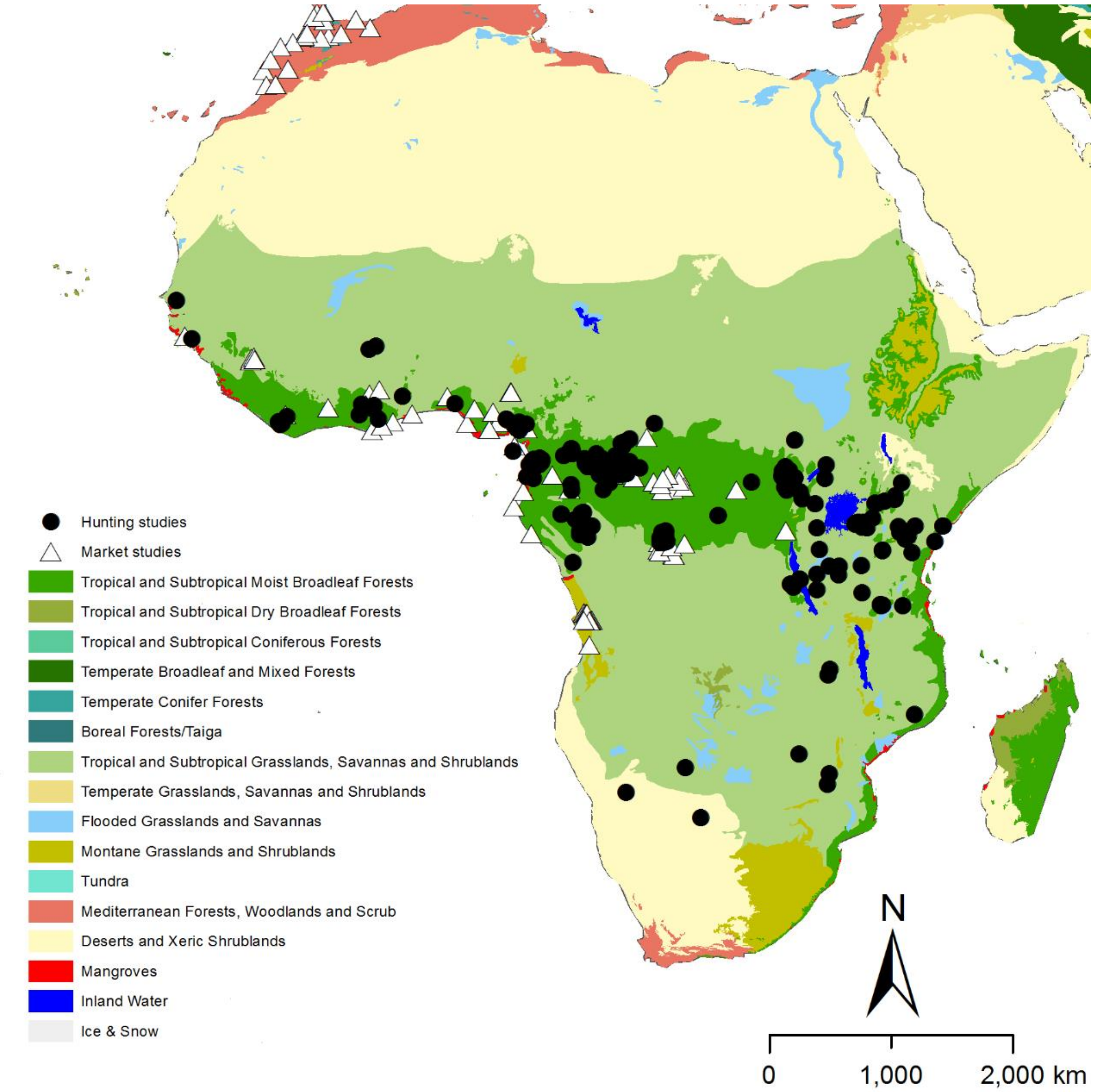

Figure 2.5. Sites at which hunting (black circles) and market (white triangles) studies have taken place in Africa, and are held within the OFFTAKE database. Colours show the distribution of biomes (Olson et al. 2001).

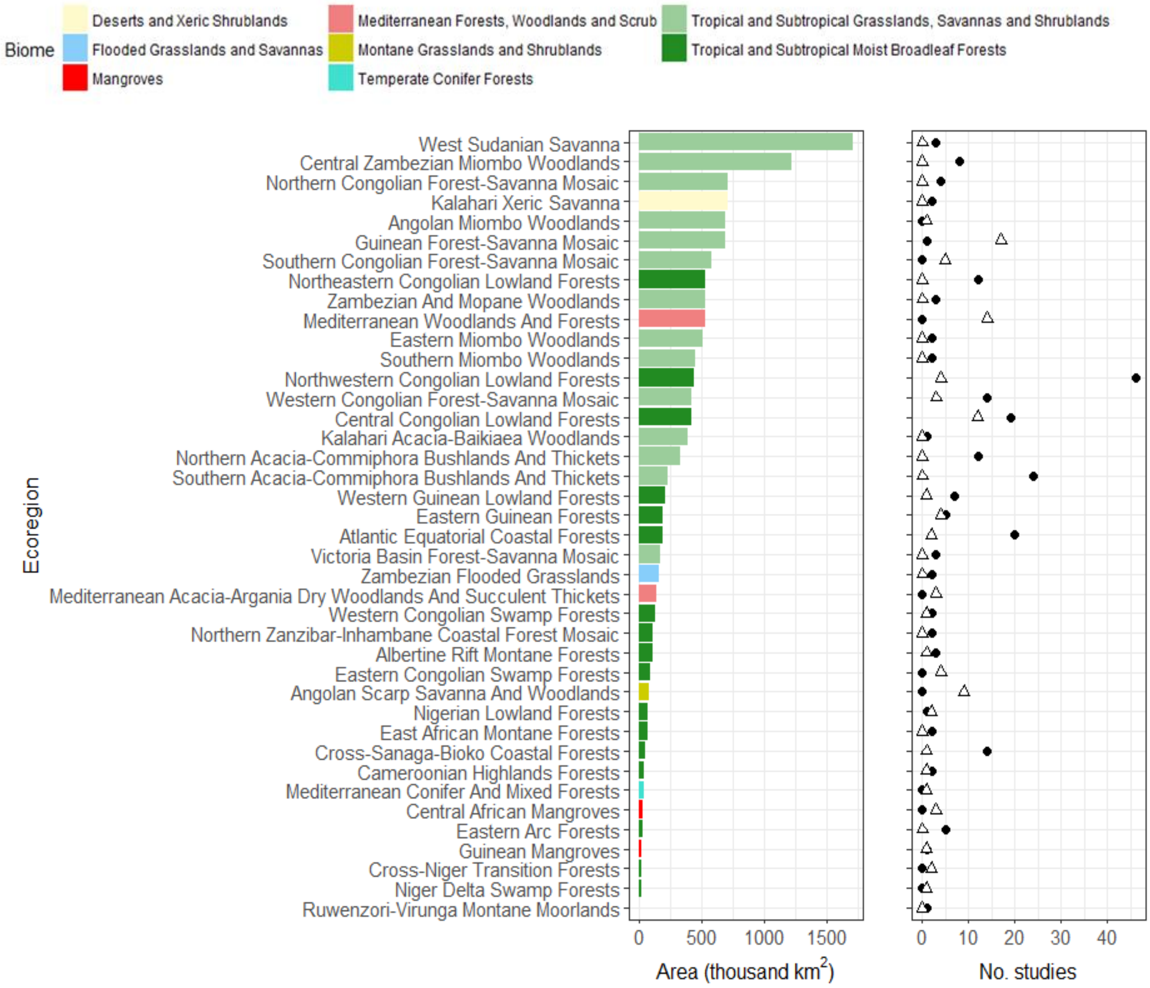

Figure 2.6. The area (left) and number of studies (right) per ecoregion. Hunting studies are indicated as black circles, and market studies as white triangles. Colours of bars show the biome that the ecoregion is located within.

2.3.3 Taxonomic coverage

In total, 318 species were identified to species level in the database as harvested or sold, and belong to 5 Classes (Figure 2.7): Amphibia (from 1 Order), Aves (14 Orders), Gastropoda (1 Order), Mammalia (15) and Reptilia (3). The largest numbers of species from hunting studies were identified from the Order Cetartiodacyla (58 species) and from market studies from the Primates (46). When grouped by UN Subregion, Middle Africa was found to have the greatest number of species represented in the database (Figure 2.8).

Of the Orders represented in the database, 47% (16 Orders) contained ≥ 50% of the total number of species within the Order that occur in Africa (Figure 2.9). The top five most speciose Orders in the database were Passeriformes (225 species), Anura (225), Squamata (161), Primates (135), and Cetartiodactyla (122). Of these top five, Primates and Cetartiodactyla were particularly well represented in the database, representing 42.2% and 52.5% of the Orders respectively. Particularly underrepresented Orders in the database were Passeriformes (2.5% represented) and Anura (0.4%), both of which contain a relatively large number of species. While Carnivora was not in the top five most speciose Orders, notably, 66.7% of the number of species in Carnivora that occur in Africa (69 species) were represented in the database.

Of the species identified to species level in the database, 93% were assessed by the IUCN Red List, while 7% were not assessed and classified as unidentified. The unidentified species comprised of mostly reptiles (20 species), but also included one species of mammal (*Scutisorex thori*) and one species of gastropod (*Archachatina marginata*). Of the species that were listed as harvested or offered for sale in the database, a total of 5 species were listed as Data Deficient (1.5%, Figure 2.10), 67.9% as Least Concern, 6.9% as Near Threatened, 9.1% as Vulnerable, 4.1% as Endangered, and 3.5% as Critically Endangered.

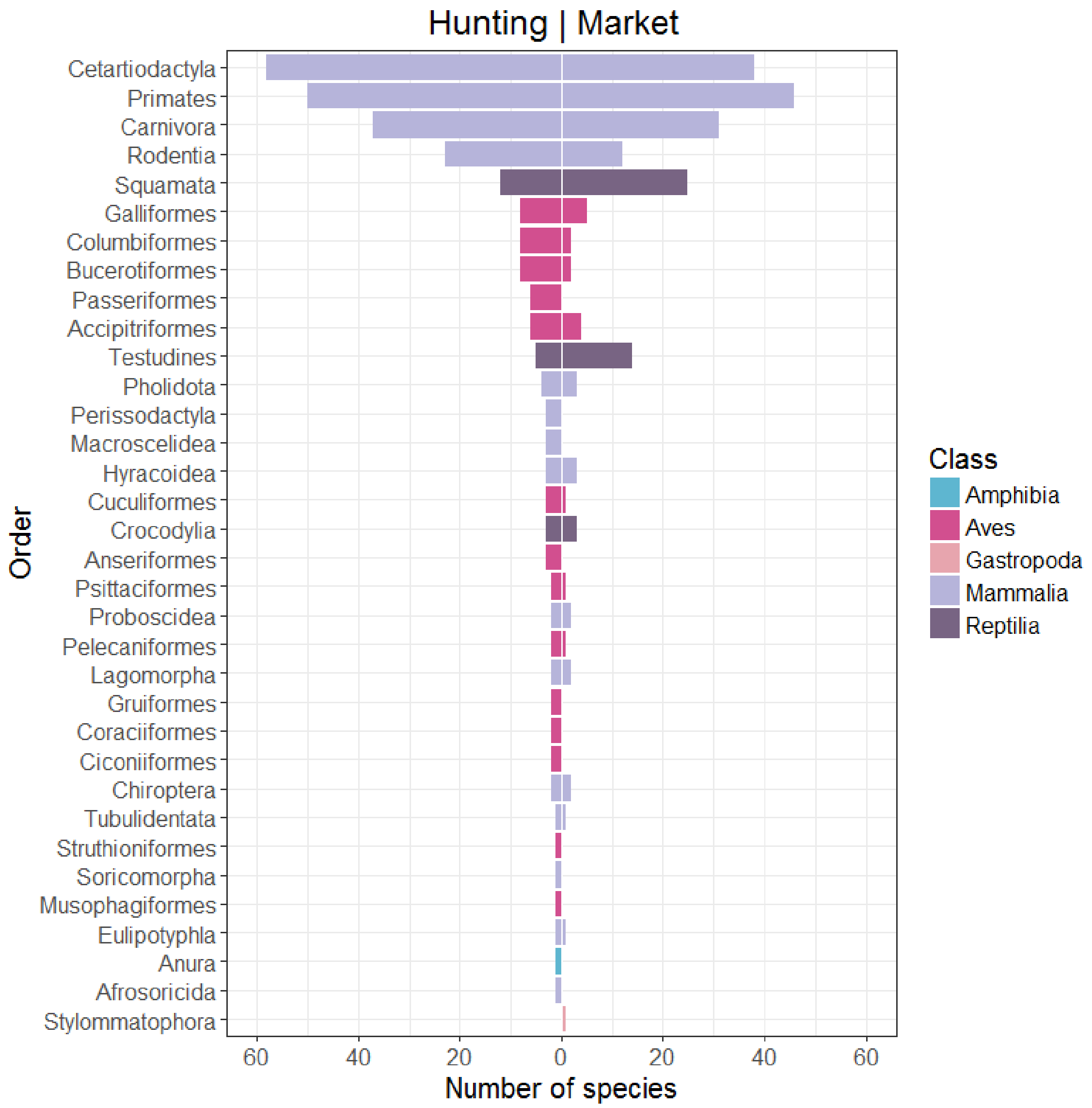

Figure 2.7. The total number of species per Order in the database from hunting (left) and market (right) studies, coloured by Class. Bars are ordered from most to least number of species per Order in hunting studies.

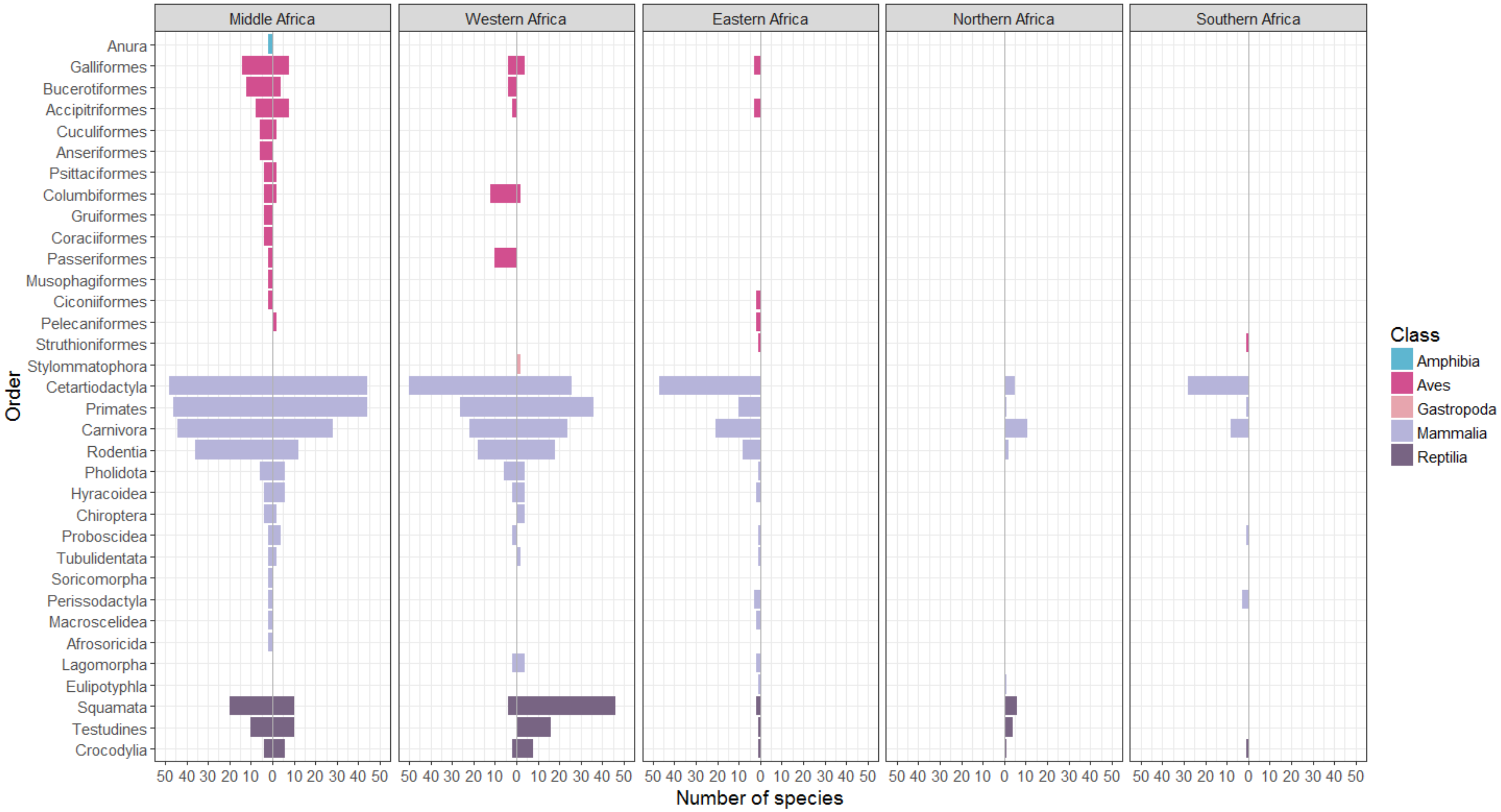

Figure 2.8. The total number of species per Order in the database from hunting (left half) and market (right) studies, grouped by UN Subregions in Africa (see inset of Figure 4). Bars are ordered alphabetically by Class, and then from most to least number of species per Order within each Class for hunting studies in Middle Africa.

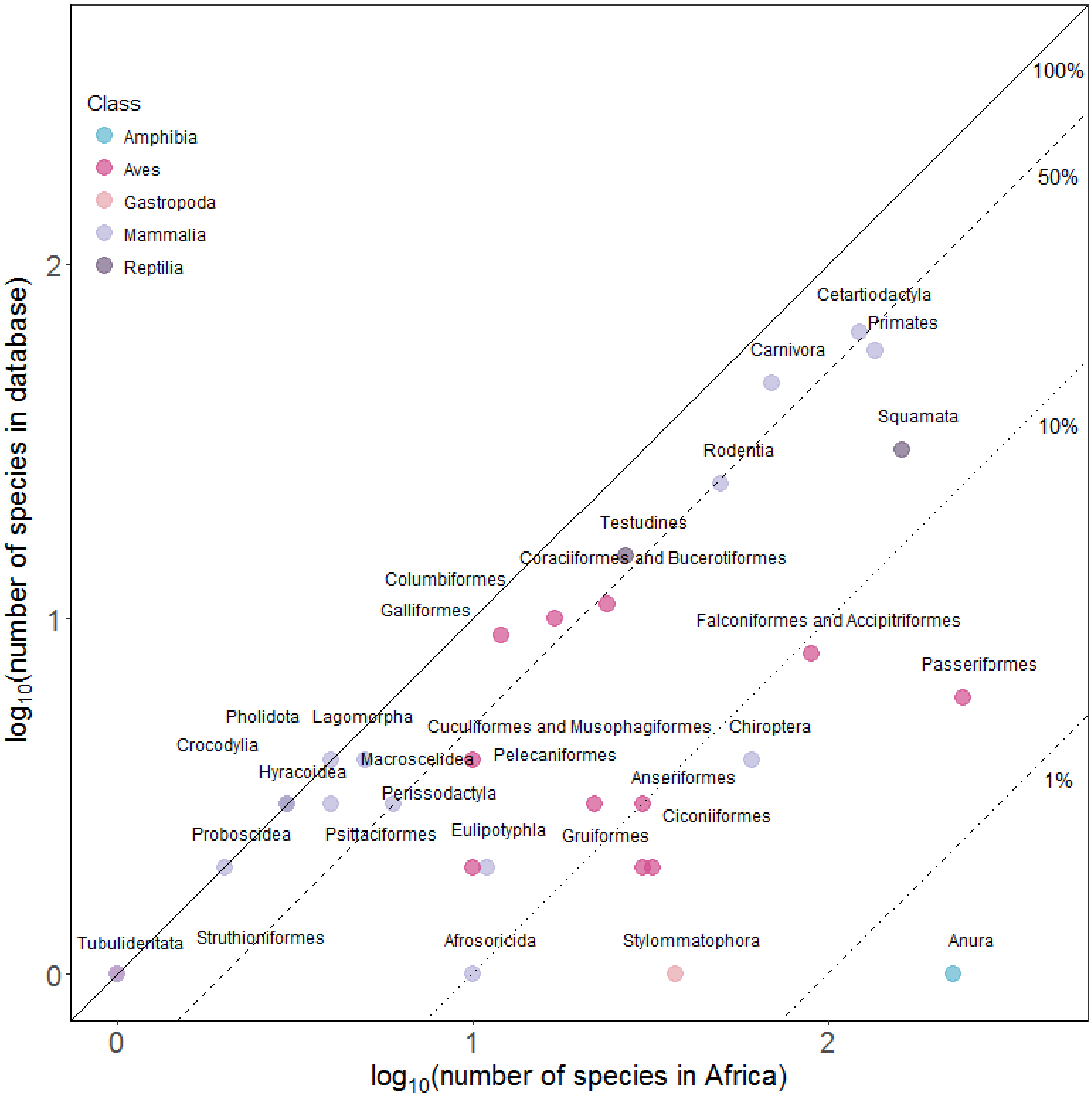

Figure 2.9. The number of species from each Order represented in the database, across all studies. Points are coloured by Class, and made translucent to show overlapping points. Lines indicate 100% (solid line), 50% (dashed), 10% (dotted), 1% (dot-dashed) representation. Data on the total number of species per Order in Africa was extracted from the online ARKive database (http://www.ARKive.org).

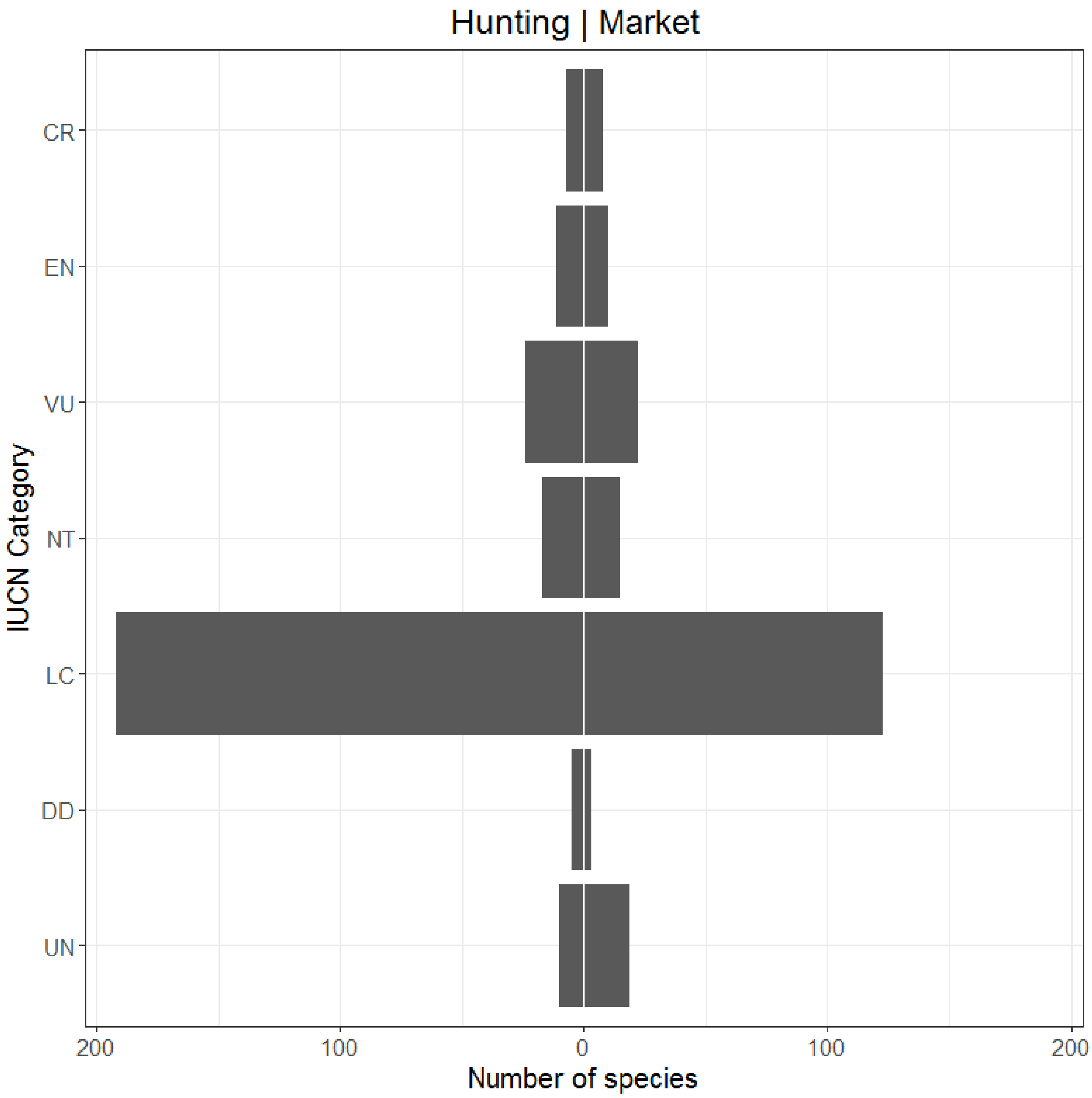

Figure 2.10. The number of species per IUCN Category represented in the database from hunting (left) and market (right) studies. The first bar (UN = Unidentified) represents species that have not been assessed by IUCN, then bars are ordered in order of IUCN Category from least to most threatened: DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, and CR = Critically Endangered.

2.4 Discussion

Through collating site-level studies on the exploitation of wildlife, I present a purpose-built database on the harvest and sale of wildlife in Africa. In total, I collated data from 137 sources and entered them into the database. Studies were conducted between 1974 and 2016, at 316 sites across 25 countries and 8 biomes in Africa. Across all studies, approximately 1.3 million animals from 318 species were recorded. Nearly half of the Orders recorded in the database were represented by at least 50% of the number of species within each Order that occur in Africa. The greatest number of species in the database were Primates and Cetartiodactyla, and accounted for a high proportion of the total number of species in Africa within each Order. Of the species recorded as harvested or at market in the database, 7.6% of the species were listed as Endangered or Critically Endangered.

Previous efforts have been made to collate sources that contain information on hunting and market sales at different sites. Ziegler et al. (2016) collated hunting information at 26 sites from 12 sources for Central Africa, while Taylor et al. (2015) collated information from 275 sites from 67 sources in West and Central Africa (but this included consumption studies). In the database presented here, ninety-eight hunting studies provided information on either the hunter territory size, or the area over which harvesting was recorded (e.g. a reserve), which was not previously recorded in Taylor et al. (2015) and exceeds the 12 sites recorded in Ziegler et al. (2016). Hunting territory size estimates are needed for area-based extrapolations of total annual wildlife harvests (see Chapter 3). Therefore, the database I present here has greatly expanded upon these previous databases both in terms of geographical scope and number of sources.

Studies were found to differ greatly in terms of sampling effort, and the level of detail provided. For example, the median number of days surveyed for market studies was smaller than that of hunting studies, which may be due to difficulties in counting carcasses discretely over long periods of time, or estimating the turnover of carcasses at the market. Furthermore, I found more sites at which time-series information was available for hunting studies than for market studies. Whilst half of the hunting studies provided information on the number of hunters surveyed, below 40% provided information on the total number of hunters at a site. Of those that provided both values, the median number of hunters surveyed was 43%. The proportion of hunters surveyed and the number of days surveyed is an important consideration for future studies given that the quantities hunted and time dedicated to hunting differs significantly between hunters (Coad 2007).

The majority of studies were found to be clustered in Middle Africa and surrounding tropical forest ecosystems, with few studies located in Southern and Northern Africa. In particular, hunting studies were conducted most frequently in Cameroon, while market studies were most frequent in Democratic Republic of Congo. It is likely that this geographic clustering is caused by a number of factors, whereby a study site is chosen based on: 1) known hunting pressure, 2) conservation concern, 3) safety for researchers, 4) ease of access for researchers, and 5) willingness of communities to engage in research. Given the number of hunting studies conducted in Cameroon, a case-study could be conducted to test whether it is possible that a database such as this one could be used for country-level analyses to guide conservation and policy efforts in Cameroon. For example, future initiatives should endeavour to include long-term monitoring into their efforts, particularly by re-sampling at sites that have already been sampled previously (as in Gill et al. 2012; Coad et al. 2013), to track changes in wildlife harvests, and ultimately enable targeted conservation actions where needed.

While a large number of species are harvested across the region, my database highlights that the greatest number of species come from the order Cetartiodactyla, corroborating research indicating that this taxon is the most important vertebrate group for human food security, providing a source of protein and micronutrients (Wilkie & Carpenter 1999). Primates, carnivores, squamates and rodents had the next greatest number of species in the database, but are also generally relatively speciose groups. The database is also particularly well represented in terms of the total number of species of Cetartiodactyla and Primates that occur in Africa (Figure 2.9). I observed a taxonomic bias in both hunting and market studies towards recording only vertebrates, where invertebrates are not often recorded at the same time; some studies further focussed on particularly charismatic groups, e.g. primates (Refisch & Koné 2005). Some speciose Orders are also only represented by a couple of species in the database, such as Anura and Passeriformes. This may be because these Orders are generally not specifically targeted or less preferred, and may only have been recorded if they were caught by an indiscriminate trap or snare. Moreover, it is known that insects and other invertebrates are consumed widely across

Africa (van Huis 2003), yet I only found one study that quantified the harvest of African land snails (Class: Gastropoda). Future studies are needed to investigate the exploitation of all wildlife, including invertebrates, to better understand the full impact that humans have on all taxa, and also in understanding the needs of different communities.

Monitoring and tracking wildlife harvests where hunting occurs (rather than at markets) is challenging, and doing so over large spatial extents and periods of time is more difficult still. Hunting studies are challenging to conduct for a number of reasons such as the requirement for extensive resources (time, infrastructure, and funds), the need to build a strong trusting relationship with a community and find communities that are willing to report wildlife harvests. Despite these difficulties, hunting studies still offer the most informative and detailed data, which can be used to answer the most pertinent questions. Given the disparities observed between the studies in the database, there is a need for the production of best practice guidelines, or a ‘toolkit’, for conducting hunting studies from which studies are standardised and aim to collect harmonised essential data variables. These data requirements should be agreed upon by researchers, conservation non-governmental organisations and donors, and would allow for greater coordination between researchers and conservation efforts. Harmonising studies by ensuring that data is comparable will enable sustainability metrics to be calculated, allow the comparison of more studies, and could be used to inform conservation decision-making and assess progress towards international agreements (e.g. UN Sustainable Development Goals).

There were a number of challenges that arose when collating disparate studies. For example, designing a database that could house information from different sources first involved collating lists of the different types of data that studies collected. Furthermore, many studies referenced in the literature were not available online or in public libraries, and were found by contacting researchers with paper copies of reports and unpublished non-governmental organisation (NGO) reports which were no longer available from the authors themselves. Here, I have illustrated the archival potential of the database created in this thesis, which could act as a hub for storage of data from past, present, and future studies. Quantifying the harvests of wildlife by communities is important to further understand sustainability, and potential risks to wildlife and people. The hunting and trade of wildlife has been shown to have implications for nutrition (Fa et al. 2015b), zoonotic disease transmission (Wolfe et al. 2005; Cantlay et al. 2017), ecosystem health (Young et al. 2016), livelihoods (van Vliet & Nasi 2008), and culture (Buij et al. 2016; Svensson et al. 2016). Databases such as that presented here, and analyses and information derived from such databases, are needed to demonstrate to governments that natural resources provide essential ecosystem services to millions of the world's most vulnerable people.

3 Quantifying the harvest of wildlife in Central Africa

3.1 Abstract

The overexploitation of wildlife has recently been identified as one of the main pressures on wildlife globally. However, efforts for conservation action and policy cannot be targeted without first knowing what quantities of wildlife are being harvested, and which areas might be experiencing high harvest levels. Using a wealth of information collated from decades of studies on the harvest of wild vertebrates in Central Africa, we compare three different methods to estimate the total annual harvest. Furthermore, we investigate the environmental and socio-economic factors that predict wildlife harvests using a mixed modelling approach, and use significant factors to spatially extrapolate wildlife harvests. Depending on the methods used, our estimates of total harvest varied between 1 and 5.5 million tonnes per year. Hunters located closer to protected areas harvested significantly more biomass per annum. We produced a map of wildlife harvest and estimated that 1.6 million tonnes of wildlife are harvested in Central Africa per year, which is lower than previous estimates. Our study has implications for future efforts to quantify harvests, and identifies areas of past research bias and future research priority. We demonstrate how a mapping approach can be used to identify likely areas experiencing high levels of hunting, providing a means of targeting future conservation policy and action.

3.2 Introduction

Humankind has exploited wildlife for millennia (Abernethy et al. 2013), yet with human population growth and technological advancements, it has never been more important to understand the exploitation of natural resources. The unsustainable exploitation of wildlife, hereafter ‘overexploitation’, has been identified as one of the main pressures driving species closer to extinction (Maxwell et al. 2016), so much so that humans have now been described as unsustainable ‘super predators’ (Darimont et al. 2015). In the tropics, mammal and bird relative abundance declined by 80% and 50% respectively in hunted areas compared with areas with no hunting (Benítez-López et al. 2017). Wildlife is an important source of food and livelihoods for millions of people across the tropics

(Brashares et al. 2004, 2011), and so declines in wild animal populations present a threat to both wildlife and the people who rely on it (Weinbaum et al. 2013). To identify overexploitation and design conservation actions and policies that target overexploitation, we must first have comprehensive quantitative estimates of exploitation and identify the species that are exploited.

For decades, researchers have quantified the hunting, consumption, or sale of wildlife at markets at individual sites across the tropics (Taylor et al. 2015; Stafford et al. 2017). The most direct data on exploitation comes from studies which have documented all of the animals caught, hereafter ‘harvested’. Researchers often document the number of animals harvested by counting the carcasses that enter the village upon the hunters return (De Souza-Mazurek et al. 2000; Coad et al. 2013), or by directly counting the carcasses that the hunters capture (Kümpel 2006). Regional extrapolations of wildlife harvests from individual site-level studies may result in findings that do not reflect patterns across large spatial scales. However, by collating and analysing many local studies together, regional extrapolations may more accurately reflect the bigger picture. For example, Peres (2000) used wildlife harvests from 31 rural settlements to estimate that the rural populations of the Brazilian Amazon alone harvested approximately 67,000-165,000 tonnes of game vertebrates annually. Peres calculated the average annual number of animals consumed per capita, and then multiplied it by the rural population size of low income households in the Brazilian Amazon.

Whilst Africa, and particularly Central Africa, is currently one of the most biodiverse regions in the world (Gaston 2000; Olson et al. 2001), it is also the region predicted to undergo half of the world’s human population growth up to 2050 (UN DESA 2017). In Africa, at least 91 species of mammal are already threatened by hunting, let alone other lesser-studied taxonomic groups. Given the current pressures on wildlife from hunting, and predicted increases in human population, it is particularly important to understand the state of wildlife harvests in Africa. Site-level hunting studies have been combined to estimate annual harvests in Central Africa (Table 3.1). Fa et al. (2002) estimated that approximately 4.9 million tonnes of wild meat were extracted from Congo Basin forests annually, by calculating the annual number of individual animals of each species harvested per capita. However, this study was limited to the harvest of mammals, and was only estimated from 14 sites. More recently, Fa et al. (2016) estimated that 11.6 million tonnes of wildlife are harvested annually in Central Africa, estimated by calculating the annual biomass of wildlife harvested per capita. However, this study, whilst increasing the number of sites to 26, included hunting camps as well as villages as separate sites. All of the aforementioned studies did not consider how representative the sites were of the potential sites in the region, and did not adequately account for variation between studies (e.g. biome, country, length of study, and method of data collection), both of which could lead to biased estimates.

Table 3.1. Estimates of annual terrestrial vertebrate harvest in Central Africa from previous studies. Dashes represent unknown values.

Annual harvest per square kilometre (km^2 yr^{-1})	Unit	Mean or Median	Total annual biomass (million tonnes yr^{-1})	Area	No. Sites	Source
213.1	kg	-	4.9	Congo Basin[a]	14	Fa et al. (2002)
225.7 ± 187.5	animals	Mean	11.8 ± 7.0	Congo Basin	26	Fa et al. (2016)
92 ± 78.9	kg	Mean	-	Central Africa[b]	26	Ziegler et al. (2016)
156	kg	Median	-	Central Africa	26	Ziegler et al. (2016)

[a] Congo basin refers to the forested regions of the basin itself.

[b] Central Africa refers to the countries: Cameroon, Central African Republic, Democratic Republic of Congo, Equatorial Guinea, Gabon, and Republic of Congo.

Spatial analyses of the socio-economic drivers and environmental drivers of wildlife harvests may enable the identification of areas that are more intensely harvested. Attempts have been made to map wildlife harvests in Central Africa. Fa et al. (2016) produced a map of harvest rates by combining the calculated annual biomass per capita with a map of human population. To our knowledge, only one attempt has been made to investigate the drivers of wildlife harvests spatially in Central Africa. Ziegler et al. (2016) used predictions from a random forest model including road density, distance to protected area and population density as predictors to map annual harvest per square kilometre. However, both studies were limited by their sample size, and the methods used did not account for differences between sites adequately. Other environmental and socio-economic factors have been implicated as drivers of wildlife harvest. For example, the accessibility of an area for humans, measured as the travel time to major settlement, has been shown to have a significant effect on wildlife declines associated with hunting pressure (Benítez-López et al. 2017).

Here, we compare how different methods of estimating annual wildlife harvest across Central Africa influence regional estimates of wildlife harvests, and investigate the drivers of wildlife harvests, using the most comprehensive database of wildlife harvests yet. Firstly, we demonstrate and compare three non-spatial methods to estimate the annual harvest of wild vertebrates in Central Africa by extrapolating across 1) number of hunters, 2) rural population, and 3) the area hunted. Secondly, we investigate potential environmental and socio-economic drivers of wild meat harvests (e.g. access to market, distance to road, biome, and distance to protected area) and demonstrate a method to spatially extrapolate an estimate of total annual terrestrial vertebrate harvests. Furthermore, we discuss the scale of wildlife exploitation in Central Africa, potential ways forward, and priorities for future research efforts.

3.3 Methods

3.3.1 Data

3.3.1.1 Hunting data

We searched the literature for sources that quantified the number of individual vertebrates (mammals, birds and reptiles) harvested at a known location and time period in Central Africa, here defined as Cameroon, Central African Republic, Democratic Republic of Congo (DRC), Equatorial Guinea, Gabon, and Republic of Congo. Sources may be published literature, grey literature, or MSc/PhD theses. Sources were included if they a) collected data on the hunting of terrestrial vertebrates at a known location and time period, b) collected data using a published methodology, and c) reported geographic coordinates of the sites sampled, or where it was possible to obtain coordinates by locating the site using Google Earth. Each source was allocated an identification code.

Each source may have sampled multiple sites, each of which we refer to as a ‘study’. The number of days over which data was collected in a study was extracted, hereafter ‘study duration'. We calculated the middle date between the start and end date of data collection for each study, hereafter 'mid-year'. We also extracted the following information from each study where possible: the area over which vertebrates were hunted (hereafter 'hunting territory'), hunter survey effort (i.e. the proportion of hunters surveyed out of the total number of hunters at the site), and the human population at the site. For studies that did not report this information, we contacted authors directly (non-responses were collate in a separate folder). In studies where the hunting territory was displayed in a figure in the source but the area was not quantified, we used the area and polygon tools in Google Earth to calculate the hunting territory.

Studies reported wildlife harvests in terms of the number of individuals harvested. For each species reportedly hunted, we extracted information on body mass from Myhrvold et al. (2015) only. In cases where animals were not identified to species level, we assigned them the mean body mass of the most taxonomically resolved level possible e.g. genus or family. To model total biomass of wildlife harvested per study, we multiplied the number of individuals harvested per species by their respective body mass, and summed the total weights of all species.

Not all studies provided information on the total number of hunters, the total human population of the site, or the hunting territory. For studies with missing information we calculated estimates using the complete data from other studies, hereafter 'gap-filled', in the following way. We calculated the median proportion of hunters at sites with known number of hunters and site population. Then, we estimated the number of hunters or total site population based on the median proportion across the other sites. We allocated the median hunter territory size, that was calculated only from the sites which measured it, to sites that did not report hunter territory.

3.3.1.2 Environmental and socio-economic data

For each site, we used existing spatial datasets to extract a number of environmental and socio-economic variables (Table 3.2) using ArcGIS version 10 (ESRI 2011). The accessibility layer, was estimated as the travel time by land and navigable river to the nearest city of $\geq$ 50,000 people (i.e. more accessible areas have shorter travel times), hereafter 'accessibility'. Human population counts and accessibility were calculated for the year 2000, which is approximately the middle year of the harvest data.

All maps had a native reference system of Geographic WGS84, and were reprojected into the Africa Albers Equal Area Conic projection before distance calculations were made. Distances to nearest protected area and nearest road were calculated as the Euclidean distance, with sites inside protected areas or on roads set at 0 km, and were calculated at a 1 km resolution (0.0083 decimal degrees).

Estimates of rural human population have been used previously to extrapolate the likely population engaged in wildlife harvest and consumption (e.g. Peres 2000). To produce a map of rural human population that estimated approximately the same rural population as the UNPD (2014), we removed towns and cities from the WorldPop map by removing grid cells where the human population count was > 120 people per km^2.

Table 3.2. Environmental and socio-economic layers

Layer	Name and Version	Native Resolution (decimal degrees)	Source
Human Population Count	WorldPop	0.0083’	1
Protected Areas	World Database of Protected Areas	NA	2
Roads	gROADS Version 1	NA	3
Accessibility	Global Map of Accessibility	0.0083’	4
Land Cover Class	Global Land Cover 2000	0.0083’	5

[1] Linard et al. (2012)

[2] IUCN & UNEP-WCMC (2017)

[3] CIESIN / Columbia University and ITOS / University of Georgia (2013)

[4] Nelson (2008)

[5] Bartholomé & Belward, (2005)

To ensure we had enough data points per land cover class, we aggregated land cover classes in the following way: closed evergreen lowland forest, submontane forest, montane forest, deciduous woodland, swamp forest, closed deciduous forest, and mangrove were aggregated into one ‘forest’ category, and Mosaic Forest / Croplands, and Mosaic / Savanna classes were aggregated into one ‘mosaic’ category.

3.3.2 Testing site representativeness

We tested whether the sites for which we obtained harvest data were representative of settlements within Central Africa in terms of their distance to road, distance to protected area, accessibility, and human population. We calculated the distance to the nearest road and the human population count as described above, for all known settlements in Central Africa. We obtained coordinates of known settlements in Central Africa by compiling country-level datasets from the World Resources Institute (http://www.datasets.wri.org). We used the human population count data per grid cell because population data at the settlement level was not available. Using nonparametric two sample Kolmogorov-Smirnov tests (Massey 1951) we tested whether the sites with harvest data are sampled from the same distribution as all Central African settlements for distance to road, distance to protected area, accessibility, and human population.

3.3.3 Non-spatial quantification of wildlife harvest

Different studies collected harvest data over different periods of time and using different sampling methodologies. To ensure that studies are comparable, we calculated the total biomass harvested per hunter per year. Firstly, for each study, we divided the summed total study biomass harvested across species by the number of hunters surveyed, and the number of days a study was sampled for, and then multiplied by 365.

It is possible that studies that sampled over periods of time < 365 days may over- or underestimate mean wildlife harvest rates if, for example, studies occurred in a peak hunting season. We tested whether the annual harvest per hunter differed for studies sampled for < 365 days compared with those that sampled ≥ 365 days using a nonparametric two sample Kolmogorov-Smirnov test, due to non-normal distribution and unequal variances of the two groups (Massey 1951).

To better triangulate the total vertebrate biomass harvested (kilograms) in Central Africa, we calculated three different estimates for comparison. To test whether gap filling studies influenced our estimates, we calculated total annual vertebrate harvest using all studies (including gap filling), and using a subset of studies that did not require gap filling, for each of the three methods described below.

3.3.3.1 Extrapolating by number of hunters

There are $i = 1,2,\ldots n$ sites for which harvest data was collated, and then used in the following extrapolations. For each site i, we have information on the annual biomass harvested by the surveyed hunters b_i, the number of hunters surveyed s_i, the total number of hunters h_i, and the total population p_i.

To calculate the annual biomass harvested in Central Africa extrapolating by number of hunters (B_h), we calculated the median annual harvest per hunter, and multiplied this value by an estimate of the number of rural hunters in Central Africa. To estimate the number of rural hunters we extracted the rural human population of Central Africa (P) from the Urban and Rural Population by Age and Sex dataset (UNPD 2014) for the year 2000, and multiplied it by the median proportion of people that were hunters across sites. We also presented estimates of B_h using the upper and lower interquartile ranges (IQR) of the median proportion of hunters across sites, to investigate the variation between estimates. This method assumes that the proportion of rural people hunting is the same across Central Africa.

$$B_h = \mathrm{median}_i^n \left(\frac{b_i}{s_i}\right) \cdot \mathrm{median}_i^n \left(\frac{h_i}{p_i}\right) \cdot P$$

3.3.3.2 Extrapolating by rural people

To calculate the annual biomass harvested extrapolating by rural population (B_r), we first calculated the biomass harvested per hunter per site as above (b_i / s_i), and multiplied this by total number of hunters at a site (h_i), and divided by the total human population at the site (p_i). Then, we multiplied the median annual harvest per rural person across sites by the total rural human population in Central Africa (P). This method assumes that an evenly spread proportion of rural people harvest wildlife.

$$B_r = \mathrm{median}_i^n \left(\frac{\frac{b_i}{s_i} \cdot h_i}{p_i}\right) \cdot P$$

3.3.3.3 Extrapolating by area

To calculate the annual biomass harvested extrapolated by area (B_a), we first calculated the annual biomass harvested per hunter per site (b_i / s_i), and multiplied this by total number of hunters at a site (h_i), and divided by the hunting territory (a_i). We then multiplied the median annual harvest per square kilometre across sites by the total area of Central Africa (A). This method assumed that our calculated estimate of hunting territory size is representative across Central Africa.

$$B_a = \mathrm{median}_i^n \left(\frac{\frac{b_i}{s_i} \cdot h_i}{a_i} \right) \cdot A$$

3.3.4 Spatial analyses of environmental and socio-economic determinants of wildlife harvest

To test whether the wildlife harvested per hunter can be predicted by the environmental and socio-economic characteristics of a site, we fitted a linear mixed effects model (using all studies, including those for which we gap-filled) with the annual vertebrate biomass of wildlife harvested per hunter fitted as the response variable. Human population, mid-year, accessibility, distance to road, distance to protected area, and habitat type were considered as predictor variables (Table 3.2). All variables apart from habitat type were fitted as continuous effects, which were tested for correlations by using Pearson correlation tests.

To account for some of the variation between sites that might be introduced due to sampling effort and study duration, we weighted the mixed effects models by the summative score of:

1. Studies that sample for a whole year include possible seasonal variation of wildlife harvests. We therefore gave studies that sampled ≥ 365 days a higher score (score of 2), and those < 365 days a score of 1 (Figure 3.1A).
2. The subset of hunters surveyed in the study could influence the overall harvest estimates if particularly active or inactive hunters participated in the study. We

therefore scored studies that sampled ≤ 35% hunters at a site as 1, > 35% and ≤ 75% as 2, and > 75% as 3 (Figure 3.1B).

3. We also acknowledge the difference between studies that provided a complete set of data (i.e. the following data were available for the study: the number of hunters surveyed, the total number of hunters, the site population, and the hunter territory), and those for which we needed to gap fill. We scored studies as 2 if they provided all information, and as 1 if we calculated site estimates.

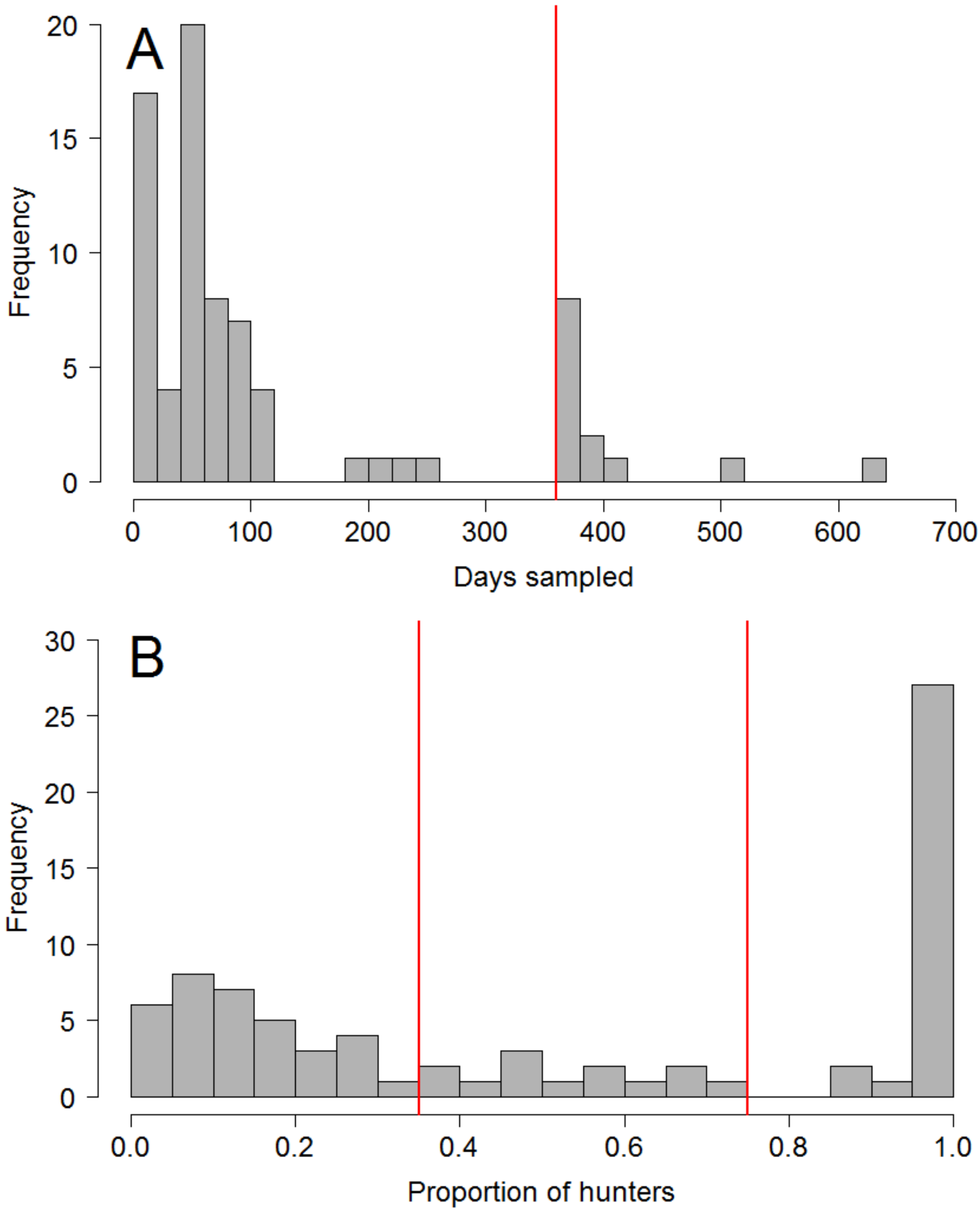

Figure 3.1. The distribution of A) the number of days that studies were sampled, and B) the proportion of hunters that were sampled across studies. Red lines show the cut-off points listed in the model weighting description.

The response variable was log transformed prior to analyses to remove heteroscedasticity. Continuous variables were scaled before model selection. To avoid over-fitting our models we did not consider interactions. The Source ID was included as a random effect in the model to account for some of the variation that may be introduced by the proximity of sites or the sampling methodology (Bolker et al. 2008). We selected the best model using backwards model selection, by incrementally removing variables and comparing model fit between models by using chi-squared tests on the log-likelihood values (Zuur et al. 2009). We tested whether quadratic polynomials of continuous variables should be included before we tested for linear effects. Models were fitted using the lme4 package (Bates et al. 2015) in R version 3.2.5 (R Core Team 2016).

We used the coefficients of the mixed-effects model containing only significant terms to spatially extrapolate wildlife harvests across Central Africa. We extrapolated to all grid cells with habitat type of forest or mosaic, but did not extrapolate beyond the range of our environmental and socio-economic variables.

3.4 Results

3.4.1 Data

We found 22 sources that contained the required data, and contained data for 77 studies at 74 sites in Central Africa (Figure 3.2A), spanning 1990 - 2015. The median study duration was 53 days (IQR 36 - 115). The median proportion of hunters at a site was 0.129 (IQR 0.08 - 0.21, n = 54), and the mean hunter territory size was 99 km^2 (IQR 60 – 184 km^2, n = 41), and was used for studies that did not provide this information.

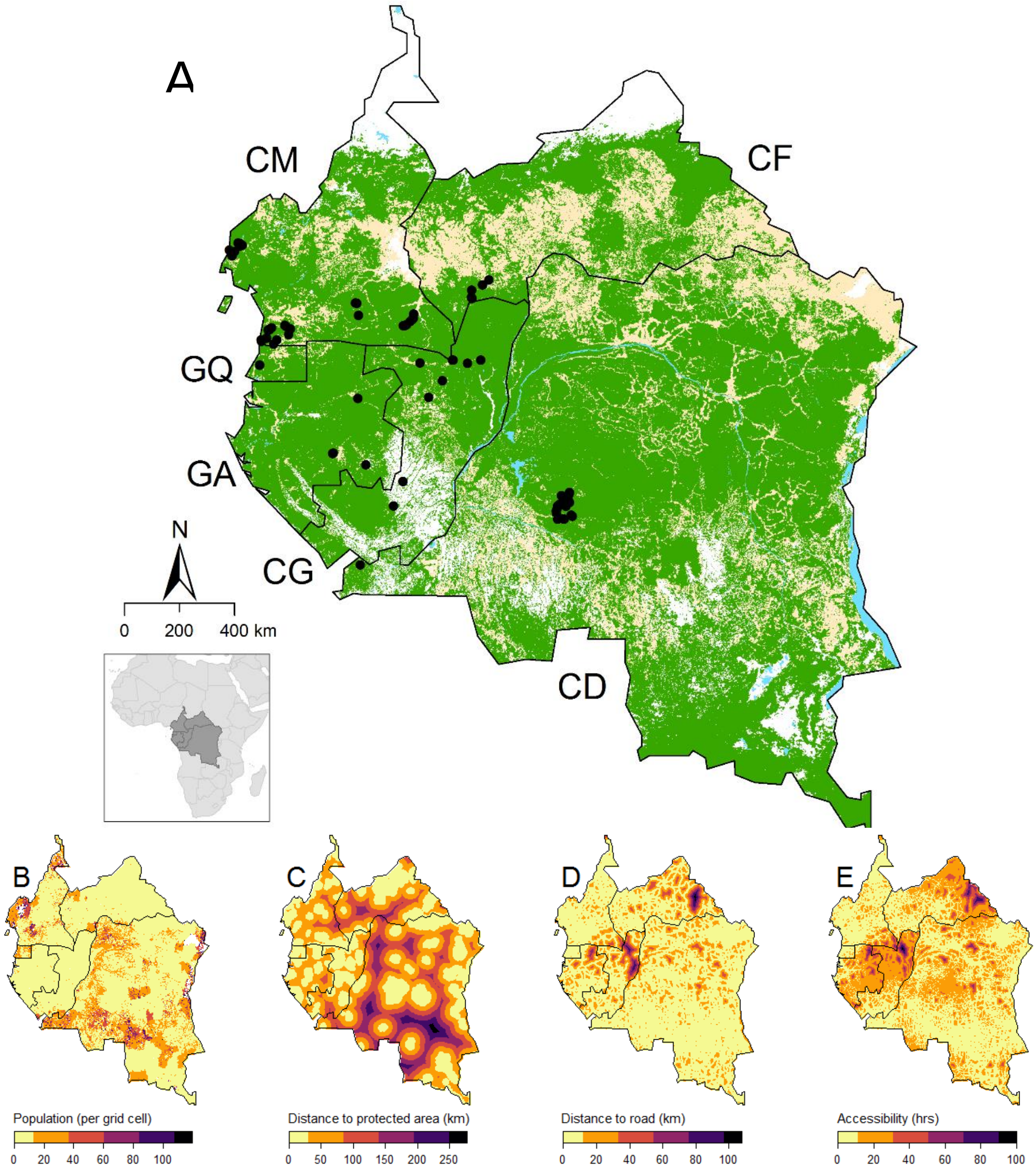

Figure 3.2. Sites (black points) for which we have harvest data from 77 studies across Central Africa in A) aggregated forest (green) and mosaic (yellow) habitat classes. Habitats for which we do not have data (white) and water (blue). Black lines show country borders, and the inset shows the locations of Central African countries within Africa. Layers used as predictor variables are shown for B) human population count from Linard et al. (2012), C) distance to nearest protected area, D) distance to nearest road, and E) accessibility. CM = Cameroon, CF = Central African Republic, CG = Republic of Congo, CD = Democratic Republic of Congo, GQ = Equatorial Guinea and GA = Gabon.

3.4.2 Testing site representativeness

We found that our sites had significantly lower human population count (median 6.6 people compared to 13.4 people, D = 0.312, p < 0.001, Figure 3.3A), were located significantly closer to protected areas (median 19.1 km compared to 51.9 km, D = 0.337, p < 0.001, Figure 3.3B), and were significantly less accessible than for all settlements (median 5.8 hours compared to 4.1 hours, Kolmogorov-Smirnov test D = 0.182, p = 0.014, Figure 3.3D). However, the sites for which we have data were representative of all settlements in Central Africa in terms of their distance to road (median of 1 km for both groups, K-S test D = 0.123, p = 0.205, Figure 3.3C).

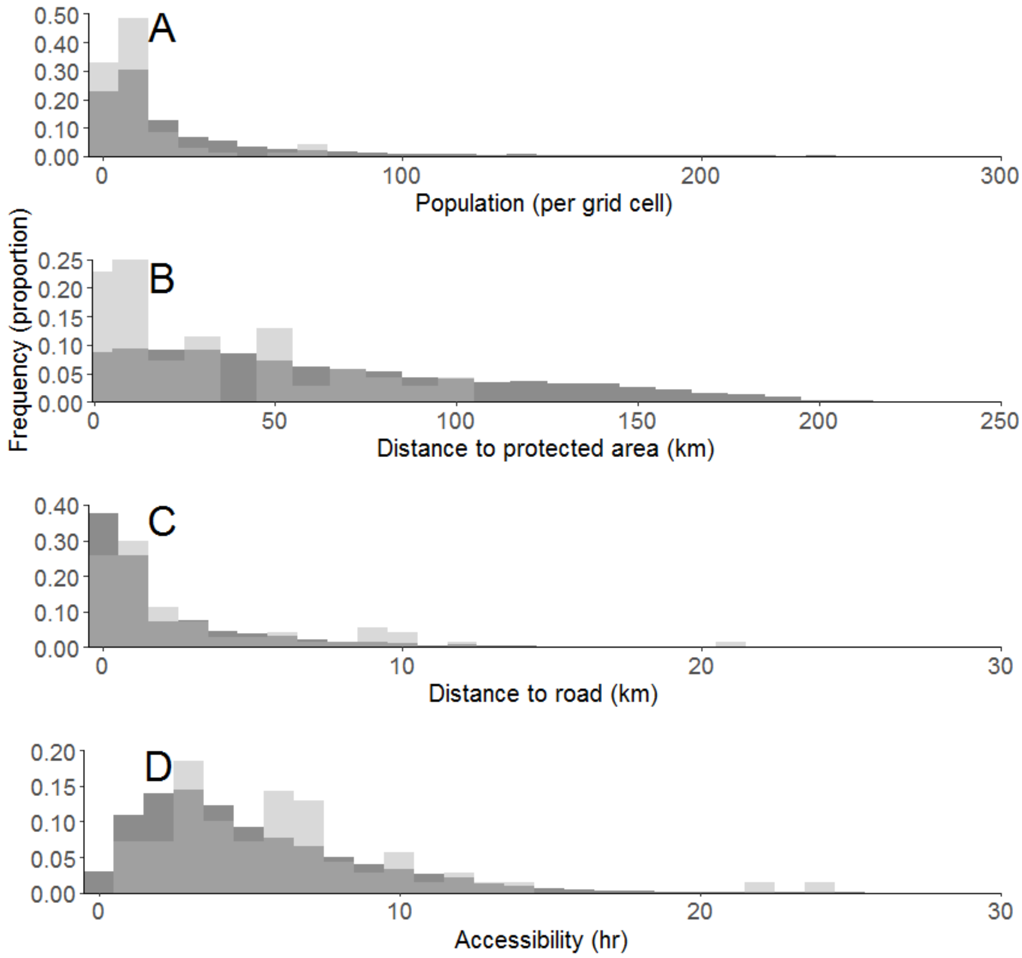

Figure 3.3. Distribution of all settlements in Central Africa (dark grey, n = 38,580 settlements) and sites for which we have wild meat data (light grey, n = 75 sites) for A) human population count from (Linard et al. 2012), B) distance to protected area, C) distance to road, and D) accessibility. X-axes on plots have been cropped to better visualise trends.

3.4.3 Non-spatial quantification of wildlife harvest

Using all datasets, including gap-filling, we found that depending on the extrapolation method used, estimates of total annual vertebrate harvest varied between 1 and 5.5 million tonnes. We estimate that 5.1 (2.5-9.4) or 5.5 (3.0-9.6) million tonnes were harvested in Central Africa if we extrapolated by rural human population or hunters, respectively, whilst we estimate that 1 million (IQR 0.6-2.7) tonnes of wildlife were harvested annually if we extrapolated by area (Table 3.3).

Using the subset of datasets that contained all the required information, we estimate that 6.2 (2.8-11.0) or 5.5 (2.7-10.2) million tonnes were harvested if we extrapolated by rural human population or hunters, respectively, whilst we estimate that 1.6 million (IQR 0.6-4.0) tonnes of wild meat were harvested annually if we extrapolated by area. Furthermore, we found that the annual biomass harvested per hunter from studies sampled for ≥ 365 days were sampled from the same distribution as those sampled < 365 days (median 490 kg when sampled for ≥ 365 days compared to 1102 kg when sampled < 365 days, K-S test: $D = 0.384$, $p = 0.053$, $n = 72$), but were nearly significantly different.

The variation between estimates is caused by differences in extrapolation method, namely the difference between extrapolating over total area or by total number of rural people. For extrapolations by rural hunters, we have also presented the total annual biomass estimates when calculated using the upper and lower quantiles of rural hunter estimates.

Table 3.3. Estimated biomass of wild meat extracted annually in Central Africa, based on three methods.

			Total annual biomass (million tonnes) and IQR		
Method	No. sites	Median kg/yr (IQR)	Median proportion of hunters (0.129)	1st quartile hunter proportion	3rd quartile hunter proportion
Hunter	Full (77)	987 (532 - 1705)	5.5 (3.0 – 9.6)	3.4 (1.8 – 5.9)	9.0 (4.8 – 15.5)
	Subset (72)	987 (476 - 1819)	5.5 (2.7 – 10.2)	3.4 (1.6 – 6.3)	9.0 (4.3 - 16.5)
Rural	Full (77)	119 (58 - 218)	5.1 (2.5 – 9.4)	NA	NA
	Subset (52)	143 (64 - 253)	6.2 (2.8 – 11.0)	NA	NA
Area (km^2)	Full (77)	248 (138 - 665)	1.0 (0.6 – 2.7)	NA	NA
	Subset (49)	402 (142 - 974)	1.6 (0.6 – 4.0)	NA	NA

5,000,000,000 kg = 5 million metric tonnes.

3.4.4 Spatial analyses of environmental and socio-economic determinants of wildlife harvest

For the environmental and socio-economic variables across sites, we found that the accessibility of sites was significantly correlated with the distance to nearest road ($r = 0.92$, $p < 0.001$, Figure 3.4). The mid-year of the study was significantly correlated with accessibility ($r = -0.39$, $p < 0.001$) and distance to nearest road ($r = -0.35$, $p = 0.002$). We included accessibility in the model selection, instead of distance to road and mid-year, because it is effectively a measure of 'distance to market', and considers navigable rivers, roads, and penetrability of land cover. We did not include year in the model because it was correlated with accessibility.

Hunters at sites closer to protected areas hunted significantly more wildlife per year than those located further away ($\chi^2_{3,4} = 4.946$, $p = 0.0262$, $n = 77$, Estimate = -0.327 and std. error = 0.144 for log-transformed total annual harvest, Figure 3.5). The minimum adequate model with distance to protected area had a marginal R-squared of 5% (proportion of variance explained by the fixed effects) and a conditional R-squared of 31% (variance explained by fixed and random effects). When we re-ran models with only studies that were not gap filled, the effect of distance to protected area remained ($\chi^2_{3,4} = 5.6658$, $p = 0.0173$, $n = 72$) but explained slightly more of the variance (marginal = 6%, conditional = 35%). However, we found no significant effect of human population density, year of study, or habitat type on the annual wildlife harvest (Table 3.4).

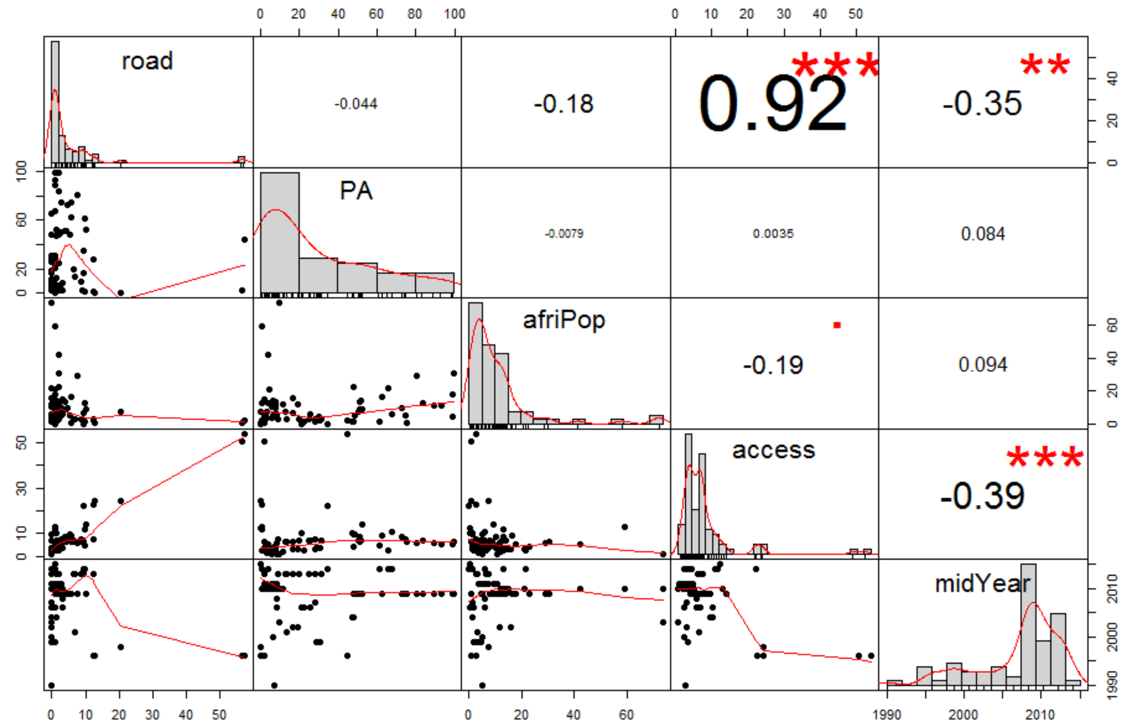

Figure 3.4. Correlation matrix of continuous variables that were included in the mixed-effects models. Numbers inside the grid show the correlation coefficients. Text size of coefficients and number of red stars represent significance of correlation, where * is significant at the $p < 0.05$ level, ** at $p < 0.01$, and *** at $p < 0.001$. 'road' = distance to nearest road, 'PA' = distance to nearest protected area, 'afriPop' = human population count, 'access' = accessibility, and 'midYear' = year of study.

We used the minimum adequate model including the distance to nearest protected area as the only statistically significant predictor, to map annual wildlife harvests per hunter across Central Africa. The predicted annual harvest per hunter per grid cell was multiplied by 12.9% of the human population within each grid cell to estimate the total annual biomass of wildlife harvested per grid cell (Figure 3.6). Summing the predicted annual harvested wild meat across all grid cells, we estimate that 1.6 million tonnes of wildlife are harvested annually across Central Africa. We note that areas with high annual harvests include: the Southwest and Northwest provinces of Cameroon, and the Western side of the Albertine Rift region, Sankuru province, Transfrontier Mayombe region, and Haut-Lomami province of the Democratic Republic of Congo (numbers 1 – 5, Figure 3.6).

Table 3.4. Statistics from the backwards model selection from the full linear mixed effects model for annual biomass of wildlife harvested per hunter. ΔAIC has been included to show the change in Akaike information criterion (AIC) when the term is dropped from the model. * highlights statistical significance at the p < 0.05 level. Polynomial terms (poly) are included for continuous variables.

Term removed	poly	Coefficient (scaled)	χ^2	df	p	ΔAIC
Human population	2	0.012	0.01	1	0.905	-1.98
Accessibility	2	-0.085	0.97	1	0.326	-1.04
Distance to protected area	2	-0.048	0.32	1	0.570	-1.67
Human population	1	-0.069	0.49	1	0.482	-1.51
Accessibility	1	0.129	1.39	1	0.239	-0.62
Habitat		0.289 (Mosaic)	2.86	1	0.091	0.86
Distance to protected area	1	-0.327	4.95	1	0.026*	2.95

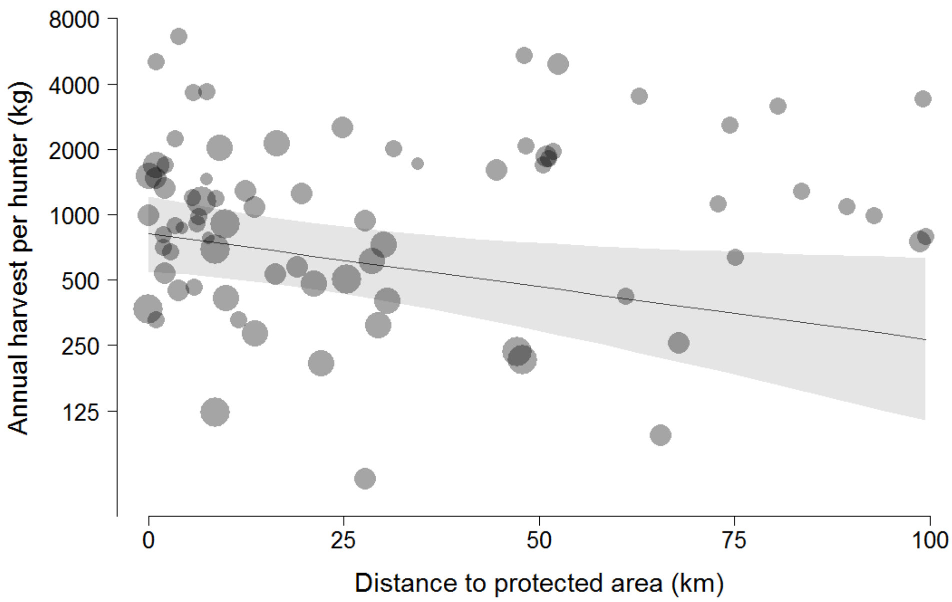

Figure 3.5. The annual harvest of terrestrial vertebrates per hunter (kg) at varying distances from nearest protected area in Central Africa. Points represent individual studies (n = 77), and are translucent to show density of points. Studies located inside protected areas have a distance to protected area of 0 km. Trend line shows the significant relationship from a linear mixed effects model with 95% confidence intervals (grey shading).

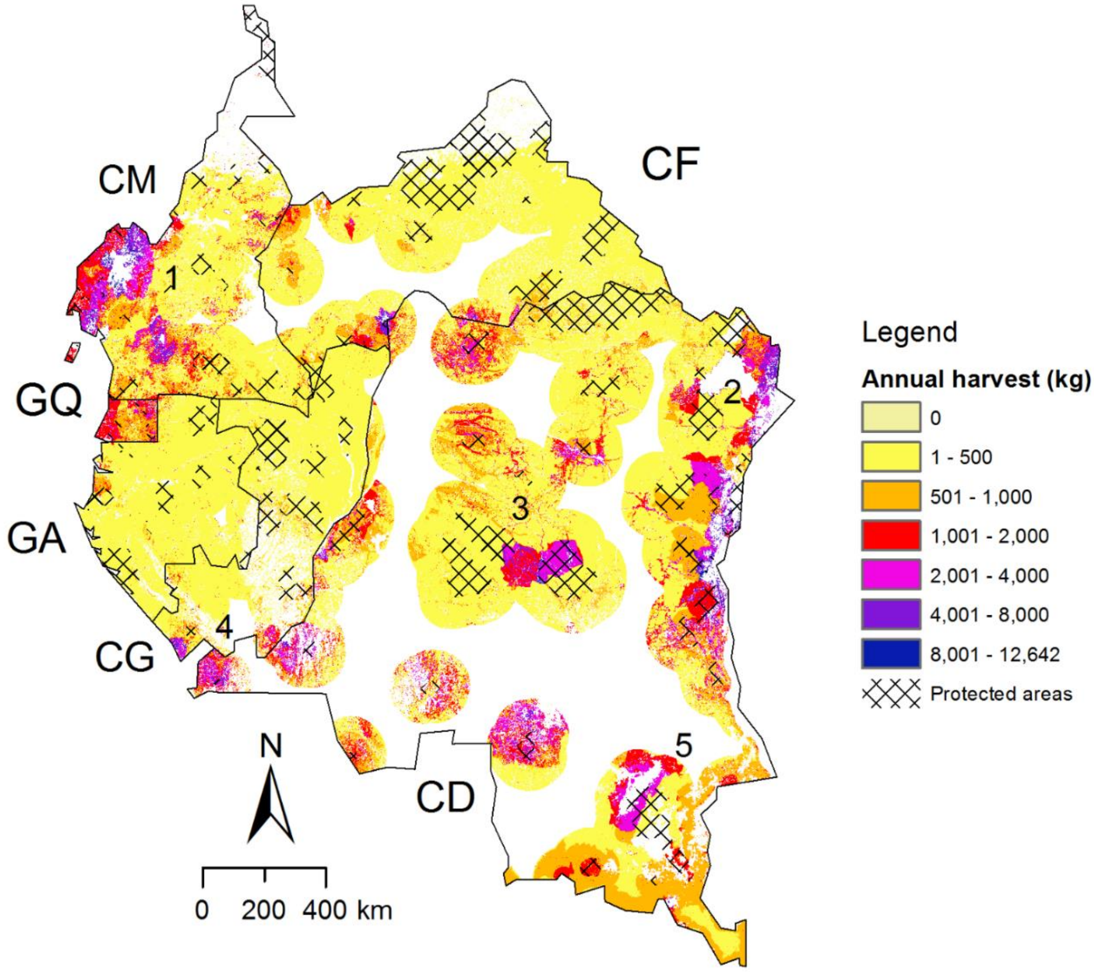

Figure 3.6. Distribution of total annual biomass (kg) of wildlife harvested across Central Africa based on distance to protected area, and multiplied by 12.9% of the rural population to show estimated hunting pressure. Predictions are based on a linear mixed effects model, and protected areas are shown in crosshatch. Grid cells for habitat types without data, grid cells that exceed the range of our protected area data, or if the number of people exceeded 120 people per cell are shown in white. 1 = Southwest and Northwest provinces, 2 = Western side of the Albertine Rift region, 3 = Sankuru province, 4 = Transfrontier Mayombe region, and 5 = Haut-Lomami province. See Figure 2 for country labels.

3.5 Discussion

Overexploitation of wildlife has recently been identified as one of the main threats facing biodiversity, yet without information on the quantity of wildlife harvested, it is difficult to identify when and where exploitation is unsustainable. We set out to investigate the methods to estimate wildlife harvests, and the drivers that influence the quantity harvested across Central Africa.

Quantifying the harvest of terrestrial wildlife across large areas is difficult, and understanding how different methods of estimating harvests vary is important to produce a range within which the actual harvests fall. Using data from across Central Africa, we estimated that the total harvest of wild vertebrates every year in this region was between 1 and 5.5 million tonnes using extrapolations based on area or human population. When incorporating spatially explicit environmental parameters into our extrapolations, we estimated a total of 1.6 million tonnes of wildlife were harvested. Our results span the range of previous estimates, e.g. 1 million tonnes consumed in the Congo Basin (Wilkie & Carpenter 1999) and 5 million tonnes harvested (Fa et al. 2002b), but highlight that estimates can vary widely dependant on extrapolation methods. Extrapolating across rural population assumed that a proportion of people in every rural settlement are hunters and that the proportion does not vary with socio-economic and environmental parameters, yet extrapolating across area assumes that hunting territories do not overlap and that every area is hunted.

Our study found that hunters closer to protected areas harvested significantly more wildlife than hunters further away, corroborating the findings of Ziegler et al. (2016). This is likely due to the higher availabilities and densities of wildlife inside protected areas, which could be acting as a source population for hunted areas outside the protected area boundaries, acting as 'sinks' (Mockrin et al. 2011). Although, hunting has been shown to reduce mammal populations even inside protected areas (Benítez-López et al. 2017), and it is important to note that the total biomass of wildlife differs between sites. Benítez-López et al. (2017) found that wildlife in hunted areas was more depleted in areas that are more accessible to humans. We did not find a statistically significant association between accessibility and total annual harvests, which may indicate that hunters shift to whatever species are available given declines in more preferred large-bodied species

(Cowlishaw et al. 2005a; Fa et al. 2015a). Knowing how long a particular area has been harvested for, in addition to the hunting pressure may be useful, given that areas that have been harvested over a longer period of time could be at the end of a depletion gradient, although in Latin America length of harvest period was not found to be a significant predictor of the taxonomic composition of harvests (Stafford et al. 2017).

Spatially extrapolating annual biomass harvests enables the identification of areas that are predicted to have high hunting pressure. From our map, which includes human population, we note that the following areas (numbered as in Figure 3.6) have some of the highest predicted biomass harvested per grid cell: 1) the Southwest and Northwest provinces in Cameroon near to Korup National Park, Rumpi Hills and Banyang-Mbo Protected Areas, and the Bakossi Mountains Wildlife Reserve; 2) the western side of the Albertine Rift, particularly in the Northeast corner of Oriental province near Garamba National Park; 3) Sankuru province in between Salonga National Parks and Sankuru Nature Reserve; 4) the Democratic Republic of Congo portion of the transfrontier Mayombe forest; and 5) Haut-Lomami province, north of Upemba National Park. Evidence from near Sankuru suggests that hunting pressure is high in this region, with 62-73% of households listing hunting in their top three sources of income (Colom 2006).

Wildlife harvest studies usually quantify the harvest of vertebrates that were hunted by men only. However, women and children also hunt and gather smaller wildlife such as birds, insects, squirrels and amphibians opportunistically (Muchaal & Ngandjui 1999; Cowlishaw et al. 2005b; Carpaneto et al. 2007; Gallois et al. 2015). Amphibians (e. g. Efenakpo et al. 2015), insects (Kitanishi 1995; van Huis 2003), and invertebrates such as African land snails (Cowlishaw et al. 2005b; Allebone-Webb 2009) are regularly consumed by communities in Sub-Saharan Africa. For example, 10% of the animal protein consumed came from 65 species of insect in a study in the Democratic Republic of Congo (deFoliart 1999). Therefore, studies that only quantify hunting by men, or vertebrate harvests, will underestimate total wildlife harvests. In addition, some methods estimate wildlife harvests, but may underestimate the quantity of killed wildlife and the impact it may have on wildlife populations (Peres 2000). For example, studies may not include animals that rotted in traps e.g. 11% of carcasses were found to be rotten, inedible or scavenged at sites in Tanzania (Nielsen 2006), and 8% of all animals caught at sites in Gabon were rotten (Coad 2007). Mortality of animals that were injured from hunting but escaped is also rarely quantified (but see Yasuoka 2006 that reports 101 escapes from 198 snared animals). Therefore, the estimates presented here, while more detailed than previous estimates, may still be conservative estimates of the total biomass of wildlife harvested.

Site level human population data for Central Africa are not available, therefore we used a gridded human population count layer which itself is based on a model (Linard et al. 2012). While it is possible to acquire information on settlement locations, it is currently not possible to obtain standardised population data for each settlement across Africa, hindering our ability to predict vertebrate exploitation accurately. We extrapolated by a static proportion of rural people that are likely to be hunters, but spatially explicit estimates of human population per settlement would allow us to include a dynamic estimate of the proportion of hunters depending on population size at a particular settlement. Abernethy et al. (2010) found that the number of hunters per capita decreased with increasing village population, and assert that accurate estimates of annual harvest for large settlements are more difficult to obtain. Thus, our estimates based on human population are likely to overestimate wildlife harvests in areas with higher populations. The sites for which we had harvest data were also found to be located in slightly less populated areas in comparison with the distribution of all settlements in Central Africa, highlighting a bias in our data, and together with static proportions of hunters, may result in overestimating the total annual biomass harvested. If data on settlement location and population are available, information on hunter territories could better be applied in harvest mapping efforts, for example, mapping could be conducted only for areas within a specified distance from settlements.

The method used here to estimate total annual wild meat harvests uses data collected at different periods of time to calculate one estimate. Wildlife harvests may be changing over time given increasing human population density and increases in the availability and use of guns. In rural Gabon, when asked why wildlife was declining, many hunters stated either an increase in hunting or gun hunting as the main reason (Coad et al 2013). In the two Gabonese villages included in our analyses, the number of gun hunting trips almost doubled (100% increase) between 2004 and 2010 (Coad et al 2013). Recently, a study in Malabo, Equatorial Guinea, showed that the number of carcasses on a wild meat market killed from gun-hunting increased by approximately 275% between 1998 and 2010

(Cronin et al. 2015). Furthermore, as access to previously ‘wild’ areas increases due to expansions of roads and mining, hunting in these areas tends to follow (Watson et al. 2016; Kleinschroth & Healey 2017; Spira et al. 2017). Therefore, it is important that future research not only investigates the effects of increasing gun use, and how hunting practices may be changing over time, but also the spatial extent of hunting as landscapes become more accessible.

In this study, we demonstrate that by collating site-level hunting studies, the total annual wildlife harvest can be extrapolated, but that estimates vary depending on the assumptions made in the extrapolation method. This study builds upon decades of research on the hunting of wildlife in Central Africa, and investigates the harvest of wildlife in this region in more detail than any study to date. By doing so, we have been able identify areas of research bias, we recommend that studies investigate the hunting at sites with higher human populations, and in mosaic environments. Moreover, current studies have also focussed on identifying areas where hunting occurs, but not on identifying areas where hunting does not occur. Identifying no-hunting areas may allow for more accurate estimates of total wildlife harvest, which may currently be overestimated. In addition, there is a lack of studies in Northern, Central and Eastern DRC, and northern Central African Republic, and future studies should investigate total wildlife harvests from all members of a community, including the harvest of invertebrates.

4 Indicators for wild animal offtake: methods and case study for African mammals and birds

4.1 Abstract

Unsustainable exploitation of wild animals is one of the greatest threats to biodiversity and to millions of people depending on wild meat for food and income. The international conservation and development community has committed to implement plans for sustainable production, consumption and use of natural resources, and requested development of monitoring systems of bushmeat offtake and trade. Although offtake monitoring systems and indicators for marine species are more developed, information on harvesting terrestrial species is limited. Building on approaches developed to monitor exploitation of fisheries and population trends, we have proposed two novel indicators for harvested terrestrial species: the mean body mass indicator (MBMI) assessing whether hunters are relying increasingly on smaller or larger species over time, as a measure of defaunation, by tracking the body mass composition of harvested species within samples across various sites and dates; and the offtake pressure indicator (OPI) as a measure of harvesting pressure on groups of wild animals within a region by combining multiple time series of the number of harvested individuals across species. We applied these two indicators to recently compiled data for West and Central African mammals and birds. Our exploratory analyses show that mean body mass of harvested mammals decreased while that of birds rose between 1966/1975 and 2010 as measured by the MBMI. For both mammals and birds the OPI increased substantially during the observed time period. Given our results, time-series data and data collated from multiple sources are useful to investigate trends in body mass of hunted species and offtake volumes. In the absence of comprehensive monitoring systems, we suggest that the two indicators developed in our study are adequate proxies of wildlife offtake, which together with additional data can inform conservation policies and actions at regional and global scales.

4.2 Introduction

Unsustainable exploitation is one of the greatest threats to terrestrial (Schipper et al. 2008) and marine (Costello et al. 2010) wild animals. Simultaneously, exploitation of wild animals for food, referred to as ‘wild meat’ globally or ‘bushmeat’, as it is known in Africa (Milner-Gulland et al. 2003), is a major source of animal protein for more than a billion of the world’s poorest people (Brashares et al. 2014). Because of these contrasting issues, world leaders committed through the Convention on Biological Diversity (CBD) to “take steps to achieve or have implemented plans for sustainable production and consumption and have kept the impacts of use of natural resources well within safe ecological limits” (Aichi target 4, CBD 2010). Since 2008, the CBD requires Parties to comply with recommendations, resolutions and decisions related to ‘bushmeat’ issues, and the 11th Conference of the Parties of the CBD explicitly called for the development of “appropriate monitoring systems of bushmeat offtake and trade” (Decision XI/25, CBD 2012). However, limited progress has been made towards developing a comprehensive monitoring system of wild animal offtake, especially for terrestrial species.

An effective monitoring system requires indicators that represent and explain the condition of a monitored variable over time (Jones et al. 2011), usually comprising drivers, pressures, states and responses for multiple species and geographic scales (Sparks et al. 2011). Although a number of biodiversity indicators have been developed, especially to assess trends in ‘state’ of habitats, e.g. natural habitat extent (Tittensor et al. 2014), and vertebrate species, e.g. Living Planet Index or LPI (Loh et al. 2005), few indicators exist that can inform on key aspects of pressures, responses and benefits (Balmford et al. 2005; Mace & Baillie 2007; Walpole et al. 2009; Tittensor et al. 2014). Indicators of pressures on wild animals, e.g. levels of harvest or offtake, or on the benefits derived from wild animal use, e.g. consumption rates, are relatively well developed for marine species, but poorly advanced for terrestrial species.

Knowledge of the spatial and temporal patterns of marine fish stock exploitation has progressed over past decades because of the wealth of data available (Pauly 2007, FAO Statistics Division 2015) from globally available fish stock assessments (Milner-Gulland & Akçakaya 2001; Worm et al. 2009). Estimates of the absolute biomass of fish stocks exploited by fisheries are widely considered as the gold standard for fisheries indicators (e.g. Kleisner et al. 2013). For example, Pauly (2007) produced an indicator for the state of marine fisheries based on the plethora of catch data, classifying fisheries from developing to collapsed. The Large Fish Indicator (LFI), another widely used indicator, captures trends in the biomass contribution to the catch of larger individuals or species, which is a response to exploitation, i.e. curtailment of size structure (e.g. Greenstreet et al. 2011; Shephard et al. 2011). However, these indicators based on landing records likely underestimate exploitation because not all harvest is reported e.g. bycatch, wastage. These two types of indicators, the former utilizing the number of fish caught at a site and the latter the body mass of fish caught to assess changes in stocks over time, provide insights into pressure and benefit of fisheries. The same approaches can be applied to terrestrial species.

For terrestrial species, development of exploitation indicators has largely been hampered by a lack of data from long-term monitoring across multiple scales (Weinbaum et al. 2013). Recently, however, Tierney et al. (2014), using time series of vertebrate abundance from the LPI, produced two indicators for wild commodities: the Utilized Species Index (USI) and Harvest Index (HI). The USI uses population data categorized at the species level as 'utilized' by humans according to multiple sources including the International Union for Conservation of Nature (IUCN) Red List (IUCN 2009) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Trade Database (2009). The HI tracks the sustainability of offtake by combining harvest and population data. Both, USI and HI, are based on population trends, rather than direct measures of trends in exploitation pressure. Further, both indicators may actually provide conservative estimates of exploitation pressure because not all populations of a species categorized as 'utilized' are necessarily impacted by exploitation. Other indicators of wild meat exploitation have collated data from market surveys or on consumption (e.g. Crookes et al. 2006; Brashares et al. 2011; Fa et al. 2015a), thereby capturing offtake over larger areas, rather than using more spatially explicit offtake data. Other studies have measured wildlife offtake at village or trap level, providing information on actual numbers of individuals hunted at known sites (e.g. Noss 1999), often restricted to individual villages (e.g. van Vliet & Nasi 2008; Kümpel et al. 2010). Currently these data have not been used to inform indicators of regional or global trends, though offtake studies from individual villages are becoming more readily available, and at a small number of sites, analyses of data over time have been possible (Gill et al. 2012; Coad et al. 2013).

We apply approaches developed for monitoring fisheries offtake and population trends to develop indicators of terrestrial wild meat exploitation. First, we outline two indicators.

The first, based on ‘snapshot data’, focusses on investigating trends in the mean body mass of species hunted, analogous to the LFI, and a second investigates trends in offtake by combining time-series data collected at individual sites. Finally, using recently compiled data on wild meat for West and Central Africa (Taylor et al. 2015) supplemented with additional African data from the literature, we conduct exploratory analyses to demonstrate the utility of these data and indicators.

4.3 Methods

We use the term ‘offtake’ to describe the number of individuals removed from the environment through hunting or harvesting by humans. Although data on wild animal offtake, consumption, and trade at markets are available, we restrict our analyses to offtake data as these provide information on actual numbers of individuals harvested at a known site, whereas consumption and market data provide less spatially explicit information because knowledge of the likely harvest site is lost along the commodity chain (Cowlishaw et al. 2005b).

To investigate trends in offtake over time and space, data need to be collated from a variety of sources, often gathered for different purposes. As no standard protocol exists for offtake studies, such compilation includes studies that differ in their taxonomic, geographic, seasonal and temporal coverage and may also vary in other aspects such as ethnic group, hunting technique, targeted species, taboo animals, hunting area, hunting effort, alternative livelihoods, researcher effort, and timing and duration of data collection. Although in practice researchers might concentrate on certain areas and taxa, based on their interests, conservation priorities, socio-political conditions, or may focus on areas of particularly high harvest, here we assume that there is no systematic bias in sampling effort and sites that could affect our analyses.

Data on offtake were collated from a variety of ‘sources’, where source is a published paper, report from a non-governmental organization, or Ph.D. dissertation or master’s thesis. Each source contains one or more ‘samples’; each sample is a record of the overall wild meat offtake collected at a specific time and site using a specific sampling method. For example, a source providing offtake data for two sites surveyed in both February and October, would be structured as a single source containing four samples, one for each month and site. We assigned a unique identifier (ID) to each sample, unless the sample is part of a time series. We only included data on harvested individuals that could be identified taxonomically to at least Class. We separated data into two categories based on the duration over which they were collected, as follows:

1. Snapshot data: ‘Snapshot’ data refers to samples collected at one site over a continuous period of time within 18 months (Coad et al. 2013). An example of snapshot data is an offtake survey conducted between January and July 2010 in Putu Town, Liberia (Greengrass 2011). These samples may not have recorded offtake throughout an entire year, so may not capture differences in seasonality. Wild animal offtake in Africa is often seasonally dependent, affected by climatic conditions, availability of species, and socio-economic factors such as other financial opportunities for hunters (Allebone-Webb et al. 2011).

2. Time-series data: Time-series data refers to continuous or repeated sampling over multiple years using the same method at the same site and time of year. An example of a time series is data on putty-nosed monkeys (*Cercopithecus nictitans*) hunted each year between 1998 and 2008 in northern Republic of Congo (Riddell 2010; Wildlife Conservation Society Noubale-Ndoki Project 1998-2007, *unpublished data*).

We outline two offtake indicators, one based on snapshot data, i.e. the mean body mass indicator (MBMI), to investigate trends in body mass of offtake as a proxy for species composition, and another, i.e. the offtake pressure indicator (OPI), based on time-series data, to examine trends in offtake over time across multiple sites.

4.3.1 Two offtake indicators

4.3.1.1 Mean body mass indicator

We assessed whether all snapshot data, collected across different sites and times, could be used to develop an indicator of changes over time in the composition of hunted species. We proposed using mean body mass within each sample as a proxy of species composition, where a drop from larger to smaller species may indicate a process of defaunation of a habitat (Dirzo et al. 2014). This is analogous to the LFI, which captures changes over time in the contribution of biomass from large fish to the catch (see above, Greenstreet et al. 2011; Shephard et al. 2011). We expected this indicator to decrease if the proportion of small-bodied species increased within the catch over time, either because large-bodied species were extirpated or more smaller-bodied species were being harvested.

An MBMI was calculated by fitting a trend line to the arithmetic mean body mass of the total offtake for each sample for every year, weighted by the number of species harvested. Each sample was weighted by the number of species within the sample, assuming that the number of species is a proxy for sampling effort and to down-weight studies with single or few species. However, differences among studies in the number of species reported may also be caused by other factors such as differences in habitat, site, or harvesting pressure. We attempted to account for this heterogeneity among data sources by including ID and country as random factors, and weighting by number of species, in our statistical analyses.

Body mass data for mammals were collated from Jones et al. (2009) and Kingdon (1997) and for birds from Dunning (2008). For those individuals that were not identified to species level, we assigned the mean body mass of related taxa found in Africa to the most resolved level taxonomically. To investigate whether year, country and ID explained any of the variation in mean body mass among samples we used a linear mixed effects modelling framework, with model selection based on likelihood ratio tests (Zuur et al. 2009). We specified year as a fixed effect and tested for non-linear relationships by including up to third order polynomial terms. To account for autocorrelation within the data we compared random factor structures including ID and the country where each sample was collected as random effects. As our datasets are limited to a small number of countries (8 countries) with few observations each (≤ 8 studies per country), we fitted country as a random effect (Clark and Linzer 2015), however as more data become available fixed effects and interactions among country and year should be explored. All analyses were conducted in the R statistical computing software (version 3.0.1, R Core Team 2013) with linear mixed effects models fitted in the lme4 package (version 1.1-7, Bates et al. 2014).

4.3.1.2 Offtake pressure indicator

The offtake pressure exerted on terrestrial species can be represented by the overall trend in number of individuals harvested of each species across sites and years. Time series of multiple species harvested can be aggregated and indexed to calculate an overall trend in the number of individuals harvested. We hypothesize this indicator to increase with increasing number of individuals harvested reflecting an increase in overall hunting pressure, although individual species may decrease.

To quantify trends in offtake pressure, we developed an OPI that combines multiple time series of harvested species. The OPI uses the same method as developed for the LPI (equations 1 to 4 in Collen et al. 2009) to aggregate time series across species and sites using the chain method. The chain method calculates the logarithm of the ratio of the number of individuals harvested, i.e. offtake, for successive years. The mean value of the logarithm of the ratio was calculated for species that had more than 1 time series. For any year within a species-specific time series in which the offtake was 0, the mean offtake across years was calculated and 1% of that mean added to each 0 before calculating the index. Missing data points were imputed using log-linear interpolation. Once species-specific means were calculated for each year, the overall mean logarithm of the ratio of the offtake was calculated, weighting each species equally. The index was set to 1 in the first year where data are available. We calculated 95% confidence intervals (CI) for each annual index value using the LPI bootstrap resampling technique (Collen et al. 2009) with 1000 iterations.

Trends in offtake pressure may have occurred before the earliest data were collected, and the ‘starting point’ of hunting, or hunting at high pressure, will likely differ among sites. Therefore OPI trends need to be interpreted carefully.

The OPI is limited because time series data are non-independent of each other, i.e. there are time series for several species for each source and site. Like the LPI, averaging across species-specific time series obscures trends for individual species. For example in Makao-Linganga (1998-2008) the offtake of 12 species increased, whereas 4 decreased and 14 remained stable. The chain method implemented to produce the OPI is limited because these data were not initially collected through a specifically designed initiative that ensures continuity of data collection. Loh et al. (2005) discuss few differences between the chain method and least-squares linear modelling results for the LPI, and suggest that the least-squares approach would allow the use of full datasets without having to interpolate missing values. More time series datasets would allow the least-squares approach to be employed more robustly and other non-linear responses, e.g. using generalized additive models, to be explored.

4.3.2 Data for exploratory analyses

We extracted all offtake data for mammals and birds from the West and Central African bushmeat database (Taylor et al. 2015). As Taylor et al. (2015) only collated sources investigating all species hunted at each site, we supplemented these data with sources that studied individual species, or partial or full communities. We searched for additional sources from the ISI Web of Science (Thomson Reuters 2014), Imperial College Conservation Science thesis archive (http://www.iccs.org.uk/publications/thesis-archive-general/) and reference lists. If sources did not contain all information required, we contacted the authors for raw data. We separated data into snapshot and time-series data as outlined previously.

Time series were generated by compiling data from multiple sources that sampled at the same site using the same method in different years. When different sources were sampled during different times of the year, we only included data for matching dates. For example, Coad (2007) collected data from October 2003 to February 2005, whereas Schleicher (2010) collected data at the same sites using the same methods from June to August 2010.We therefore used data from June to August from both sources (Coad et al. 2013) and assigned one ID. Some species were reported to be harvested in only some years of a time series, and sources did not always report absence of species. When a species was reported to have been harvested in at least one year, we assumed it was not harvested in all other years when not reported and added zeros to complete the time series for the species.

We calculated both indices separately for mammals and birds separately to investigate whether the offtake trends differed between these groups. With more time series available, the OPI could be disaggregated by taxonomic groups; guilds, e.g. herbivores, carnivores; threatened species; and areas, e.g. protected areas or countries, as well as using more complex analysis techniques including interactions.

4.4 Results

4.4.1 Data

We extracted data for 18 sources with 41 samples across 29 sites from the West and Central African bushmeat database (Taylor et al. 2015), and another 11 sources with 18 samples across 14 sites from our searches. In total, we compiled data from 29 sources across 43 sites (Figure 4.1) for 59 samples (Sabater Pi 1981; Ichikawa 1983; Kano & Asato 1994; Colell et al. 1994; Amubode 1995; Kitanishi 1995; Dethier 1995; Jeanmart 1998; Muchaal & Ngandjui 1999; Noss 1999; Hart 2000; Fimbel et al. 2000; Fa & Yuste 2001; Kümpel 2006; Yasuoka 2006; Brown 2007; Willcox & Nambu 2007; Carpaneto et al. 2007; Coad 2007; Abugiche 2008; Rist et al. 2008; Mbete et al. 2010; Riddell 2010; Schleicher 2010; Greengrass 2011; Linder & Oates 2011; Mockrin et al. 2011; Gill et al. 2012; Wildlife Conservation Society Noubale-Ndoki Project 1998-2007, *unpublished data*).

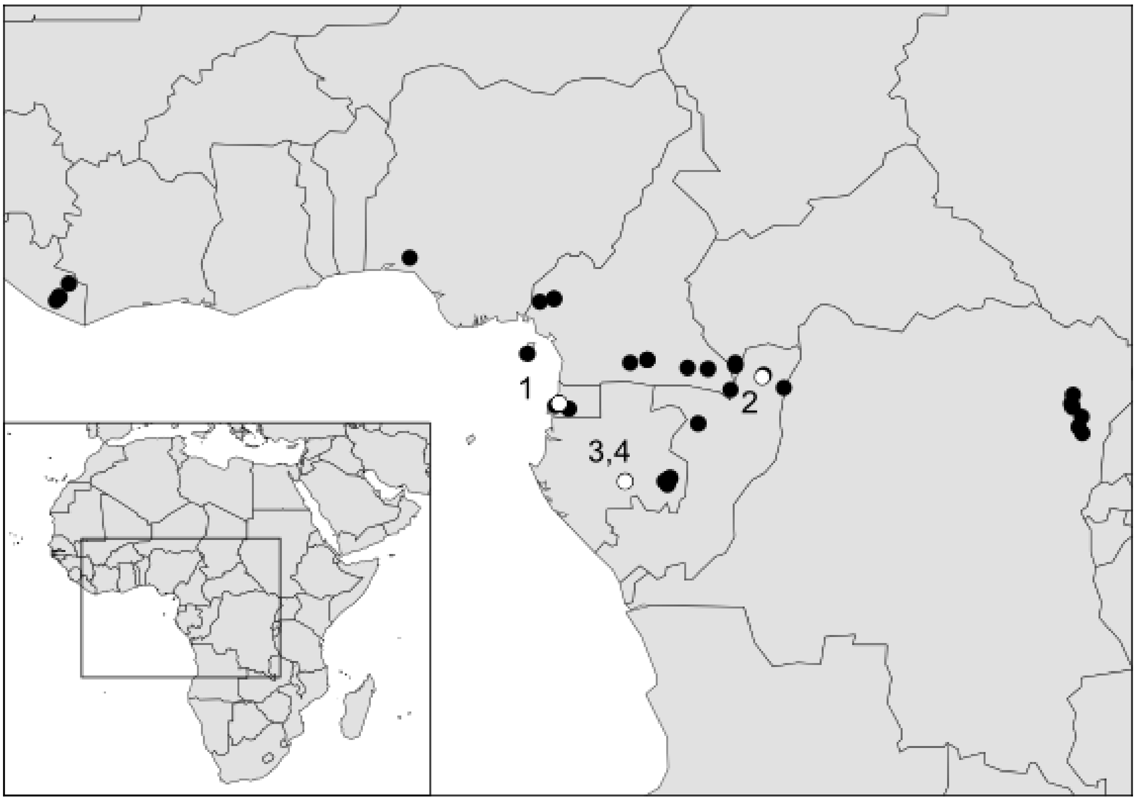

Figure 4.1. Sites in West and Central Africa at which offtake data were collected and used to calculate the mean body mass indicator (black and white circles) and the offtake pressure indicator (white circles). Numbers correspond to time series: 1- Sendje, Equatorial Guinea; 2 - Makao-Linganga, Republic of the Congo; 3 - Dibouka, Gabon; and 4 - Kouagna, Gabon (Table 1, Figure 3C). Inset shows the area of Africa where sites are located.

The majority of data were identified to species level (90.3%) or genus level (92.7%). Of these data, 99.5% were identified to at least Class level, and included in our analyses. We collated data for 114 species (101 mammals and 13 birds) collected between 1966 and 2010, with the majority of samples collected between 1985 and 2010. Most data sources (26 sources or 92.9%) represented snapshot data.

4.4.2 Mean body mass indicator

We used data from all 29 sources, encompassing 65,803 harvested individuals, to calculate the MBMI for mammals and birds separately. Data for mammals (59 samples) were available from 1966 to 2010 and for birds (20 samples) from 1975 to 2010.

The MBMI for mammals decreased significantly between 1961 and 2010 (Figure 4.2; slope ± s.e.: -0.380 ± 0.144 kg/yr; minimum adequate model: mean body mass ~ year +

(1| ID) + (1|country), $\chi^2_{4,5}$ = 4.8, p = 0.028). However, for birds it increased significantly between 1975 and 2010 (0.055 ± 0.029 kg/yr; mean body mass ~ year + (1| ID), $\chi^2_{3,4}$ = 5.5, p = 0.018). For mammals, including the random effect of *country* resulted in a ΔAIC of 10.75, whereas for birds, *country* effects were non-significant and dropped from the model.

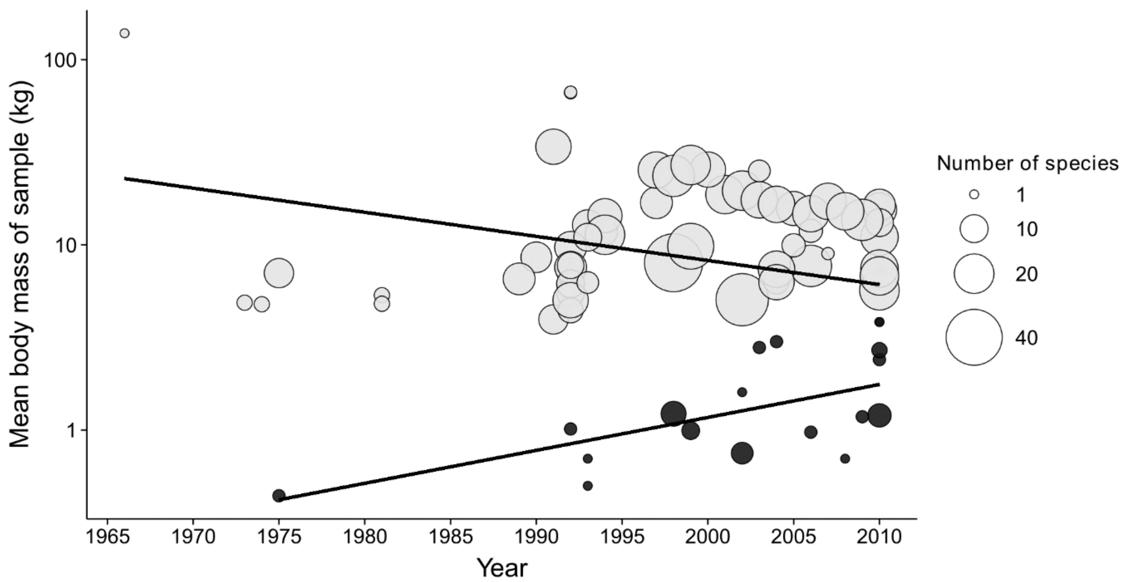

Figure 4.2. Mean body mass indicator for mammals (grey circles) and birds (black circles) in West and Central Africa. Circles represent offtake samples and are scaled by the number of species harvested within each sample; lines are fitted using linear mixed effects models. Samples are plotted on a logarithmic scale. Note that excluding outliers, 1966 for mammals and 1975 for birds, did not substantially alter the fitted lines.

4.4.3 Offtake pressure indicator

We identified time series from four sites in Central Africa (Table 4.1) representing 124 species- and site-specific time series.

Table 4.1. Details about sites, years sampled, and sample period for four time series used to calculate the offtake pressure indicator. Sample sites are shown in Figure 4.1.

Source number. Site name, country	Years (sample period)	No. of species mammal / bird	No. of individuals mammal / bird	Source
1. Sendje, Equatorial Guinea	1998, 2003, 2010 (5 May – 26 June)	30 / 9	1,313 / 65	Fa and García Yuste 2001, Kumpel 2006, Gill 2010
2. Makao-Linganga, Republic of the Congo	1998 - 2007, 2008 (all year)	26 / 3	12,141 / 38	Nouabale-Ndoki Project 1998 - 2007, Riddell 2010
3. Dibouka, Gabon	2004, 2010 (14 June - 12 August)	24 / 5	327 / 25	Coad 2007, Schleicher 2010
4. Kouagna, Gabon	2004, 2010 (14 June - 12 August)	24 / 3	342 / 3	Coad 2007, Schleicher 2010

Between 1998 and 2010, the OPI for mammals increased significantly by 231% to an index value of 3.31 (95% confidence interval: 1.95 - 5.82; Figure 4.3A). For birds, the OPI increased to 9.73 (95% confidence interval: 3.78 - 27.09; Figure 4.3B) between 1998 and 2010, an overall increase of 873%.

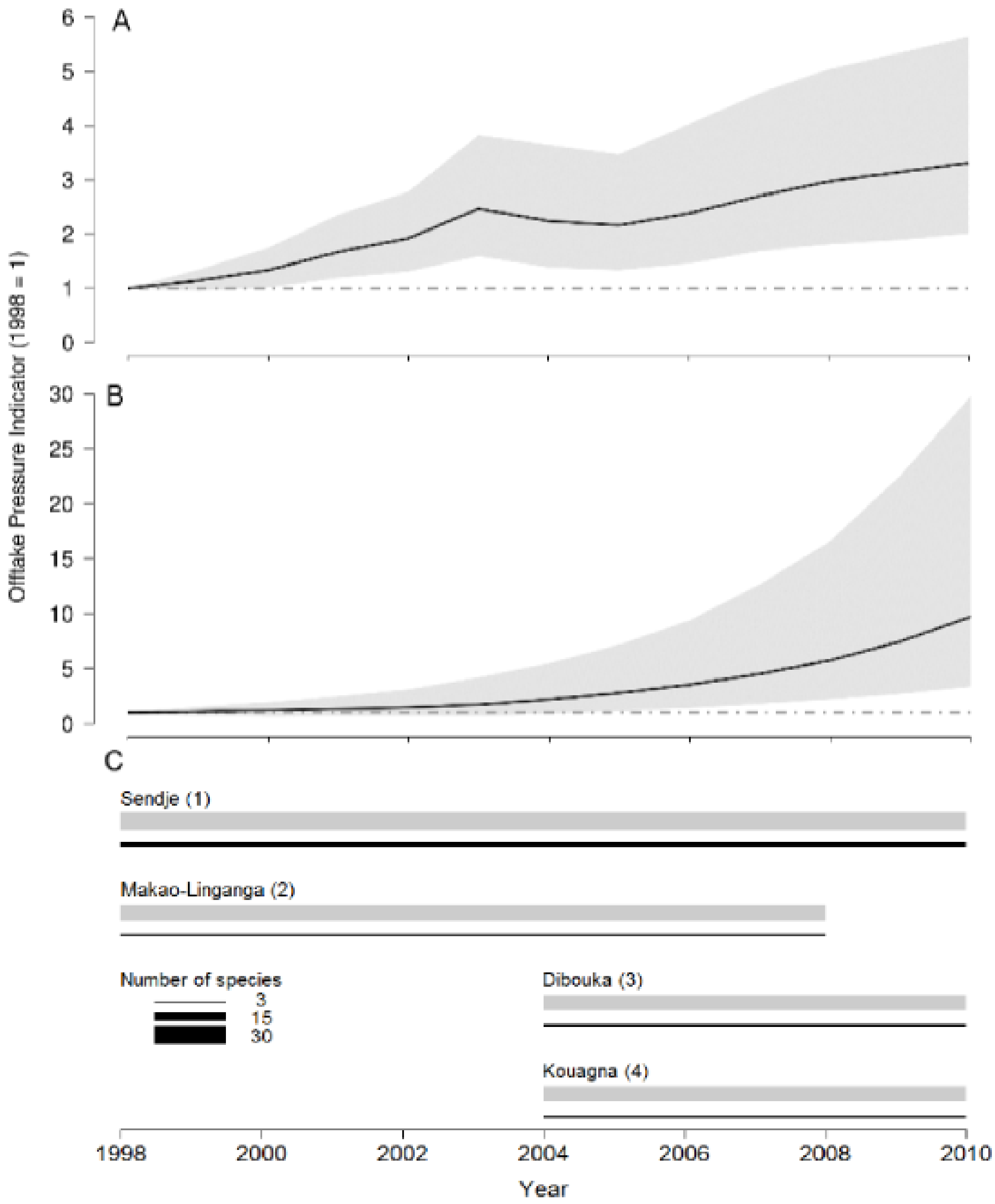

Figure 4.3. Offtake pressure indicator for mammals (A) and birds (B) in Central Africa and the distribution of time-series data at the four sites listed in Table 4.1 (C). The indicator is set to 1 for the first year where data are available (dotted horizontal line). Shading (A and B) represents ± 95% confidence intervals generated with 1000 bootstrap replicates. Width of bars (C) represents the number of mammal (grey) and bird (black) species sampled at four sites (numbers refer to sample sites shown in Figure 4.1 and Table 4.1).

4.5 Discussion

Indicators tracking anthropogenic pressures exerted on wild animals are valuable for informing conservation policy and action, and in tracking efforts towards sustainability and global conservation targets (Mace & Baillie 2007; Weinbaum et al. 2013; Collen & Nicholson 2014). Currently, few indicators are available that track offtake of terrestrial species especially at broader spatial scales, despite exploitation being one of the major pressures driving wildlife declines worldwide. We have investigated and outlined two different methods to track the offtake of wild terrestrial species using data extracted from the existing literature for West and Central Africa.

4.5.1 Two offtake indicators

We showed that trends in composition of harvested species and offtake pressure can be observed when approaches used in monitoring fisheries exploitation and population trends are applied to compiled data on wild meat for West and Central Africa. Our indicators provide a means of integrating taxonomically, spatially and temporally disparate data collated from multiple sources. The two indicators provide insights into different aspects of wildlife exploitation dynamics and are useful in understanding trends in hunted wildlife in Africa. The MBMI is a proxy for temporal changes in the composition of harvested species averaged at each site, whereas the OPI provides a measure of relative change in the number of harvested individuals indexed across multiple sites and species. The currently available data allowed us to produce separate indices for the two main taxonomic groups exploited, i.e. mammals and birds. As more data become available, indicators at finer taxonomic, ecological, e.g. genera, feeding guilds, functional traits, and spatial, e.g. country or ecoregion, resolutions can be produced. Despite the limited data currently available, we provide two methodologies to calculate trends in composition of species harvested and offtake pressure that have potential for guiding conservation policies and actions.

With the data available for our exploratory analyses for West and Central African mammals and birds, we show that the composition of harvested species, as measured by the MBMI, changed and the OPI increased significantly over time. Between 1966 and 2010, the average body mass of harvested mammals declined, whereas that of birds increased between 1975 and 2010, indicating a change in the composition of species harvested, as shown by the MBMI (Figure 4.2). The indexed number of individuals harvested of both mammals and birds increased dramatically between 1998 and 2010 (Figure 4.3).

One may be tempted to compare MBMI and OPI to conclude that hunting pressure continues to increase for African species, with hunting of smaller mammals being compensated by larger birds. However, such a direct comparison is not valid because the datasets used are only partially overlapping in space and time, and were used simply to demonstrate the feasibility of applying the two indicator methodologies. Further, MBMI and OPI are calculated differently, with the former employing an arithmetic mean and the latter a geometric mean. We would, therefore, expect the MBMI to change more rapidly compared to the OPI; hence, these two indicators will not directly align. With more time series at multiple sites available, it would be possible to calculate both indicators for the same sites and compare them.

These two indicators offer potentially useful approaches to assess wildlife offtake in the absence of comprehensive monitoring schemes, especially once the limitations as outlined below have been addressed. The increase in average body mass of harvested birds, shown by the MBMI, may reflect a change in the demand for larger birds and their bills, such as the Black-casqued Hornbill (*Ceratogymna atrata*), in the Sendje time series. The MBMI may indicate that hunting down a size gradient has occurred over time across the region, which has been reported from studies at individual sites (e.g. Gill et al. 2012; Coad et al. 2013). The size of remaining mammalian fauna in the forests today will likely be generally smaller; this likely has had multiple effects on ecosystem function (Abernethy et al. 2013), including changes in forest composition (Beaune et al. 2013; Effiom et al. 2013) and nutrient cycling (Doughty et al. 2013a, 2013b; Wolf et al. 2013). Trends in both MBMI and OPI need to be interpreted carefully, especially when data from different types of hunting, e.g. subsistence and trophy, are included, because species and number of individuals hunted are likely determined by different demands.

4.5.2 Limitations and future developments

In addition to the indicator limitations discussed in the *Methods*, offtake data collection relies on the willingness and availability of hunters to participate in research, therefore sources likely sampled a subset of hunters at a site. Moreover, offtake by women and children, or that harvested for subsistence rather than trade, is often overlooked in studies, although this contribution to the harvest could be substantial (see Kümpel 2006). Hunters may also purposefully avoid, or fail to report, harvesting certain species while research is ongoing, because these species are legally protected and law enforcement is strict in their area. This is likely to be the case for gorilla (*Gorilla gorilla*) and chimpanzee (*Pan troglodytes*) hunting at Makao (site 2, Figure 4.1). Our indicator methodologies attempt to account for heterogeneity among sources. As more studies on wild meat offtake become available, more rigorous statistical analyses can control for some of these factors, although we recognize that it is impossible to account for all of them.

The MBMI uses mean body mass of the sample as a proxy for species composition; however, analogous indicators could be produced based on other traits of species. For example, to assess whether hunters rely increasingly on smaller, faster-reproducing species, indicators could incorporate the ratio of small to large animals, the ratio of *r*- to *K*-selected species (Fa et al. 2015a), or the trophic level of harvested species (Pauly & Watson 2005). Further, the MBMI is fitting a trend across samples from disparate site and taxonomic coverage, with some taxa entering and leaving the index as studies focus on particular taxa. With more data included in the MBMI the effects of taxa dropping in and out should become less of an issue.

The OPI presented here is based on 124 species-specific time series from 4 sites that overlapped sufficiently; therefore, interpreting the index should be restricted to species and sites included. Moreover, the baseline against which the index is calculated is important because trends may have occurred before the earliest data collected or started at different times among sites. This was indeed the case in the two Gabonese villages included (Coad et al. 2013).

More data on wild meat harvest are available from consumption and market trade studies. However, these data have not been included here because they usually represent a larger and often unquantified area over which wild meat has been harvested. Furthermore, comparing and combining data collected on consumption and trade with offtake data is not without difficulties (Allebone-Webb et al. 2011). Indicators utilizing consumption and market data, separately or in combination, could offer additional insights into the wild meat harvest dynamics.

4.5.3 Conclusions

Our indicator methods suggest that existing heterogeneous data from multiple sources can be used to gain information about aspects of wild meat offtake dynamics. We can use not only time series datasets but also the more commonly collected snapshot data. The quality and quantity of data used to produce an indicator affects how representative the indicator is (Collen & Nicholson 2014); therefore, investigating multiple indicators based on the most readily available data over large spatial scales may improve the chances of producing more representative indicators. Furthermore, identifying causal links between changes in pressure on, and the state of, wild animal populations is often difficult. The wild animal offtake indicators showcased here have the potential to establish such linkages when combined with indicators of state to potentially estimate sustainable exploitation.

Our analyses are based on data collected over 40 years by many researchers, and even with this amount of effort, the indicators are limited in what they can show, highlighting the likely large investment required to produce robust and sensitive indicators that can inform policy. To gain more detailed insights into wild meat dynamics by applying these novel indicators in the future, existing data on wild meat offtake need to be collated and new data collected, ideally by systematic monitoring schemes (e.g. Système de suivi de la filière “viande de brousse” en Afrique Centrale, Ringuet et al. 2010) enabled by innovative technologies, such as mobile telephone apps. Establishing a monitoring network for wildlife hunting and trade could provide data for future large-scale long-term indicator analyses. Existing global data on terrestrial wild meat offtake, consumption, and trade are currently being collated by the OFFTAKE database (http://www.offtake.org). This database encompasses the West and Central African bushmeat database (Taylor et al. 2015) and welcomes additional data. Using these data in predictive modelling, ground-truthed by field studies, will likely help guide conservation decisions. The indicators explored here, given more data over space and time, could prove informative for assessments of wildlife exploitation as both a threat to wild animals and a benefit to people at local, national and global scales.

5 Trends in the harvests of wildlife in Central Africa

5.1 Abstract

Overexploitation has resulted in declines of wildlife, causing disruptions to ecosystem functions, interactions and services, with implications for both wildlife and people. Yet, methods to track exploitation and identify overexploitation are limited. We collated data from the literature quantifying the harvest of vertebrates across Central Africa to investigate trends in the mean body mass and taxonomic composition of harvested individuals, across varying levels of human accessibility and over time. We found that the mean body mass of harvested mammals was lower in more accessible areas, and decreased over time; however, the trend over time did not hold when elephants were excluded. In the least accessible areas, we found that higher proportions of preferentially targeted medium-sized bovids and suids were found to be harvested. In addition, we found that lower proportions of vertebrates harvested were small-bodied animals such as rodents, pangolins, carnivores, birds, and reptiles in the least accessible areas. Furthermore, we found that primates and pangolins are contributing increasingly greater proportions of the total individuals harvested over time. Our results suggest that it may be possible to use such information as a crude method to track exploitation.

5.2 Introduction

In many parts of the world, wildlife is hunted and exploited as an important source of nutrition and livelihoods for millions of people (Brashares et al. 2004; Weinbaum et al. 2013; Abernethy et al. 2016). Simultaneously, the overexploitation of wildlife, the unsustainable harvest of wildlife, has been identified as one of the main pressures driving global species declines (Maxwell et al. 2016). In particular, it is in tropical regions, which house over half of the world's species (Corlett & Primack 2010), where exploitation is commonplace. The tropics is also a region where people rely on wildlife and so overexploitation presents a major threat to both wildlife and people. Despite the unequivocal importance of wildlife, there is a global paucity of data on exploitation (Joppa et al. 2016), without which it is difficult to identify when and where exploitation is unsustainable.

In Africa, humans have occupied tropical forests and hunted wildlife for millennia (Barton et al. 2012), and African wildlife is thought to be more resilient to hunting because of coevolution alongside humans. Nowadays, overexploitation represents one of the largest environmental challenges in Africa (Abernethy et al. 2016). Wildlife, hereafter referring to terrestrial vertebrates, is hunted for a variety of reasons across Africa, such as food and livelihoods (Abernethy et al. 2013), traditional medicine, cultural practices, and trade (Walters et al. 2014; Buij et al. 2016). Studies have shown that hunting for livelihoods is increasingly common (Abernethy et al. 2016) and that the international trade in wildlife is increasing, e.g. the trade in African pangolins to Asia (Gomez et al. 2016). Growing human populations, industry, and infrastructure facilitate increasing access to remote areas (Lewis et al. 2015), while advances in hunting technology enable the hunting of arboreal and larger-bodied species (van Vliet & Nasi 2008). Since the 1960s and 70s, the use of guns and wire-snares by hunters has become increasingly widespread, although traditional methods, such as traps, are also still being used (Walters et al. 2015). In some places, the transition to gun-hunting has led to an increase in the biomass harvested per hunter (Coad et al. 2013). Together, these factors are thought to have resulted in increased commercial hunting (Lahm 2001; Starkey 2004; Fa & Brown 2009) and sale (Cronin et al. 2015) of wildlife over time.

Defaunation, defined as “the global extinction of faunal species and populations, and the decline in abundance of individuals within populations”, has profound cascading consequences for wildlife and people (Young et al. 2016). Ecological consequences of defaunation, such as changes in seed dispersal, seedling functional trait composition, carbon storage, and trophic relationships have already been documented (Effiom et al. 2013; Peres et al. 2016; Young et al. 2016). Defaunation may also have major implications for human food security, health, and disease spread. In rural Africa, ungulates are the most harvested taxa, accounting for between 36-95% of the total harvest (Wilkie & Carpenter 1999), and can be the main source of animal protein. For example, in Gabon, wild meat can contribute more than 100% of the recommended daily protein for people in rural areas and up to 48% in urban areas (Cawthorn & Hoffman 2015). Therefore, changes in the availability of ungulates may have implications for food security, i.e. access to sufficient, safe and nutritious food, especially for rural people. Declines in large-bodied vertebrates have been shown to increase rodent abundance, and consequently increase landscape-level prevalence of rodent-borne diseases in east

African savannahs (Young et al. 2014). The hunting, butchering and consumption of wildlife has been linked with the transmission of zoonotic diseases, such as Ebola (Alexander et al. 2015), and anthrax-like diseases (Antonation et al. 2016). Despite a long history of hunting and consuming wildlife, zoonotic disease risk is of global importance today due to increasing human populations, international trade (Smith et al. 2012), and contact with wildlife.

Hunting has already caused the local extirpation of wildlife from some areas of Africa (Lahm 1996; Maisels et al. 2001; Milner-Gulland et al. 2003; van Vliet et al. 2007), exemplifying past predictions of an "empty forest" (Redford 1992). For example, a recent meta-analysis showed that in hunted areas, tropical mammal and bird abundances were reduced by 83% and 58% respectively, in comparison to unhunted areas (Benítez-López et al. 2017). Gradients of defaunation have been identified by conducting wildlife abundance surveys at varying distances from roads and settlements. In Gabon, the species assemblage composition changes with distance to settlements and roads, and is correlated with intensity of hunting closer to villages and roads (Laurance et al. 2006; Koerner et al. 2017), highlighting that distance-based measures are a good proxy for hunting pressure. Species respond differently to hunting pressure, for example studies have shown that rodents and small duikers are more abundant in hunted areas (Effiom et al. 2013; Yasuoka et al. 2015) and closer to settlements (Henschel et al. 2011; Benítez-López et al. 2017).

In Central Africa, studies have investigated wildlife harvests at the local village level over past decades (Taylor et al. 2015); these studies quantified the number of individuals harvested per species, hereafter referred to as 'harvest profiles'. Harvest profiles have been shown to be an indicator of wildlife abundance (Kümpel et al. 2008; Fa & Brown 2009), e.g. decreases in the abundance of wildlife are reflected as relatively fewer individuals harvested, thus changes in harvest profiles are thought to reflect defaunation (Franzen 2006). Hunters tend to selectively harvest the largest available animals first (Coad 2007; Dirzo et al. 2014), and so a higher proportion of smaller-bodied animals may reflect defaunation, e.g. rodents make up an increasingly greater proportion of the total catch as hunting intensity increases (Yasuoka et al. 2015). Furthermore, Yasuoka et al. (2015) showed that in areas of higher hunting intensity medium-sized duikers (*Cephalophus* spp.) declined in abundance, allowing an increase of the smaller blue duiker (*Philantomba monticola*), until both taxa declined in the highest pressure zones, a pattern that was reflected in the harvest profile. Ingram et al. (2015) proposed tracking the mean body mass of harvested wildlife over time as an indicator of defaunation, called the Mean Body Mass Indicator (MBMI), which was recently applied to time-series data for three villages in Cameroon (Avila et al. 2017). Few studies have investigated patterns of wildlife harvests over time or large spatial scales. For example, Petrozzi et al. (2016) investigated temporal trends in the taxonomic composition and trophic level of species offered for sale at sixteen wild meat markets in West and Central Africa. However, the ability of market data to reflect defaunation is questionable, because a) often only a subset of marketable species are sold on markets, b) species that are sold only make up a fraction of those hunted, and c) the area over which animals on a market are sourced can be large and unknown. In the absence of time-series data at multiple sites across regions, collating harvest profiles across different sites provides an opportunity to investigate how wildlife harvests may have changed over time and space, as possible indicators of defaunation.

Here, we investigate evidence for defaunation across Central Africa by analysing a database of existing studies investigating the harvest of wildlife, collated from published and grey literature. Assuming that human accessibility is a proxy for hunting intensity, we use data collected at different points in time at sites with varying levels of accessibility to investigate whether: 1) the average body mass of harvested vertebrates (i.e. the MBMI) changes over time and/or across a gradient of accessibility, and 2) the taxonomic composition of harvested vertebrates, measured as the proportion of different taxonomic groups of the total harvest, changes over time and/or accessibility.

5.3 Methods

5.3.1 Hunting data

To investigate patterns in the wildlife harvested in Central Africa, we first collated data on vertebrate harvest profiles (individuals harvested per species) from a variety of ‘sources’ (published papers, reports from nongovernmental organisations, PhD or Master’s theses, or unpublished data collected using a published methodology) that quantified harvest profiles at known locations over known time periods. We searched for sources using a snowballing technique (Noy 2008), and searched reference lists and online libraries. Here we defined Central Africa as encompassing Cameroon, Central

African Republic, Democratic Republic of Congo, Equatorial Guinea, Gabon, and the Republic of Congo (Figure 5.1).

A source may have collected data at multiple locations, which we separated into ‘studies’. Each study provided details of the site, start and end dates of the sampling period, species and number of individuals hunted. We excluded studies that conducted partial sampling, e.g. sampled specific taxonomic groups only, or where site coordinates were not available from the authors and could not be acquired by referencing maps in the source with Google Earth.

Some studies collected data over multiple years. To investigate trends over time, we allocated data to a particular year by calculating the mid-date of the sampling period, hereafter ‘samples’. Studies that collected data over multiple years were divided into samples if the data was temporally resolved. We included studies with a sample period of less than 2 years in length and that could not be divided into samples, as one sample. We excluded studies with sample periods over 2 years and where data were not resolved enough to allocate to separate years. We assigned a unique identification code to sources, ‘SourceID’, and studies, ‘StudyID’.

To separate species into size classes, we assigned each individual vertebrate the species-specific body mass from Myhrvold et al. (2015). For individuals not identified to species level, we used the mean body mass of the members of a genus or family that occur in Africa, identified from IUCN Extent of Occurrence maps (IUCN 2016).

5.3.2 Accessibility and land cover data

We extracted the accessibility of each site, defined as the estimated travel time to the nearest city of ≥ 50,000 people in the year 2000, from the Global Map of Accessibility (Nelson, 2008) using ArcGIS version 10 (ESRI, 2011). We chose this dataset because it estimates travel time by land or water (including navigable rivers) and represents conditions in 2000, about the mid-point of when the hunting data was collected. We extracted land cover data for each site from the Global Land Cover 2000 dataset (Bartholomé & Belward 2005) and aggregated land cover classes into two categories to allow reasonable sample sizes per class: all forest classes (closed evergreen lowland forest, submontane forest, montane forest, deciduous woodland, swamp forest, closed deciduous forest, and mangrove) were aggregated into one 'forest' category, and Mosaic Forest / Croplands, and Mosaic / Savanna classes were aggregated into one 'mosaic' category.

5.3.3 Trends in mean body mass

We defined the mean body mass of a sample as the arithmetic mean of the body masses from all individuals caught within a sample, as outlined by Ingram et al. (2015), and studies for which the mean body mass was zero were not included. To test whether the mean body mass of birds or mammals across all samples changed over time or with accessibility, we fitted two separate linear mixed effects models (Zuur et al. 2009) using the lme4 package (Bates et al. 2015) in R version 3.2.5 (R Core Team 2016). The log-transformed mean body mass of birds or mammals within each sample was the response variable, and year and the log-transformed travel time (up to second order polynomial) were included as fixed effects with a random effects structure as described below. Continuous fixed effects were scaled before analyses. The fixed effects were selected using backward model simplification based on likelihood ratio tests (Zuur et al. 2009). StudyID nested within SourceID were included as random factors to control for some of the variation due to research methods and site. Samples were weighted within the model by the square root of the total number of vertebrates harvested, as a crude proxy for sample size.

5.3.4 Trends in taxonomic composition

To investigate trends in the proportions of different taxonomic groups across harvest profiles, the 'taxonomic composition', we calculated the proportion of individuals from different taxonomic groups out of the total number of vertebrates in each sample. Taxonomic groups representing the most commonly harvested groups of species found across Central Africa included: birds (Class: Aves), reptiles (Class: Reptilia), carnivores (Order: Carnivora), primates (Order: Primates), rodents (Order: Rodentia), bovids (Family: Bovidae), suids (Family: Suidae), and pangolins (Family: Manidae). We separated bovids into three size classes, small (≤5kg), medium (>5 and <20 kg), and large (≥20kg), because bovids of different sizes are known to respond differently to hunting pressure (Yasuoka et al. 2015).

To investigate changes in the proportion of any given group across samples we used arcsine-transformed proportions as the response variable to deal with zeros and very low proportions (Andreano et al. 2015). We fitted separate linear mixed effects models for each taxonomic group and bovid size classes, with log-transformed travel time (up to second order polynomial), year (up to second order polynomial), and land cover category as predictor variables. We did not include interaction terms due to small sample size relative to the number of predictor variables. Individual terms were included in models with significant interaction terms (Crawley 2007). Models were selected and weights included as described above. We did not adjust the p-values of our models because 1) p-value adjustment increases the likelihood of making type II errors, and increases the need for increasing sample size due to substantial reduction in statistical power (Feise 2002; Nakagawa 2004), and 2) the proportions analysed are not independent given that if the proportion of one taxonomic group increases another must decrease, and so we are not testing multiple separate hypotheses (Armstrong 2014).

5.4 Results

5.4.1 Data

We collated data that met our inclusion criteria from 41 sources, representing 103 studies and 114 samples that investigated the vertebrates at 98 sites (Figure 5.1). In total, the samples represented 72,321 individual vertebrates harvested between 1982 and 2016. Overall, on average per sample, most of the vertebrates harvested were bovids (46% ; 28% small, 13% medium, and 5% large), followed by 21% rodents, 15% primates, 4% reptiles, 3% carnivores, 3% pigs, 3% pangolins and 2% birds, and 3% other taxa.

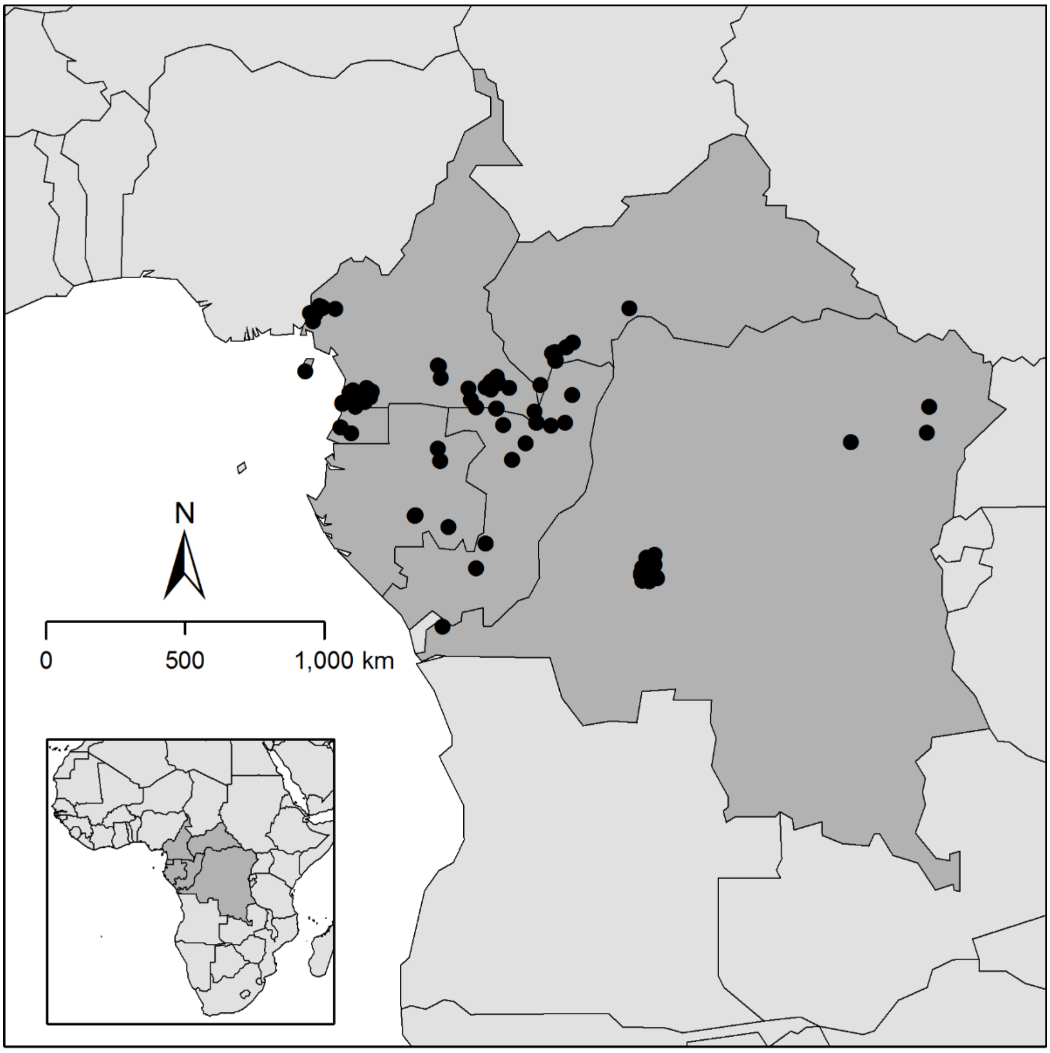

Figure 5.1. Locations of hunting sites (black points) across Central African countries (dark grey shading).

5.4.2 Trends in mean body mass

We observed statistically significantly lower mean body mass of mammals (~17kg compared to 5kg; $\chi^2_{4,5} = 9.77$, $p < 0.001$, n = 112 samples, Figure 5.2A) harvested in the most accessible areas (i.e. low travel time) compared to the least accessible areas; this trend held when elephants were removed from samples ($\chi^2_{4,5} = 15.57$, $p < 0.001$, Figure 5.2B). We found no significant trends with accessibility for birds (n = 65).

We found that the mean body mass of harvested mammals significantly decreased over time ($\chi^2_{5,6} = 4.05$, $p = 0.044$, Figure 5.2C); however this trend is not significant when elephants were removed from the samples (Figure 5.2D). We found no significant trends for birds over time.

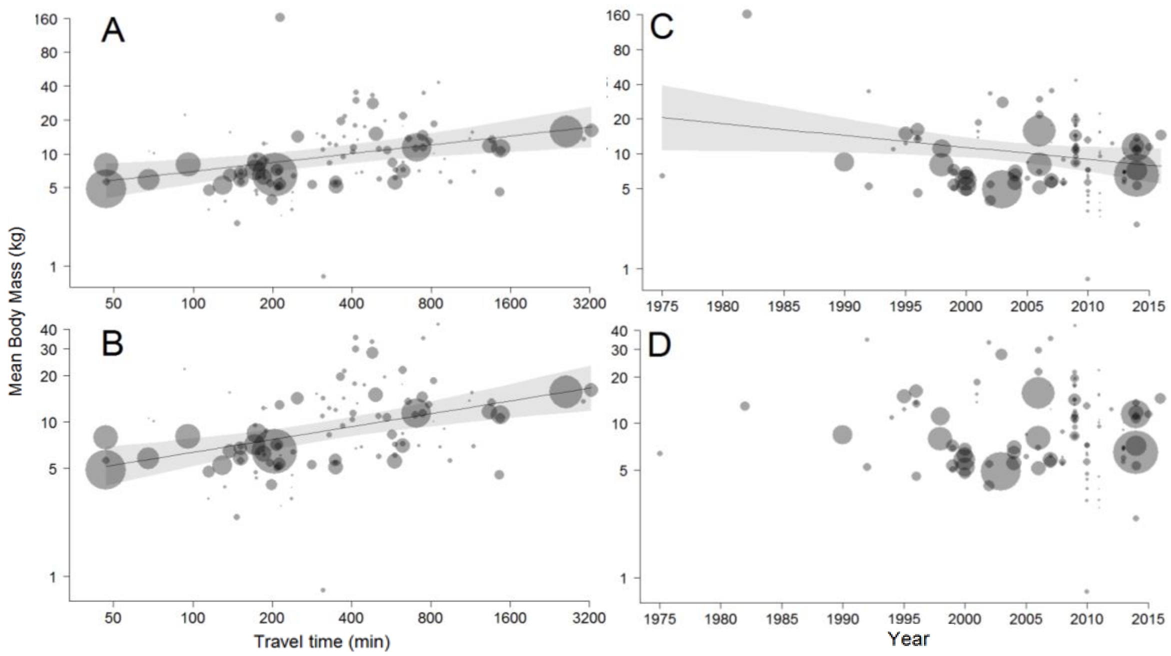

Figure 5.2. The mean body mass for harvested mammals with travel time to nearest settlement of ≥50,000 people (from Nelson (2008)) with (A) and without (B) elephants, and over time with (C) and without (D) elephants in Central Africa (n = 112 samples). Points are translucent to show density of points, and sized by the square-root of the total number of harvested individuals (8 - 9985). Significant trend lines and 95% CI (shading) are fitted using a linear mixed effects model.

5.4.3 Trends in taxonomic composition

As human accessibility decreased (i.e. a higher travel time from major settlements), we observed a statistically significant linear increase in the proportion of medium-sized bovids ($\chi^2_{4,5} = 4.69$, $p = 0.030$, Figure 5.3A: increase from ~5% to 19% with accessibility from 0.8 to 54 hours travel time) and suids ($\chi^2_{4,5} = 22.50$, $p < 0.001$, Figure 5.3B: ~0.03% to 6%) across samples. In the least accessible areas to humans, we also observed a statistically significant linear decrease in the proportion of rodents ($\chi^2_{4,5} = 16.65$, $p < 0.001$, Figure 5.3C: ~ 35% to 4%) and pangolins ($\chi^2_{6,7} = 15.37$, $p < 0.001$, Figure 5.3D: ~6% to 0.1%), and a near statistically significant decrease for carnivores ($\chi^2_{4,5} = 3.79$, $p = 0.052$, Figure 5.3E: ~4% to 1%). A similar trend was observed for the proportion of reptiles ($\chi^2_{5,6} = 10.93$, $p = 0.0009$, Figure 5.3F: quadratic decrease ~6% to 2%), and birds ($\chi^2_{4,5} = 6.52$, $p = 0.011$, Figure 5.3G: linear decrease ~2% to 0.2%) as accessibility to people increased.

We found a marginally significant increase in the proportion of pangolins ($\chi^2_{6,7} = 3.78$, $p = 0.052$, Figure 5.4A) and primates ($\chi^2_{4,5} = 3.83$, $p = 0.050$, Figure 5.4B) harvested over time. We observed no significant changes in the proportion of any other taxonomic group over time. Whilst we could not include interaction terms in our model, we found no correlation between log-transformed accessibility and time (Pearson's correlation test: $r = -0.053$, $p = 0.576$).

In addition, we found that samples conducted in the forest land cover category had a significantly higher proportion of pangolins than those in the mosaic category (forest: 2.4 ± 1.4 % [mean ± standard deviation], mosaic: 0.67 ± 0.63 %; $\chi^2_{6,7} = 9.41$, $p = 0.002$). We observed no significant effect of land cover category for any other taxonomic group.

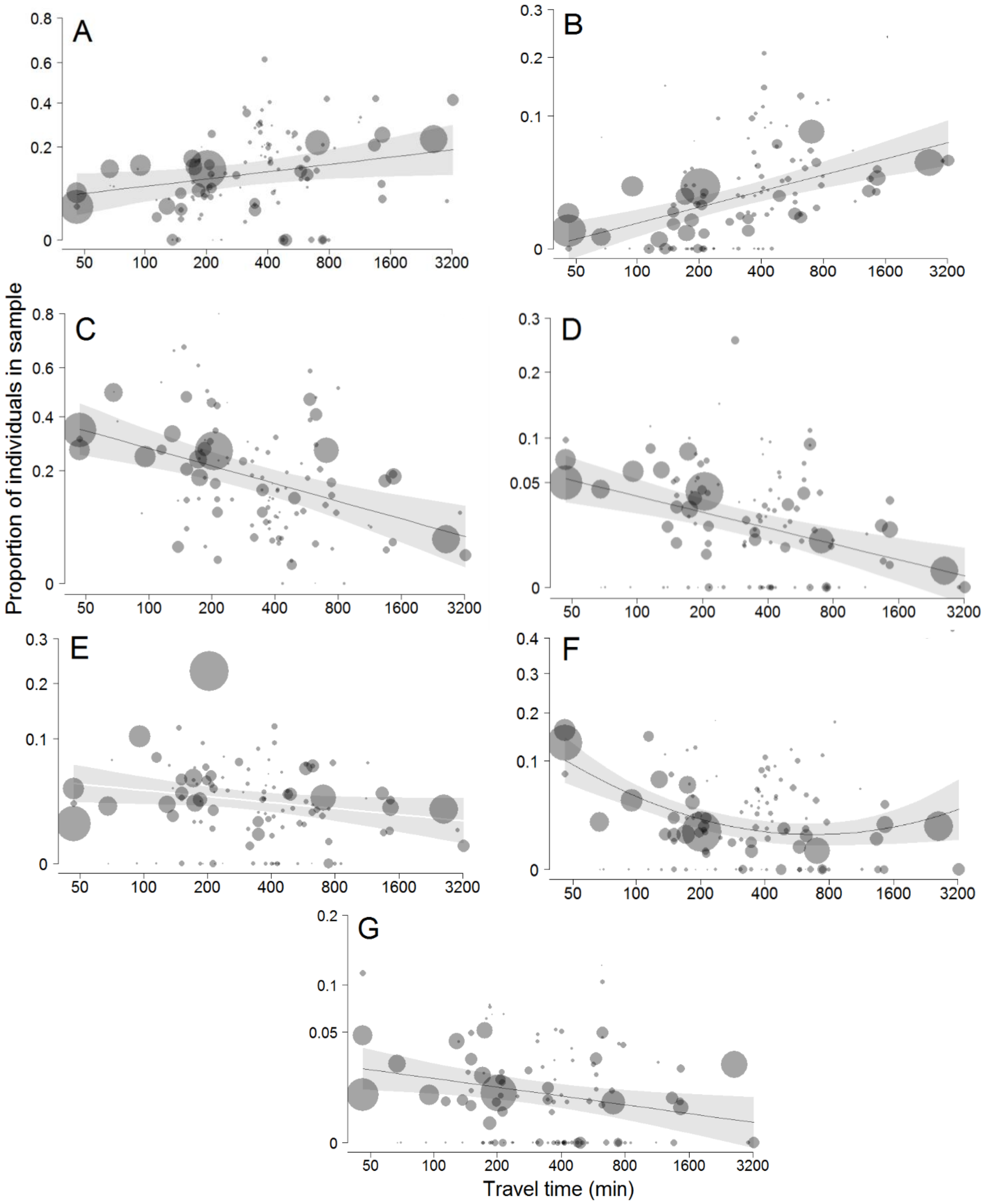

Figure 5.3. Trends in the proportion of vertebrates that were larger-bodied A) medium-sized Bovidae, B) Suidae, and smaller-bodied C) Rodentia, D) Manidae, E) Carnivora, F) Reptilia, or G) Aves, across Central African samples (n = 114 samples) against travel time to nearest major settlement. Points are translucent to show density of points. Significant trend lines (grey) and 95% CI (shading) are fitted using a linear mixed effects model. The white line shows a near statistically significant effect for carnivores (p = 0.052).

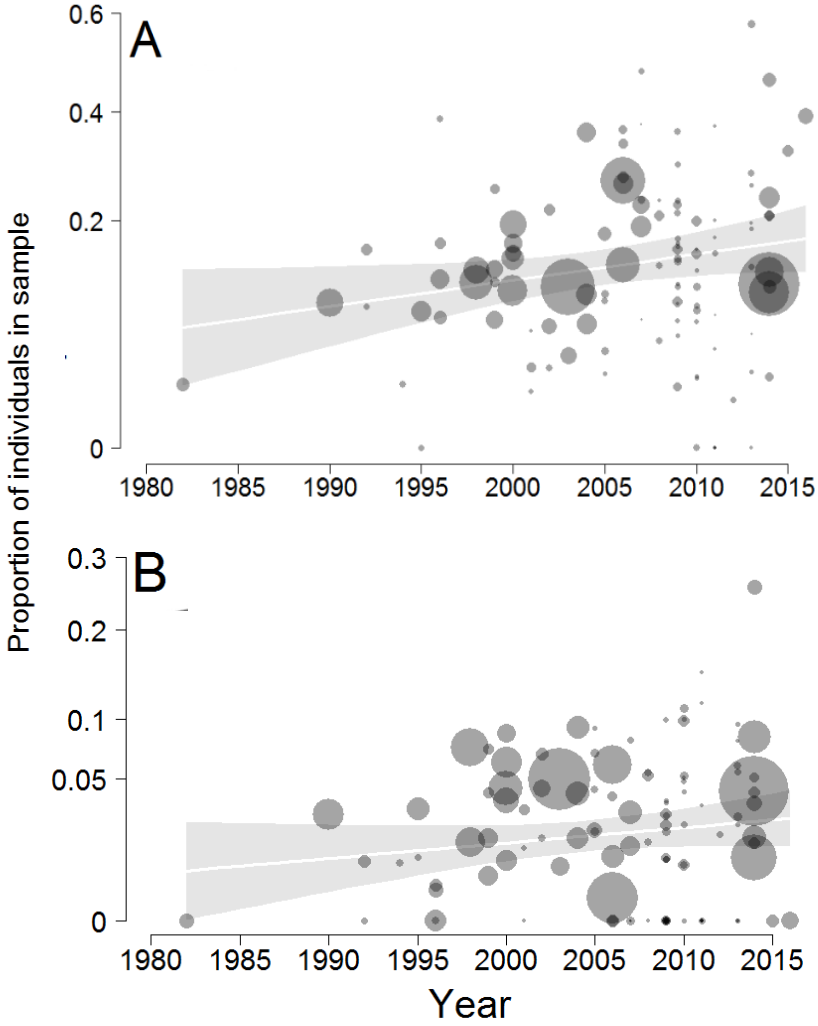

Figure 5.4. Trends in the proportion of vertebrates that are A) Primates and B) Manidae across samples (n = 114 samples) between 1982 and 2016 in Central Africa. Points are translucent to show density of points. The white lines show near statistically significant effects of time for primates (p = 0.05) and pangolins (p = 0.052) and 95% CI (shading) are fitted using a linear mixed effects model.

5.5 Discussion

Using data spanning more than three decades, we provide the first comprehensive analyses of trends in harvested wildlife in Central Africa. Across samples, we found that the average body mass of harvested mammals, but not birds, was significantly lower at sites that are most accessible to humans. Furthermore, we found that the taxonomic composition of the samples differed depending on the accessibility of the area to humans: the proportion of harvested medium-sized bovids and suids was significantly higher in the least accessible areas, while the proportions of harvested rodents, pangolins, birds, carnivores, and reptiles was lower in the least accessible areas. Over time, we found evidence of a marginally significant increase in the proportion of harvested primates and pangolins in samples over time, but not for other taxa.

Lower mean body masses of mammals harvested in the areas that are most accessible to humans, assumed to have higher hunting pressure than the least accessible areas, may be indicative of the defaunation of larger-bodied species given that they are more threatened by hunting (Dirzo et al. 2014; Ripple et al. 2016a). While we did not observe any trends with accessibility for large bovids, we did find that the proportion of medium-sized bovids and suids across samples was significantly lower in the most accessible areas, which are preferentially targeted by village hunters (Abernethy et al. 2016). Studies have shown that larger bovids have already been extirpated in many areas (e.g. Lahm 1996; Maisels et al. 2001; Jimoh et al. 2013), potentially leaving medium-sized wildlife as the primary target of hunters. Our results are consistent with studies that have shown the local extirpation of medium-sized bay duikers in north-east Gabon (van Vliet et al. 2007) and in the Oban Hills region of Nigeria (Jimoh et al. 2013), and reduced abundance of red duikers (~18.8 kg) closer to roads (Fimbel et al. 2000). Whilst our results suggest that the mean body mass of harvested mammals is decreasing over time, consistent with preliminary results from Ingram et al. (2015), it should be noted that our analyses are limited because trends in body mass can be skewed by very heavy species such as elephants, which can be orders of magnitude heavier than other vertebrates in the region. If harvest profiles are a good predictor of wildlife availability (Fa & Brown 2009), and higher hunting pressure leads to the decline of medium and large-bodied species (Yasuoka et al. 2015), our results suggests that defaunation of the species may have occurred in some of the most accessible places. In addition to implications for wildlife populations and people, declines may have implications for predators competing for food with humans and driving changes in their feeding habits and abundance (Henschel et al. 2011).

Harvest profiles from the most accessible areas, had significantly higher proportions of smaller-bodied vertebrates including rodents, pangolins, carnivores, reptiles and birds. These trends may explain why we also found that the average body mass of mammals caught is lower in more accessible areas. In addition, we found evidence that both pangolins and primates are accounting for greater proportions of harvest profiles over time. Our results, while across a larger area, are consistent with wildlife surveys which showed increases in the abundance of smaller-bodied taxa such as birds and rodents nearer to settlements where hunting pressure is typically higher (Laurance et al. 2006; Coad 2007; Koerner et al. 2017). Defaunation of preferred larger species necessitates the hunting of other species, which may be facilitated by the increased availability and use of guns (Walters et al. 2015; Abere et al. 2016). For example, increases in the use and availability of guns in the region over time may lead to increased primate hunting (Kümpel et al. 2008; Walters et al. 2015). Cultural taboos in some areas act as an ‘invisible’ system of local resource management and wildlife conservation (Colding & Folke 2001), but may not apply to commercial or migrant hunters, and may therefore allow the hunting of wildlife protected by taboos in some places. Defaunation of large-bodied species and primates may have major implications for seed dispersal, regeneration, and carbon storage capabilities in tropical forests (Effiom et al. 2013; Peres et al. 2016). Further, if people are increasingly hunting primates, this may represent a potential zoonotic disease risk (Peeters et al. 2002; Zheng et al. 2010).

Our study is limited because if the proportion of one taxonomic group has declined, the proportion of another would increase, which means we cannot ascertain whether increasing proportions also means increasing numbers of animals are being harvested. Our analyses of trends over time are also limited because they do not represent time-series at the same site, and more generally, hunting studies rely on the willingness of hunters to take part in the study or allow their wildlife harvests to be monitored, and so each source may represent a subset of hunters. Engagement with subsistence hunting communities may be the key to tracking exploitation, and to ensure sustainable use of wildlife and the success of long-term community-based approaches. To further test whether harvest profiles can be a useful tool to investigate hunting patterns and defaunation, future studies should test whether the composition of harvests does reflect the abundance of wildlife at sites (e.g. Kümpel 2006), by combining hunting with wildlife abundance studies at the same sites. If so, information from harvest profiles could be used by local communities and conservation practitioners as one metric to monitor changes in harvests and potentially as a proxy of the availability of wildlife. While tracking changes in harvest profiles does have limitations, it may be a more feasible monitoring method when resources are scarce.

Our study highlights the potential landscape scale pressures on wildlife from hunting. If defaunation is occurring in the most accessible areas, then efforts are needed to monitor both wildlife populations and hunting activities, to protect wildlife and support the millions of people who rely on wildlife. To understand which species are resilient to hunting, basic ecological data on the vital rates of hunted wildlife is needed, particularly for smaller lesser-studied species. In addition, we suggest that further studies are needed to investigate the ecological effects of defaunation, but also the implications for human health, nutrition and food security. Foremost, we suggest that more data are needed and that time-series studies be conducted to assess the impacts of hunting over time and across accessibility gradients at landscape scales.

Here, we show how harvest profiles collected at different time periods and in different locations across Central Africa can be used to track trends in the availability of wildlife at the landscape scale. If the world is to gain a better understanding of the exploitation of wildlife, decision-makers should enact proposals to monitor the hunting of wildlife in collaboration with local communities, needed to better understand how to protect wildlife and the needs of people in the region.

6 Assessing Africa-wide pangolin exploitation by scaling local data

6.1 Abstract

Overexploitation is one of the main pressures driving wildlife closer to extinction, yet broad-scale data to evaluate species' declines are limited. Using African pangolins (Family: Pholidota) as a case study, we demonstrate that collating local-scale data can provide crucial information on regional trends in exploitation of threatened species to inform conservation actions and policy. We estimate that 0.4-2.7 million pangolins are hunted annually in Central African forests. The number of pangolins hunted has increased by ~150% and the proportion of pangolins of all vertebrates hunted increased from 0.04% to 1.83% over the past four decades. However, there were no trends in pangolins observed at markets, suggesting use of alternative supply chains. The price of giant (*Smutsia gigantea*) and arboreal (*Phataginus sp.*) pangolins in urban markets has increased 5.8 and 2.3 times respectively, mirroring trends in Asian pangolins. Efforts and resources are needed to increase law enforcement and population monitoring, and investigate linkages between subsistence hunting and illegal wildlife trade.

6.2 Introduction

Overexploitation is one of the main pressures causing species' declines and local extinctions (Maxwell et al. 2016; Ducatez & Shine 2017). Currently, broad-scale data on the exploitation of terrestrial wildlife, needed to inform conservation policy and action, are lacking (Joppa et al. 2016). Information on wildlife harvests can be difficult to collect because, at times, hunters and traffickers operate secretly to avoid law enforcement, and may be unwilling to disclose what they have harvested (Keane et al. 2008). Law enforcement and seizures data have been used to quantify exploitation of threatened species, however, these data suffer from detection biases and underestimation (Gavin et al. 2010). Instead, collating local-scale hunting studies may provide more accurate estimates of the number of animals hunted and relevant information to aid conservation efforts, complementing seizures data (Sánchez-Mercado et al. 2016).

Pangolins (Family: Manidae), a group of African and Asian scaly mammals, are considered to be ‘the most heavily trafficked wild mammal in the world’, and are hunted and traded for food and traditional medicines (Challender et al. 2014). They are also used in rituals, art, and magic among communities across Africa (Soewu & Sodeinde 2015) and Asia (e.g. Mahmood et al. 2012). Despite a long history of exploitation, pangolin populations in Asia have declined dramatically (estimated 90% decline of Chinese pangolin [*Manis pentadactyla*] since the 1960s; Wu et al. 2004). All four Asian pangolin species are listed as ‘Critically Endangered’ or ‘Endangered’ on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species due to past, present, and predicted population declines driven by growing demand for meat and scales (Challender et al. 2014), and compounded by low reproductive rates (Newton et al. 2008; Challender et al. 2012; Cheng et al. 2017). In addition, commercial trade, and international trade of wild-caught pangolins has been banned (CITES 2016).

In comparison to Asian pangolins, less is known about the African species: white-bellied (*Phataginus tricuspis*), black-bellied (*P. tetradactyla*), giant ground (*Smutsia gigantea*), and Temminck’s ground pangolin (*S. temminckii*). They are currently classified as ‘Vulnerable’ by the IUCN (Pietersen et al. 2014a; Waterman et al. 2014a, 2014b, 2014c), and international trade was recently banned (CITES 2016). African pangolin populations are assumed to be declining, because of habitat degradation and loss (Challender et al. 2014), hunting, and increasing demand from international markets (Challender & Hywood 2012). However, little is known about population sizes, reproductive potential, and African pangolin trade. Mounting evidence suggests that as the availability of Asian pangolins declines and international trade flows increase, traders are increasingly supplying the currently more abundant and less expensive African pangolins to meet Asian demand (Challender & Hywood 2012).

Seizures of pangolins and their derivatives (e.g. scales and skins) from Africa destined for Asia are increasing (Heinrich et al. 2016) with over 53 tonnes seized in 2013 (Flocken 2015), and more than 1 million pangolins trafficked globally since 2000 as estimated from illegal trade data (IUCN SSC Pangolin Specialist Group 2016). These estimates likely represent a fraction of all pangolins traded, and an even smaller proportion of the number of pangolins hunted.

Many studies have monitored wildlife hunting and/or markets at local scales across Africa (e.g. Crookes et al. 2006; Coad et al. 2013). Collating data from these studies allows us to infer trends, produce indicators of overall rarity and demand at a regional scale, and provide information to aid conservation efforts. Here, we collate data from local-scale hunting and market studies to provide the first comprehensive assessment of the exploitation of African pangolins by estimating (i) the total number of pangolins hunted annually; (ii) temporal trends in the proportion of pangolins of all animals hunted or observed at wild meat markets and; (iii) trends in the price of pangolins over time as an indicator of changes in demand or rarity (Courchamp et al. 2006).

6.3 Materials and methods

6.3.1 Data

We collated data on the number of individual vertebrates hunted or observed at wild meat markets in a particular area and time period across Africa from a variety of ‘sources’ (published papers, reports from nongovernmental organisations, PhD or Master’s theses, or unpublished data collected using a published methodology) using a snowballing technique (Noy 2008), and searching reference lists and online libraries. Where sources did not provide detailed data on animals hunted or observed at markets, we contacted the authors for raw data. Where available, we extracted information on use (e.g. consumed, sold), hunting method (e.g. gun, snare), sex, age category (as assessed by the authors), and price of whole animals observed at markets.

Each source could contain one or more ‘studies’, where each ‘study’ collected data using a specific sampling methodology at a location, and was assigned a unique StudyID. Each study provided data on the location (hereafter ‘site’), market type (urban or rural), start and end date, species and number of individuals hunted (hunting studies), hereafter referred to as ‘the catch’, or observed at wild meat markets (market studies), hereafter ‘markets’. Studies were included that collected data on all vertebrate taxa hunted/observed at market at a site within a specified time, i.e. we excluded single-taxon studies, e.g. those that only reported primate hunting, and partial sampling).

To investigate trends over time, we allocated data from studies to the years in which the data were collected. Studies spanning multiple years, including studies of less than a year's duration, were separated into annual 'samples' if temporally resolved raw data were available and could be separated and allocated to a year (n = 16 studies). Studies that provided temporally unresolved data, i.e. one value per species for the entire study duration, were included if the study duration was ≤ 500 days to allow reasonable allocation of data to individual years, while including studies that sampled slightly longer than one year. All samples were allocated to a year by calculating the mid-date between the start and end dates.

6.3.2 Estimating total catch of pangolins in Central African forests

Most studies that have human population and hunting territory size data available were located in Central African forests, we therefore restricted the estimates of total pangolin catch to this region. We define Central African forests as the forests in Cameroon, Central African Republic, Equatorial Guinea, Gabon, Democratic Republic of Congo, and Republic of Congo. We used three methods to estimate the total annual catch of pangolins in Central African forests from hunting studies. For the first method, we calculated the median annual number of pangolins hunted per area multiplied by the total likely hunted forest area, calculated as the forest area within 10km of a settlement (Text S1). For the other two methods, we calculated the median annual number of pangolins hunted per rural person multiplied by either of two independent estimates of the total rural population (CIESIN 2011; UNPD 2014; see Text S1 and Figure S1). To assess change over time, we repeated the analyses for samples collected before and after 2000 (Text S2), to permit comparison with Heinrich et al. (2016) showing an increase in seizures of African pangolins destined for Asia after 2000.

6.3.3 Trends in pangolins hunted and observed at market

To investigate trends of pangolins hunted or observed at markets, we calculated the percentage of individuals from all African pangolin species combined among the total number of vertebrates in the catch or at markets within each sample, from hunting or market studies, respectively. We fitted linear mixed effects models (Zuur et al. 2009) using the lme4 package (Bates et al. 2015) in R version 3.2.4 (R Core Team 2016), and selected the final model using backward model simplification based on likelihood ratio tests. Arcsine-transformed percentages of pangolins in the catch or at markets were modelled separately as the response variable (Andreano et al. 2015), with year and a second order polynomial of year as fixed effects. As random factors we included StudyID nested within SourceID to control for some of the variation due to research methods and site, and Country to account for variation among countries. Within the statistical models, the percentage of pangolins were weighted by the total number of animals within each sample as a proxy for sample size. Furthermore, we assessed overall trends that may influence our results (such as body mass, accessibility, and sample duration, see Text S3), and assessed whether the inclusion of the small number of early studies affected overall trends (Text S5).

6.3.4 Trends in prices

To investigate trends in prices of whole pangolin carcasses at markets, we adjusted all prices in Central African Francs (CFA) to 2015 prices by controlling for inflation using the Consumer Price Index (CPI) (The World Bank 2017). We fitted mixed effects models for arboreal and giant ground pangolins with log-transformed price as the response variable, interaction of year and market type (rural or urban) as a fixed effect, and SourceID as a random effect to control for some of the variation due to research methods and site. StudyID was not needed in these analyses because studies were not different from sources.

Separately, we calculated the price ratios of pangolins (averaged when multiple prices were reported per site and source) relative to three commonly hunted and similarly sized species using unadjusted prices, to control for changes in prices of traded vertebrates. We calculated price ratios for blue duiker (*Philantomba monticola*), African brush-tailed porcupine (*Atherurus africanus*), and greater cane rat (*Thryonomys swinderianus*), using fresh carcass prices where specified. We investigated price ratio trends for arboreal pangolins (*Phataginus* sp.) as insufficient price data were available for ground pangolins (*Smutsia* sp.). Mixed effects models were fitted for each of the prices ratios as described above.

6.4 Results

6.4.1 Data

We collated data from 68 sources that met our inclusion criteria (Table S1), separated into 161 studies and 204 samples, accounting for 348,807 individual vertebrates. Of these, 152 samples had information on 71,716 individual vertebrates in the catch and 52 samples investigated 277,091 individuals at markets, of which 2,059 and 7,005 individuals were pangolins, respectively. Across all samples, 8,166 individuals were identified as arboreal pangolins (*Phataginus* sp.) and 300 as ground pangolins (*Smutsia* sp.), with a further 578 only identified to family (Manidae).

Pangolins were hunted at 71 of 113 (63%) sites in 10 of 14 (71%) countries, and observed at 18 of 36 (50%) markets in all seven countries for which we have data (Figure 6.1). On average, over time and across countries, per sample, pangolins represented 2.1 ± 0.27% (mean ± SE) of vertebrates in the catch and 1.4 ± 0.23% at markets.

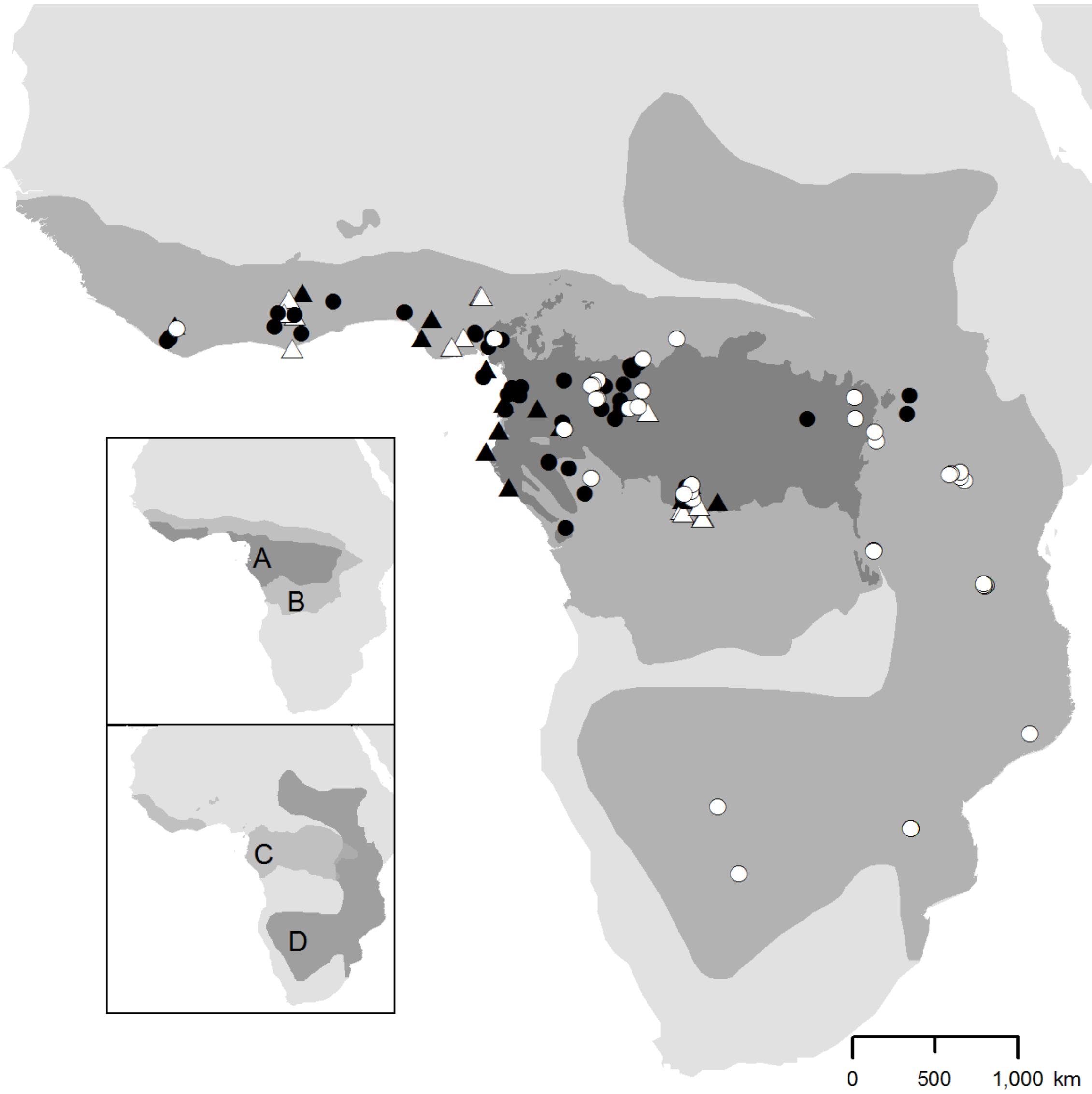

Figure 6.1. Sites where pangolins have been observed in the catch (filled circles) and at markets (filled triangles) from 113 hunting (circles) and 36 market (triangle) sites across Africa. Combined extent of occurrence (grey shading) for the four African pangolins (Pietersen et al. 2014a; Waterman et al. 2014a, 2014b, 2014c), shown separately in insets for *Phataginus tetradactyla* (A), *P. tricuspis* (B), *Smutsia gigantea* (C), and *S. temminckii* (D). Central African forests shown as the WWF Tropical and Subtropical Moist Broadleaf Forests ecoregion clipped by Central African countries and the extent of occurrence of African pangolins (dark grey; Olson et al. 2001).

The sex composition of pangolins in the catch was 49% female, 45% male, with 6% of unknown sex (n = 560 pangolins from 10 sources). Most (50%) were adults, 45% juveniles and sub-adults and 5% of unknown age (n = 310 pangolins, 5 sources). Pangolins were hunted by traps and snares (54%), hand (25%), gun (16%), or other means (5%) (n = 822 pangolins, 14 sources). Pangolins were either directly consumed (50%), sold (41%), or given as gifts (9%) (n = 425 pangolins, 9 sources).

6.4.2 Estimating total catch of pangolins in Central African forests

We estimate that between 0.42-2.71 million pangolins (*Phataginus spp*. and *Smutsia gigantea*) were hunted each year in Central Africa (sampled range 1975-2014), with the two human population-based methods giving higher estimates of 1.68 million (0.22-4.76 interquartile range) and 2.71 million (0.35-7.66) pangolins (Figure 6.2; Table S1 and Figure S2). The total annual catch of pangolins has increased by an estimated 145-151% from before 2000 (range 1975-1999) to post 2000 (2000-2014) depending on estimation method (Figure 2). *S. temmickii* does not occur in Central African forests, and insufficient data were available to estimate total annual catch where it occurs.

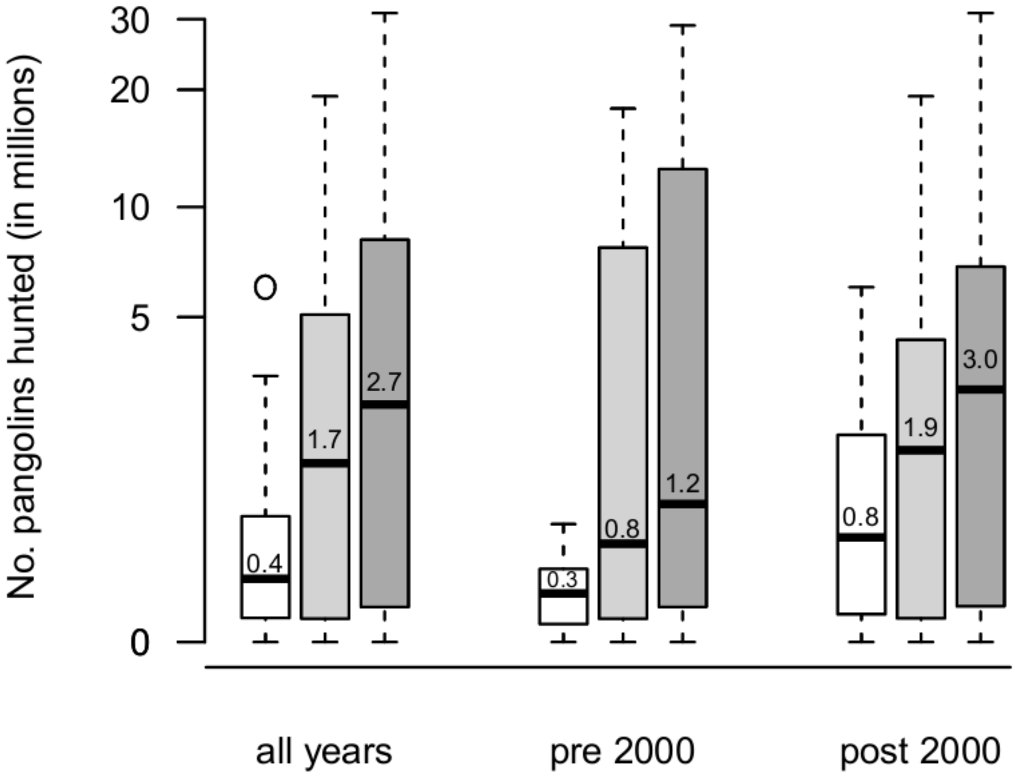

Figure 6.2. Estimates of the annual number of pangolins (Phataginus sp. and S. gigantea combined) hunted in Central African forests, median (thick lines) across all years (1975-2014) (n = 24, 44, 44 samples), pre 2000 (n = 8, 12, 12), and post 2000 (n = 16, 32, 32), based on a forest area-based method (white), and UNPD-derived (light grey) and Global Rural-Urban Mapping Project (GRUMP)-derived (dark grey) human population-based methods. Box plots show median, 1st and 3rd quartiles, with whiskers extending to extreme values no more than 1.5 times the length of the box, and points represent outliers.

6.4.3 Trends in pangolins hunted and observed at markets

The percentage of pangolins in the catch increased significantly from 0.04% in 1972 to 1.83% in 2014 (Figure 6.3A, minimum adequate model: percentage of pangolins = year + random effects of StudyID nested within SourceID, and Country, $\chi^2_{5,6}$ = 6.4, p = 0.012). For comparison, we also found no temporal trends for the main hunted taxonomic groups (Cetartiodacyla and Rodentia) (Figure S3), but we did find that pangolins account for more of the catch in the most accessible areas (Figure S4). The percentage of pangolins observed at markets did not change significantly between 1975 and 2010 (Figure 6.3B; $\chi^2_{4,5}$ = 1.9, p = 0.17).

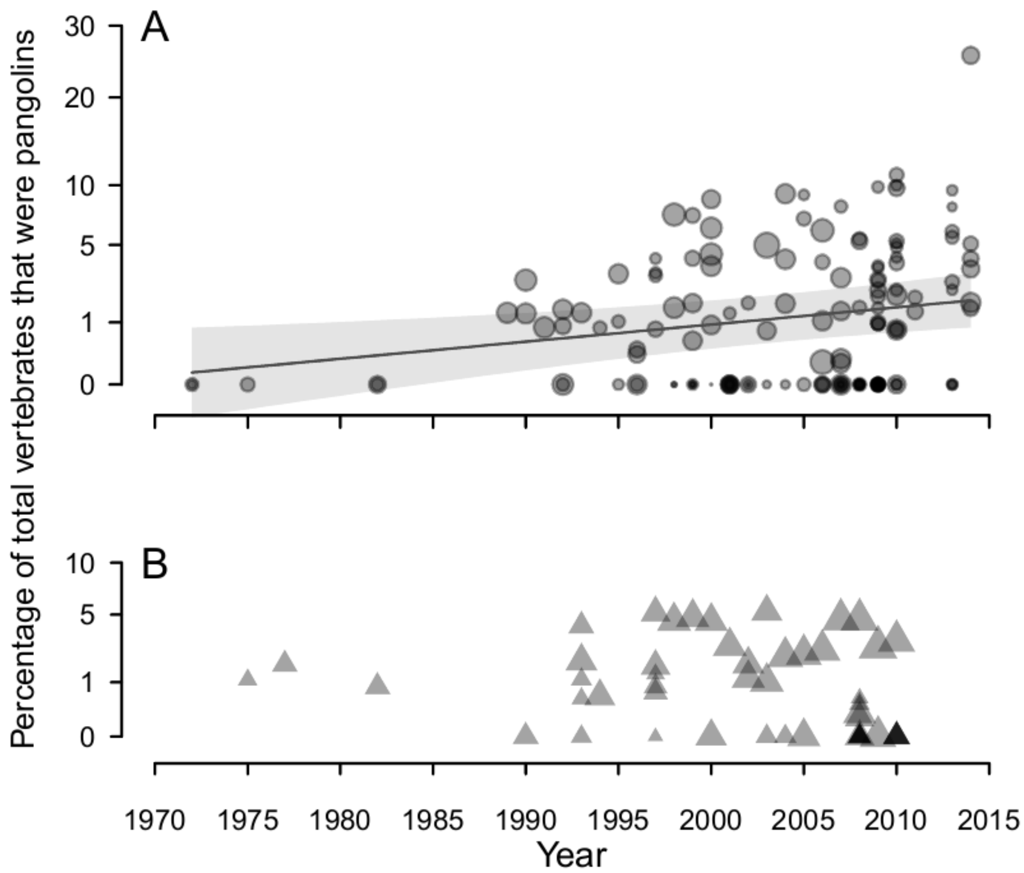

Figure 6.3. Trends in the percentage of vertebrates that were pangolins (Manidae) in the catch (A, n = 152 samples) and that were observed at markets (B, n = 52) across Africa. Samples shown as translucent points to show density of samples, and are scaled by total catch of individual vertebrates (1 – 30,196 individuals). Trend line and 95% CI (shading) fitted using a linear mixed effects model.

6.4.4 Trends in price

We collated price data for arboreal (n = 149 records) and giant ground (n= 32) pangolins from 31 sources in 5 countries. Prices for arboreal pangolins changed significantly over time, and changes differed depending on market type (Figure 6.4A, interaction: $\chi^2_{6,8}$ = 8.0, p = 0.02; urban markets increasing from ~ 3700 to 8500 Central African Francs [CFA] and rural markets decreasing slightly from 3200 to 2700 CFA). The price of giant ground pangolins increased significantly at urban markets between 1993 and 2014 from approximately 24,000 to 140,000 CFA (Figure 6.4B: $\chi^2_{3,4}$ = 3.9, p = 0.05), but not in rural ones where we have few prices (n = 8).

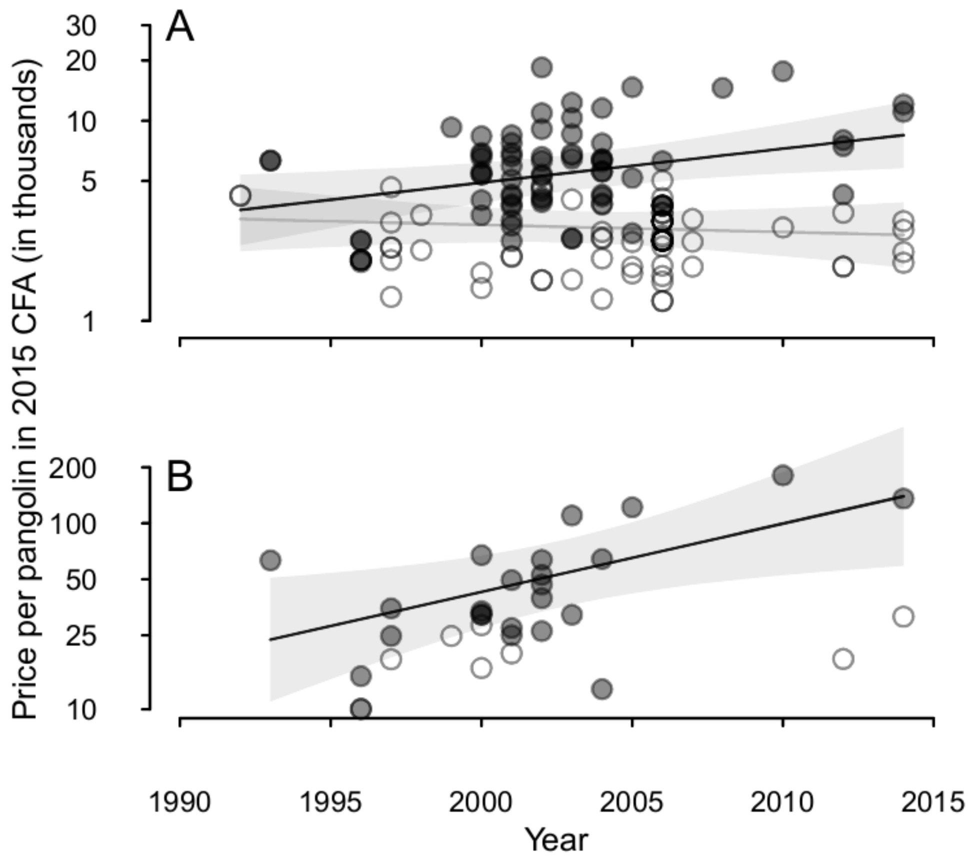

Figure 6.4. Trends in the price (in 2015 Central African Franc [CFA]) of arboreal pangolins (A, n = 149, Phataginus sp.) and of giant ground pangolins (B, n = 32, Smutsia gigantea) at urban (filled points) and rural (hollow points) markets in Central Africa, plotted on a log scale. Statistically significant (P < 0.05) trend lines (black for urban, grey for rural) and 95% CI (shading) are fitted using linear mixed effects models.

We calculated price ratios for blue duikers (n = 134 price records), brush-tailed porcupines (n = 134), and cane rats (n = 82) based on data from 31 sources collected at 85 sites in 5 countries between 1992 and 2014 (Table S1). Price ratios of arboreal pangolins to blue duikers increased significantly in urban markets (0.024 ± 0.008 ratio increase per year ± SE, Figure 6.5A, Figure S5), and decreased in rural markets (-0.017 ± 0.007 ratio decrease per year; interaction of year and market type, $\chi^2_{5,6} = 12.9$, p = 0.0003). We found no significant interaction of year and market type for the price ratio with porcupines ($\chi^2_{5,6} = 3.0$, p = 0.08) or cane rats ($\chi^2_{5,6} = 0.06$, p = 0.81), or any effect of year on the price ratios for porcupines ($\chi^2_{3,4} = 0.03$, p = 0.87) or cane rats ($\chi^2_{3,4} = 0.01$, p = 0.93).

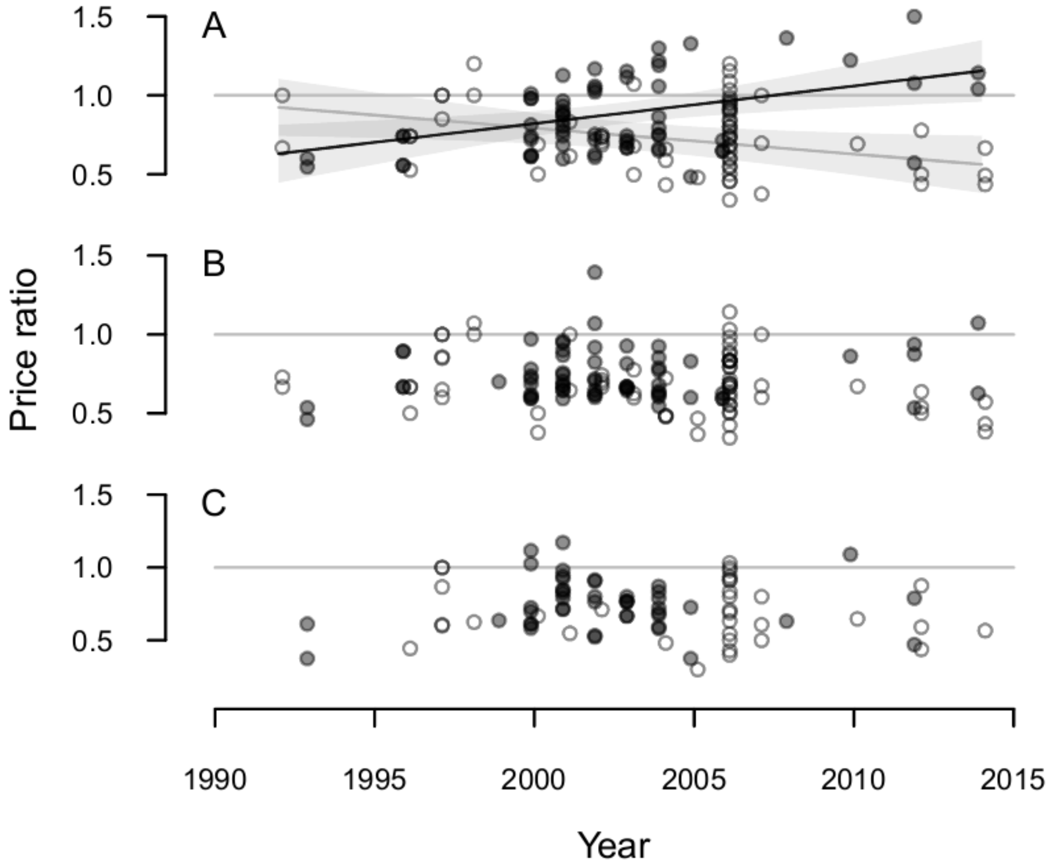

Figure 6.5. Trends in the price ratio at urban (filled points) and rural (hollow points) markets across Central Africa for arboreal pangolins (Phataginus sp.) to blue duikers (A, n = 134 price ratios), brush-tailed porcupines (B, n = 134), and greater cane rats (C, n = 82). Trend lines and 95% CI (shading) are fitted using linear mixed effects models, statistically significant ($P < 0.05$) in A for both urban (black line) and rural (grey line) markets.

6.5 Discussion

By collating local-scale studies, we provide the first regional estimates of African pangolin exploitation, revealing that pangolins are hunted and observed at markets throughout West and Central Africa, and that pressure from hunting has increased. The proportion of pangolins in the catch increased significantly over time, while the proportion observed at markets remained unchanged. We found evidence that the price of whole pangolins increased significantly at urban markets, but not at rural ones.

We estimate that 0.4-2.7 million pangolins (*P. tricuspis*, *P. tetradactyla,* and *S. gigantea*) were hunted annually in Central African forests, based on forest area- or human population-based extrapolations of average hunting levels. Our area-based estimate of ~420,000 pangolins hunted annually is consistent with a previous area-based estimate of ~400,000 *P. tricuspis*, and ~100,000 *S. gigantea* annually in Central Africa, although based on fewer studies and excluding *P. tetradactyla* (Fa & Peres 2001). Studies rely on the willingness of hunters to participate, so studies may represent only a subset of hunters at a particular site. Furthermore, hunters and traders may either fail to report illegally hunted protected species, or may not participate in studies, therefore our extrapolations are likely conservative.

Our analyses suggest that the number of pangolins hunted has increased. Comparing forest area- or population-based extrapolations of data from before and after 2000, we found a ~150% increase, although interquartile ranges overlap likely due to relatively small sample sizes. When analysing hunting samples, the percentage of pangolins out of the total catch increased significantly from ~0% to 2% over four decades. The percentage of pangolins observed at markets remained unchanged, suggesting pangolins may be traded along alternative supply chains as observed in Ghana where pangolins were often traded to wholesalers away from wild meat markets (Boakye et al. 2016), and in Gabon where Asian industry workers buy pangolins directly from hunters (Mambeya et al. unpublished). The reliability of market studies to assess exploitation has been questioned (Crookes et al. 2006) because individuals observed at markets likely represent a fraction of those hunted as traders hide illegal goods to avoid law enforcement. We cannot discern whether the observed increase in pangolins hunted is caused by (i) increased consumption, (ii) increased hunting of smaller mammals due to declines in larger species (Ingram et al. 2015), (iii) changes in hunting technology, and/or (iv) increased demand from international markets (Challender & Hywood 2012).

We provide evidence that current hunting of African pangolins is likely unsustainable. On average, 45% of individuals were either juveniles or sub-adults, an indicator of overexploitation (Weinbaum et al. 2013), although aging sub-adults is difficult and our assessment relies on the authors reporting of age. This is of concern because pangolins take up to two years to reach sexual maturity and produce only one pup annually (Soewu & Sodeinde 2015), suggesting many of the pangolins hunted had not reproduced. Traps and snares were the most common hunting method (54%), however, the use of wire snares is illegal in all pangolin range states because they are effectively "blind" to the species trapped, but law enforcers often ignore or tolerate snaring (LAGA 2015). Effective law enforcement is needed, and should include stricter controls of snaring, such as snare specialist teams (Gandiwa et al. 2013), the elimination of corruption, and the provision of alternative protein sources and incomes.

We found substantial price increases for giant ground pangolins at urban markets, which may suggest that early signs of increased demand may not yet have been passed down to rural hunters, or that prices are responding to increased demand that is unmet by hunters because of depletion. We found small increases in prices and price ratios for arboreal pangolins in urban markets that, while increasing slowly, appear to be following the increasing trend of prices in Asia (Newton et al. 2008). Anecdotal evidence suggests that rural hunters may not yet know the value of pangolins elsewhere (Mambeya et al. unpublished).

While CITES provides a mandate for sustainable international wildlife trade, recently banning trade of all pangolin species (Challender & Waterman 2017), it does not provide enforcement mechanisms on the ground. To implement the trade ban, governments, law enforcement officials, and conservationists need to better understand the supply chains of pangolins from Africa and Asia, to implement an appropriate monitoring program, and to increase the capacity to enforce the ban and intercept illegal shipments. To better target and inform conservation efforts, tailored survey methods to accurately estimate pangolin abundance and collect vital ecological data are needed. In addition, efforts should focus on determining local demand, and when/where this leads to unsustainable hunting. For cases where pangolin hunting is unsustainable, efforts should be made to improve and increase domestic law enforcement, increase public awareness, reduce indiscriminate hunting methods such as snaring, and work with local communities to find effective solutions. Next steps should involve investigating harvests and enforcing legislations in support of country-wide conservation efforts. In addition, it is imperative that China, as one of the main consumers, considers implementation of awareness campaigns as well as increased monitoring, law enforcement and penalties. Pangolins have attracted conservation attention recently, and as people become increasingly aware of the focus on pangolin hunting, the perceptions and stigmas of pangolin hunting are also likely to change over time.

Using African pangolins as a case study, we have demonstrated that collating local-scale data from hunting and market studies can be used to assess regional trends in wildlife exploitation. Local-scale data complements seizures data, by providing estimates of local demand and more accurate estimates of total hunting rates. Together these types of data give insights into different aspects of pangolin use and trade, and paint a more complete picture of pangolin exploitation. In the absence of continent-wide species monitoring programmes, collating local-scale data can highlight pressures on wildlife, and provide detailed quantitative information on wildlife exploitation that are crucial to inform conservation action and policy.

7 Discussion

7.1 Summary of overall findings

7.1.1 A database on the exploitation of terrestrial wildlife

Ultimately, understanding whether hunting wildlife is sustainable is the main goal and overarching vision for the application of the database designed and created in this thesis. Systematically collected, long-term studies on terrestrial wildlife exploitation are rare, and methods to track terrestrial wildlife exploitation across time and large spatial scales are currently lacking. This thesis examined whether the wealth of site-level studies available can be collated and harnessed to quantify and explore patterns and trends in the exploitation of wildlife in Africa. The analysis chapters of this thesis (Chapters 3, 4, 5 and 6) act as case studies that highlight how collating disparate datasets can be used to gain a greater understanding of the magnitude and patterns of the exploitation of wildlife at a regional scale. Through this thesis, I showed that it is possible to gain novel insights into the exploitation of wildlife across Africa by collating and analysing a database of disparate site-level studies. The purpose-built database that I designed, developed, and populated for this thesis is intended to become a tool to aid in the development of conservation policies and actions.

Collating many individual studies into a database, and analysing the studies together has been a successful way of gaining a better understanding of patterns of biodiversity across large spatial scales that can be used to inform conservation policy and actions. For example, the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) database, is a global database of collated site-level studies that compare terrestrial biodiversity in different land use and intensity categories (Hudson et al. 2017). Another example is the BIOFRAG database, which can be used to investigate biodiversity responses to forest fragmentation (Pfeifer et al. 2014). These databases are available for use by other scientists and conservation practitioners, and the outputs can be used by policy makers.

The database developed in this thesis greatly expands upon previous efforts to collate data on wildlife exploitation across large spatial scales in terms of temporal, geographic, and taxonomic coverage. One advantage of collating studies in a database is the ability to identify biases in research and sampling effort. Furthermore, one can identify gaps in geographic and taxonomic sampling that currently limit our ability to understand the complete picture. Summary statistics have revealed spatial biases in the locations where the collated studies were conducted (Chapter 2), which may be caused by factors such as ease of access for researchers, safety, knowledge of willingness of communities to collaborate, or knowledge of high hunting pressure. Knowing when and where studies have been conducted is useful for identifying under-studied areas and areas where time-series studies may be conducted in the future. Despite the biases identified in Chapter 2, collating studies in a database and analysing studies together is a useful approach to better understand patterns over large areas. Analyses must take into account the distribution of the sampling locations of the studies used and draw conclusions within the context of the data.

7.1.2 Quantifying the harvest of wildlife

Previous studies have attempted to quantify the total annual harvest of wildlife in Central Africa (Fa et al. 2002b; Ziegler et al. 2016), but these studies were limited by the number of studies and did not account for differences among sampled sites. In Chapter 3, I showed that it is possible to use a database of site-level studies to investigate patterns of wildlife harvests across Central Africa. Depending on the method used to extrapolate, I found that estimates of total annual biomass harvested varied substantially. One of the main challenges in conducting this study was that human population data per settlement is not available for Africa, thus extrapolating by the number of rural people and hunters relied on human population estimates per grid cell. Secondly, not all studies collected data on the number of hunters surveyed at a site, the total number of hunters, site population, and hunter territory size, and thus extrapolations either involved fewer studies, or data gaps needed to be filled with averages. Whilst I have shown that it is possible to quantify and map the harvest of wildlife using the available data, it is likely that extrapolations would be improved with the aforementioned human population and site-level data.

7.1.3 Indicators of exploitation

7.1.3.1 Temporal trends

Whilst indicators are available that track the extent and magnitude of marine wildlife exploitation, indicators of terrestrial wildlife exploitation have been largely neglected until now. In Chapter 4, I proposed two indicators that could be used to track wildlife harvests, namely the mean body mass indicator (MBMI), and the offtake pressure indicator (OPI).

While the purpose of Chapter 4 was to develop indicators of exploitation, I also presented the preliminary results based on the data available at the time to test the indicators. Preliminary analyses from the MBMI suggested that the average size of mammals harvested had decreased over time, while that of birds had increased. In Chapter 5, I revisited the indicators proposed in Chapter 4 to further investigate trends in mean body mass. Using data from a greater number of studies, I confirmed that the mean body mass of mammals did decrease over time (but not that of birds), but that this trend did not hold when elephants were removed from the samples, indicating that the indicator is sensitive to species that are orders of magnitude heavier than most other species.

I tested whether the proportion of individuals of different harvested taxa (out of all harvested individuals) changed over time (Chapter 5). I found a borderline significant increasing trend in the proportion of individuals harvested that were pangolins and primates over time. Increases in the harvest of primates could be due to increases in gun-hunting over time (Coad 2007; Walters et al. 2015), which facilitates the hunting of arboreal and flying animals. Increases in the harvest of pangolins could be due to increased consumption, as they are a preferred species (Schenck et al. 2006), increased demand from the intercontinental trade (Challender & Hywood 2012), or decline in larger-bodied species.

7.1.3.2 Indicators of defaunation

Settlements closer to major markets have been shown to sell a greater proportion of the wildlife harvested (Brashares et al. 2011), and that hunting for commercial purposes is becoming increasingly commonplace (Abernethy et al. 2013). At a local scale, the composition of the harvested wildlife changes with distance to human settlements

(Koerner et al. 2017), and reflects the availability of wildlife (Kümpel et al. 2008; Fa & Brown 2009). In Chapter 5, I investigated whether patterns of defaunation were observable across a large area, by investigating changes in the mean body mass (using the method from the MBMI) and taxonomic composition of wildlife harvested across an accessibility gradient (measured as travel time to nearest major settlement) as indicators. I found that the mean body mass of mammals harvested was lower in the most accessible areas and that the taxonomic composition of the vertebrates harvested changed across an accessibility gradient.

Accessibility predicted the mean body mass and taxonomic composition of wildlife harvested (Chapter 5), while hunters located closer to protected areas harvested more wildlife biomass annually than those located further away (Chapter 3). The results of these two chapters complement each other for a number of reasons:

1) Wildlife populations in protected areas may act as sources for areas surrounding protected areas, so more wildlife could potentially be harvested.
2) More accessible areas could have been subjected to longer periods of hunting, or more intense hunting pressure. Larger-bodied species are known to be less resistant to hunting pressure (Yasuoka et al. 2015), and so more accessible areas could be defaunated.
3) In more accessible areas, it is likely that more opportunities exist for employment, and more alternatives exist for sources of food. Both of these could result in hunting being a secondary activity (e.g. after agriculture), or in less discriminate methods of hunting being used (e.g. snares) which require less time and catch a wider variety of species.

Overall, the methods used in Chapters 4 and 5 prove to be promising indicators that can be used to track terrestrial wildlife harvests, despite the lack of systematically collected long-term data, and results appear complimentary to spatial analyses in Chapter 3.

7.1.4 Assessing the exploitation of individual taxa

I tested whether the database could be used to investigate exploitation for one group of understudied and vulnerable species, the African pangolins (Family: Manidae). Using the harvest data available, I was able to investigate trends in the proportion of all animals harvested that were pangolins over time, and found evidence of increasing pangolin harvests over time (Chapter 6). The studies that I collated not only contained information on the number of pangolins harvested or offered for sale, but some studies contained other detailed information on price per carcass, the method used to harvest pangolins, and their end use. By collating these data, I was able to build a picture of pangolin exploitation in Africa, and investigate which hunting methods and uses of pangolins were the most common across Central Africa. Knowing such information will allow better formation of conservation measures. For example, measures could target particular hunting methods e.g. snares. Another advantage of using this approach for individual taxa is that data on when taxa were not hunted (i.e. 0 individuals were recorded as harvested in the study) can be used for studies within the species range. Ultimately, the approach demonstrated in Chapter 6 could readily be applied to other taxa, particularly those that are under-studied or threatened.

7.1.5 Limitations

Hunting studies, and occasionally market studies, often require information provided by local people who are either hunters themselves or are part of hunting communities. Obtaining information on wildlife harvesting can be difficult, and in some places, is a sensitive topic due to fear of social exclusion or law enforcement, particularly where law enforcement may be strict. Where communities will allow it, direct observation methods such as hunter-follows (e.g. Kümpel 2006) should provide more accurate and reliable information (Gavin 2010) on the quantities of wildlife harvested than indirect observations and market studies. However, direct observation is a somewhat resource intensive method, whereby numerous observers would be required to monitor the hunting patterns of a large proportion of the hunting community in a settlement, and the presence of an observer may also cause hunters to change their behaviour. In small settlements however, this method may be particularly appropriate because it is easier to obtain enough observers. Surveyors should also seek to spend time in the chosen communities to build relationships and trust with the aim of increasing the reliability of the data. Although the effectiveness will likely decrease with settlement size given the increasing number of people and decreased likelihood of building a relationship and trust with them all.

Study locations may be biased for several reasons. Study sites may have been chosen because they 1) are of interest to researchers, e.g. where hunting is known to be prevalent, 2) are relatively safe for researchers to work in, and/or 3) are relatively easy to access. Extrapolating from biased studies may overestimate total harvests if researchers preferentially conducted studies in areas where the biomass of wildlife harvested is high relative to other areas. One can test whether studies are biased by checking whether the annual harvest across sites is normally distributed, which can then inform decisions about whether the mean or median is used to extrapolate from as demonstrated in Chapter 3. Additionally, if studies are only conducted in easy to access areas, then the pressures on wildlife from hunting in the least accessible areas remain largely unknown.

Differences in the duration of studies, and the time of year that studies were conducted, are potential limitations of this thesis. Long-term time-series information was only available in a few locations. For example, continual market surveys from 1997 to 2010 at the Malabo wild meat market (Cronin et al. 2015), and hunting surveys in Makao-Linganga from 1997 to 2006 (Riddell 2010), although hunting at this site is managed. Time-series data are also available for two villages in Gabon sampled twice over six years (Coad et al. 2013), and at a village in Equatorial Guinea sampled three times over 12 years (Gill et al. 2012). The limitation of having few time-series studies is that any trends observed across time are only represented by a couple of locations. The average length of studies in the database is typically less than one year, and therefore may not include differences in hunting due to seasonality, which has been observed at some sites (Coad 2007), but not others (Kümpel 2006; Ampolo & Bikouya 2008). One could assess the importance of seasonality by plotting the monthly biomass of wildlife harvested across a year using studies for which data was available, although this method would only represent a few studies. Another method is to test for differences in the shape of the distributions of studies sampled for <365 and ≥ 365 days (e.g. Kolmogorov-Smirnov tests, Chapter 3). Studies with a duration less than one year may not include every hunting season or periods where no hunting had taken place, thus extrapolations of annual harvests may lead to overestimation. However, if the study was conducted during a period where hunting was minimal, then extrapolations could be underestimates.

I found that studies were biased in terms of the taxa for which harvest was quantified. Studies often focussed on quantifying the harvest of vertebrates, and particularly mammals. Typically, studies do not quantify harvests of invertebrates, even though they are known to be consumed widely (van Huis 2003). In a study in the Democratic Republic of Congo, 10% of the animal protein consumed by people came from 65 species of insect (deFoliart 1999). Invertebrates are also known to be an important source of food when wild meat availability declines (Vantomme et al. 2004). Zitzmann (1999) showed that the sale of one species of insect represented up to 13% of annual income in some households in Botswana. In this thesis, I estimated total annual terrestrial vertebrate harvest, however until quantities of harvests of under-studied taxa such as invertebrates are available at the site level, total terrestrial wildlife harvest will be underestimated. Therefore, it is difficult to discern the extent or magnitude of harvests, and the importance of under-studied taxa for the food security and livelihoods of people. Furthermore, without such information the sustainability and ecological consequences of invertebrate harvests is unknown.

7.1.6 Generality of the approach

Hunting is commonplace across the world (Darimont et al. 2015; Benítez-López et al. 2017), and yet no global estimates of terrestrial wildlife harvests exist despite being a global phenomenon with wide ranging implications for both people and wildlife. Whilst the aforementioned limitations exist, and I focussed on Africa in this thesis, it can be viewed as a case study to pave the way to expand the database and scale of analyses to other continents in the tropics, and ultimately the rest of the world. The methods used and indicators developed throughout this thesis can be applied to data collated for the rest of the world where available (see below discussion on Latin America and Asia). If a global database were possible, it would be particularly interesting to conduct a cross-continental analyses of quantities of wildlife harvests, drivers of hunting patterns, and the contribution of wildlife of the subsistence and livelihoods of people around the world. Further, time-series data could be aggregated into an overall Offtake Pressure Indicator (OPI), but care should be taken to interpret trends according to the local context of the time-series. Whilst the taxonomic composition of harvests differs across the world, the overall patterns may be similar, i.e. animals are hunted down a size gradient starting from large animals (Dirzo et al. 2014), and may therefore be a useful indicator of the defaunation of wildlife for other regions. Overall, the environmental and socio-economic differences between sites that may drive patterns in wildlife harvests, e.g. distance to protected areas and accessibility, may be generalizable across continents, however the effects of each variable on individual groups of taxa are likely to be different.

The approach taken in this thesis could be applied in Latin America where, in at least 78 communities, studies have investigated the harvest of mammals (Stafford et al. 2017). Moreover, several studies provide data for at least a year (e.g. Escamilla et al. 2000; Peres and Nascimento 2006), which allow for more in-depth analyses of seasonal changes, which was not available for Africa due to short study lengths.

For Asia, it is unlikely that there is sufficient harvest data to allow similar temporal or spatial analyses across large spatial scales. Whilst harvest data is available for some communities (e.g. Pangau-Adam et al. 2012), it appears that conducting research on wild meat harvests in Asia is difficult, which may be due to factors such as trust and language barriers. Furthermore, in many areas wildlife may be heavily depleted (Harrison et al. 2016), which may not attract significant research attention. However, a large number of market-based studies have taken place in Asia (e.g. Lee et al. 2005; Shepherd et al. 2007; Chow et al. 2014), which could allow for questions on the price and market turnover of carcasses to be answered.

7.2 Implications for conservation

7.2.1 Conservation action

Many approaches have been suggested to monitor and manage exploitation at a local scale to reduce pressure on wildlife. One approach for reducing hunting activities, thus reducing pressure on wildlife, is to develop alternative protein or alternative livelihoods programmes (Foerster et al. 2012; Roe et al. 2015). Currently, however, the success of such projects in Central Africa is limited, because the pressure from hunting by commercial hunters outside of the livelihood project site often dwarfs that of the hunters based at the site (Wicander & Coad 2015). In Cameroon, Yasuoka (2006) calculated that subsistence hunting was sustainable, but commercial hunting was not. Commercial hunting supplies urban areas, where wild meat is rarely a necessity due to the availability of alternatives, but studies have shown that the consumption of wild meat is frequent (Wilkie et al. 2005; Mbete et al. 2011). Efforts to reduce urban demand for wild meat may also reduce the need for commercial hunting. In areas where hunting is illegal, law enforcement may target particular areas (e.g. protected areas), or focus on regulating hunting methods (e.g. snares). Moreover, engagement with hunting communities may be the key to tracking exploitation more readily.

In rural areas, conservation actions could be sought that work with local communities to track their harvest of wildlife to ensure sustainable use of wildlife and the success of long-term community-based approaches. The indicators that I developed in Chapters 4 and 5 can be used to track exploitation over time at various scales to inform conservation decisions. For example, the indicators can be used to track exploitation over time at individual sites, or can be used to compare multiple sites. Recently, Avila et al. (2017) applied the mean body mass indicator that I developed in Chapter 4 to harvest data in three villages in Cameroon, and compared the MBMI for each village per month and by hunting method. Across time, the authors found no significant changes in the MBMI, but state that the area is likely to have relatively low hunting pressure and relatively high densities of wildlife. When comparing the MBMI for different hunting methods, the authors found that animals taken using guns had a higher mean body mass. Furthermore, Avila et al. (2017) suggested that the MBMI could be used for community-based monitoring approaches, which would allow communities to track their own harvests and understand the changing dynamics within their hunting system.

By comparing across many sites, patterns of harvests can be observed across large spatial scales, and can be used to inform global policy decisions (see pangolin example in the next section).

7.2.2 Policy

Given that the overexploitation of wildlife now represents one of the greatest pressures on biodiversity (Maxwell et al. 2016), the database and analyses presented here have important implications for future conservation policy. Consistent and accessible quantitative information is needed to inform decision-making in global policy arenas. For example, the outputs from this project could be considered as ‘Essential Biodiversity Variables’ (EBVs), defined as “a measurement required for study, reporting, and management of biodiversity change” (Pereira et al. 2013). EBVs on the exploitation of wildlife can then contribute to initiatives such as the Biodiversity Observation Network of the Group on Earth Observations (GEO BON). GEO BON aims to coordinate and facilitate biodiversity observation to support policy decisions, and is one of the GEO's Societal Benefit Areas that highlights the benefits of biodiversity to society. The database and indicators developed during this PhD may also contribute to reporting efforts on progress towards achieving the United Nations' Sustainable Development Goals. In particular, goal 2 which states that by 2020 governments commit to "ensure sustainable food production", and goal 15 which states that we must "promote implementation of sustainable management of all types of forest" (Target 15.2) and "take urgent action to end poaching and trafficking of protected species" (Target 15.7). For example, to ensure progress towards goal 2, research should focus on investigating the sustainability of the harvest of wildlife by analysing population, harvest, and life history trait data together, where available. Furthermore, the database could be used to assess how wild meat (and other wild-sourced foods if included) could contribute to achieving SDG2, which currently is assumed at zero. To do this, a consumption module could be added to the database, and analysed to quantify and map the contribution of wild-sourced foods to the diets of people. When combined with the aforementioned sustainability analysis, this would allow a sustainable contribution to be calculated and, if needed, a subsequent analysis of any nutritional 'gaps' that may remain to be estimated. Another component of goal 2 is 'better access to food' where, in areas where sustainable hunting is permitted, the size of the areas needed could be assessed using data on contemporary hunter territory sizes.

Specifically, the analyses on the exploitation of pangolins (earlier version of Chapter 6, Ingram et al. 2016) has been used to inform global policy change. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is an international intergovernmental agreement to ensure that the international trade in wild animals and plants (and their derivatives) does not threaten their existence. Both the African and the Asian pangolins were transferred from CITES Appendix II to Appendix I at the recent 17th meeting of the Conference of the Parties (Challender & Waterman 2017). Specifically, Chapter 6 informed the transfer of African pangolins to Appendix I (Challender & Waterman 2017), the most restrictive CITES Appendix, whereby the commercial and international trade in wild-caught pangolins is banned.

7.3 Recommendations for further research

7.3.1 Tracking the harvests of all wildlife

The wide range of different types of hunting and market studies, and disparities between the information that is commonly collected by studies, highlights the need for guidelines or a "tool kit" for conducting studies. While I found several studies that quantified wildlife harvests in Africa, many studies did not have sufficiently detailed data to be included in more in-depth analyses needed to better understand exploitation trends and patterns. A tool kit for harmonised and standardised data collection would therefore also maximise the use of conservation funds, and the effectiveness of regional analyses.

Through identifying the differences between a vast number of studies and investigating ways to analyse the studies simultaneously, I am now able to make the first steps towards a set of recommendations for a toolkit to harmonise future studies that monitor wildlife harvests. Any toolkit for monitoring wildlife harvests would have several components, including 1) data requirements, 2) standardised methods for collecting the data, and 3) recommendations for research needs and study regions. Here, I focus on 1) and 3), by making the data requirements needed for in-depth analyses towards understanding hunting sustainability (Table 7.1), and making recommendations for future research efforts.

Table 7.1. Data requirements for future harvest and market studies

Data type	Data
Settlement	GPS coordinates Number of people in the settlement Number of hunters
Harvested species	Species ID (Latin) Quantity harvested (report exact units, not conversions) Weight of harvested individual Sex of harvested individual
Harvest study specific	Hunting territory size Hunting tool (e.g. gun, trap) Hunting season Hunter demographics
Market study specific	Price Carcass source Market days
Survey effort	Number of days Number of hunters surveyed

The utility of market studies in understanding the sustainability of wildlife harvests has been questioned before because the animals offered for sale at markets rarely represent the total diversity of species harvested, but rather the urban demand (Allebone-Webb et al. 2011), and indicators based on the ratio of large to small animals would be biased. Although, market data has been used to infer depletion in the surrounding areas (Fa et al. 2015), but not the circumstances under which hunting may be sustainable. Therefore, hunting studies in particular are needed to better understand which species are harvested, and where. To understand the rate of harvest (biomass per person per day, or biomass per square kilometre) and therefore enable comparison between hunters and locations, hunting studies should collate information on the hunting territory size, the number of people in a settlement, the total number of hunters, and the number surveyed.

Studies that quantify the harvest of all terrestrial and aquatic wildlife at the same location are one component needed to better understand the sustainability of harvests. Crucially, hunting studies are needed in conjunction with population surveys of hunted species, and knowledge of demographic parameters of hunted species. Benítez-Lópes et al. (2017) compared population data in hunted and unhunted areas across the tropics, providing an estimate of average population declines in hunted areas. However, to provide more in-depth analyses of the effects that hunting has on wildlife populations, a measure of hunting pressure or quantity of wildlife harvested needs to be included. Such in-depth studies would provide evidence to understand the circumstances in which hunting may be sustainable. Further, hunting and wildlife populations should be monitored over time to understand how changes in the dynamics of hunting affects populations. Future studies should therefore seek to further develop indicators using hunting studies and, following the procurement of additional data, integrate them into conservation policy instruments.

The database developed in this thesis can be used to identify areas where studies have not been conducted, and to identify areas that have been previously sampled but where repeat sampling could take place to investigate trends over time. The database provides a list of the species that are harvested and offered for sale, and the areas where certain species are harvested can be identified. Spatially, western Central Africa, and in particular Cameroon, are very well sampled in Africa. For tropical forests, it would be particularly useful to sample in West African countries, and eastern Central Africa (Democratic

Republic of Congo), where data is lacking. More generally, it would be useful if future studies quantify wildlife harvests in non-forest ecosystems in Africa. Temporally, given the lack of available time-series studies (see Chapter 4), there are no areas with sufficient information over time. In Chapter 3, I identified areas where wild meat harvesting may be high relative to the surrounding areas, and so hunting studies should focus on these areas, and investigate trends over time.

Broad-scale analyses of large and disparate datasets should be considered and interpreted carefully, acknowledging the nature of the datasets. For example, Robinson and Sinovas (2018) analysed the CITES Trade Database, which captures information on the international trade of wildlife, and demonstrated that the addition of one highly-traded genera of reptile considerably altered the overall trend in traded reptiles imported into the European Union between 1996 and 2008. Thus the indicators developed here, and in the future, should be tested for their sensitivity to the addition of new studies and taxa. In addition to overall indicators of change, it is also vital to separate indicators based on other important factors e.g. taxonomic group (Order, Family etc.), functional guild, and ecoregion, to investigate the drivers of changes. Whilst an understanding of the sensitivity of indicators to new data is important, indicators also need to be sensitive to changes in the hunting system e.g. hunting tools (traditional traps to firearms), and socio-economic and cultural changes.

In addition to the inclusion of new datasets, several factors may affect the detectability of trends in the data. Weatherhead et al. (1998) list that the sample size, time-span and variability of the data, autocorrelation, and the size of the trend to be detected are all factors that affect trend detection. In this thesis, I used a mixed-effects modelling framework which allows aspects of the variability in the data to be accounted for. Further to the methods used here, future efforts should consider power analyses to understand the data requirements needed to answer different ecological questions, and may require other advanced statistical methods to take account of more components of the data (e.g. Bayesian frameworks; although large datasets are often required to make full use of their capabilities [Bolker et al. 2009]).

7.3.2 Wildlife harvests in a developing continent

Half of all global human population growth is expected to occur in Africa up to 2050 (UN DESA 2017), and will likely involve further infrastructure development such as roads and buildings to cope with rising human populations. In addition, Africa is increasingly receiving international investment for logging operations, oil, and mining for precious metals (Abernethy et al. 2016). Building roads enables access to otherwise remote areas, and facilitates hunting (Kleinschroth & Healey 2017). While the trend in Africa is towards an increasingly urbanised population (Cobbinah et al. 2015), this does not mean that hunting for wild meat will not continue. In many urban areas, wild meat is considered a luxury and is consumed in small amounts (Wilkie et al. 2016), it is considered part of local culture, or in some cases it is consumed because it is cheaper than farmed or imported meat (van Vliet & Mbazza 2011). Urban consumption of wild meat can be considerable (Wilkie & Carpenter 1999; Abernethy et al. 2013), and so large and increasing urban populations may exacerbate commercial hunting of wildlife for urban consumption. Thus, further studies should investigate how wild meat harvests and demand are changing with development and urbanisation. Studies could include the contribution of wildlife to food security, livelihoods, and zoonotic disease transmission. For example, studies recording the consumption of wildlife could easily be included in my database, which would allow urban and rural consumption to be tracked. Using data already in the database, it would be possible to investigate what proportions of wildlife are sold or consumed in different scenarios to better understand the importance of wildlife to local livelihoods and diets.

7.3.3 Defaunation

This thesis facilitates the study of defaunation by first identifying which species are hunted and sold in Africa (Chapter 2), are therefore under some level of hunting pressure and are thus candidates for hunting-induced defaunation. If we can understand the hunting thresholds (i.e. quantities harvested) that cause declines in different species groups, we may be able to use hunting studies to identify areas with potentially high defaunation risk. Chapter 3 takes steps towards identifying areas where harvests are likely to be high within Central Africa.

By investigating how the body mass and taxonomic composition of the wildlife harvested changes over time and across a gradient of accessibility to humans could be used to identify areas of defaunation, which I demonstrate in Chapter 5. These analyses showed large-bodied mammals may have already declined in the most accessible areas. If information is known on the past hunting history of some of these areas, they could be used to monitor the response of the ecosystem (e.g. floral composition) to defaunation, and cascading effects (e.g. carbon storage). For example, in some areas, one may know the length of time that an area has been hunted and the intensity of hunting. If surveys of the floral composition are conducted in these areas, it would allow for the comparison of the stages of defaunation in ecologically similar areas, and investigate changes in aboveground biomass and thus carbon storage (e.g. Peres et al. 2016). Identifying the stages of defaunation are important for understanding the levels at which ecosystems can withstand different levels of hunting. Together, the results from these chapters enable researchers to target their efforts in future studies investigating the consequences of defaunation of specific taxa or at particular locations.

Reviews on the consequences of defaunation are available (Young et al. 2016), but studies often focus on seed dispersers and large vertebrates (Effiom et al. 2013; Galetti et al. 2013; Peres et al. 2016). Attention should be paid to understanding the sustainability of harvesting smaller-bodied species and the potential ecological consequences of their decline, which has yet received little research attention. Further studies are also needed that identify the effects of defaunation within and between populations, and in the wider ecosystem context. Moreover, indicators need to be developed that identify areas at risk of defaunation from hunting, and where interventions may be developed with hunting communities.

7.4 Concluding remarks

Here, I demonstrated that the wealth of data collected over the past decades on the harvest and sale of wildlife can be used to go beyond site-level information and investigate trends and patterns in the exploitation of wildlife across large areas. Using data on African wildlife exploitation as a case study, I have highlighted the potential that such a database and analyses have for informing conservation policies and actions.

“*What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions*”

Daniel Janzen, 1974

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Appendix

Assessing Africa-wide pangolin exploitation by scaling local data

Text S1. Estimating total catch of pangolins in Central Africa

We calculated the sample-specific annual number of pangolins hunted per km2 by dividing the number of pangolins hunted by sample duration, number of hunters surveyed, and sample hunting territory area, and then multiplied this by the sample estimate of the total number of hunters and 365 days. Information on the total number of hunters and total human population at each site were extracted from the literature. To extrapolate across the Central African forests, we calculated an estimate of the likely hunted area. The likely hunted area was assumed to be a buffer with 10km radius around each settlement (as shown in Abernethy et al. 2013; Koerner et al. 2016), and overlapping buffers were merged so that they were not included multiple times. We used settlement data from national population censuses collected between 2010 and 2013 and clipped the area of Central African forests within the pangolin distribution, by the likely hunted area. We also calculated the sample-specific annual number of pangolins hunted per rural person by dividing the number of pangolins hunted by sample duration and number of hunters surveyed, and then multiplied this by the sample estimate of the ratio of total hunters to the site population (i.e. total hunters divided by population at the site) and by 365 days. This assumes no seasonality in hunting, although seasonality in the hunt has been observed at some sites (e.g.Coad 2007) but not others (e.g. Kümpel 2006; Ampolo and Bikouya 2008). Information on hunting seasons is not commonly available from published sources or authors, and hunting seasons may not coincide with climatic seasons. Studies included in our analyses may either cross multiple seasons, or are conducted in the dry or wet seasons. As data are weighted by sample size in our analyses, shorter studies that may have sampled during one season only are given lower weighting than longer studies covering multiple seasons.

The total rural population in Central African forests was estimated using two methods. Firstly, it was estimated as 20% (following Wilkie & Carpenter 1999) of the United Nations Population Division rural population estimates (UNPD 2014) for each of the six

Central African countries. Secondly, we estimated rural population by clipping the Global Rural-Urban Mapping Project (GRUMP) population count layer for 2000 (Balk et al. 2006; CIESIN et al. 2011) by the six Central African countries (Cameroon, Central African Republic, Congo Republic, Democratic Republic of Congo, Equatorial Guinea, and Gabon) by the 'best estimate' hybrid forest map where 1km grid cells were included that contained at least 50% forest (Figure S1; Schepaschenko et al. 2015) using ArcGIS version 10.0 (ESRI 2011), and by the extent of occurrence of P. tetradactyla (IUCN 2014) to represent the overlapping occurrences of the three species of pangolin occurring in Central African forests and to remove the southern forests that are not within the extent of occurrence for two of the pangolin species. Grid cells with > 10,000 people per km2 were excluded to remove large cities.

Text S2. Static forest area and human population in 2000

We used static estimates of forest area and human population in 2000 because forest area in Central Africa has not changed substantially between 2000 and 2012 in comparison to other continents (Hansen et al. 2013; Malhi et al. 2013), and accurate population changes for the rural populations living in the Central African forests is limited.

Text S3. Trends in body mass and sample duration

We assigned each individual the species-specific body mass from Myhrvold et al. (2015), or, for those individuals not identified to species, the mean body mass of the African members of a genus or family. A change in the percentage of pangolins hunted or sold over time could reflect wider changes in the average size of species caught/sold (Ingram et al. 2015), as opposed to the specific targeting of pangolins. We therefore investigated changes in the percentage of all vertebrates weighing <3 kg (the upper body mass of arboreal pangolins, Phataginus sp.) in the catch or sold at market over time. We fitted the percentage of vertebrates weighing <3 kg as the response variable, using the same model structure and predictor variables as the pangolin percentage model (see Methods: Trends in pangolins hunted and at market). Furthermore, samples with shorter durations could result in higher observed proportions of pangolins if pangolins are rare at a site but happen to be caught in the short duration. Using the same method as above, we tested this by fitting sample duration as a response variable in a linear mixed effects model. We found that neither the percentage of animals in the catch weighing less than 3 kg ($\chi^2$4,5 = 0.8, p = 0.370) nor the sample duration changed significantly over time ($\chi^2$5,6 = 2.3, p = 0.131).

Text S4. Trends in accessibility

We extracted data for each site on the travel time to major cities with a population of at least 50,000 people, hereafter ‘accessibility’ (Nelson 2008). We fitted a linear mixed effects model to the hunting data as described in the Methods (subsection: Trends in pangolins hunted and observed at market’) and included accessibility as a fixed effect. We found that year remained significant ($\chi^2$6,7 = 7.2, p = 0.007), and that the proportion of pangolins hunted was significantly higher in the most accessible areas ($\chi^2$6,7 = 4.8, p = 0.028).

Text S5. Trends in different periods of time

The trends we observe could be an artefact of few early studies. We therefore tested whether significant effects of year remain when splitting the data into two time periods for which we have the most data (1990 – 2000 and 2000 - 2015). We re-ran the models for the hunting samples for the two time periods as described in the Methods (subsection: Trends in pangolins hunted and observed at market’). We found that there was a significant effect of year for both time periods (1990 - 2000: n = 31, $\chi^2$5,6 = 10.0, p = 0.002; 2000 – 2015: n = 107, $\chi^2$5,6 = 7.1, p = 0.008).

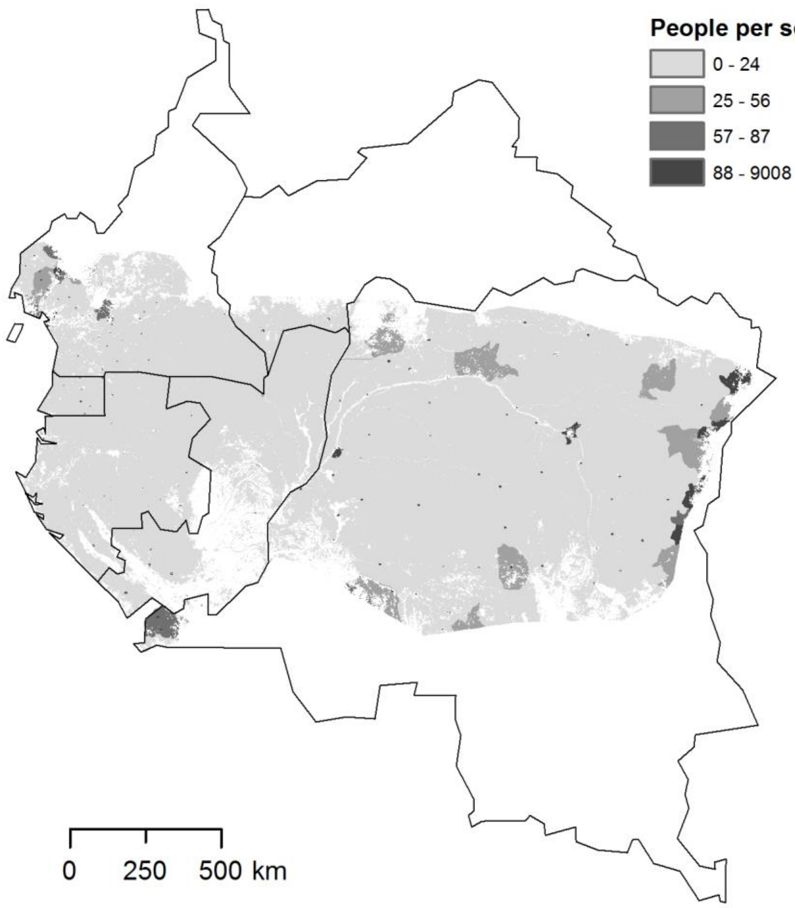

Figure S1. Human population density (Balk et al. 2006; CIESIN et al. 2011) in Central Africa (Cameroon, Central African Republic, Equatorial Guinea, Gabon, Democratic Republic of Congo, Republic of Congo) classified into groups by standard deviation, and clipped by forest distribution (Schepaschenko et al. 2015) and pangolin extent of occurrence (IUCN 2014).

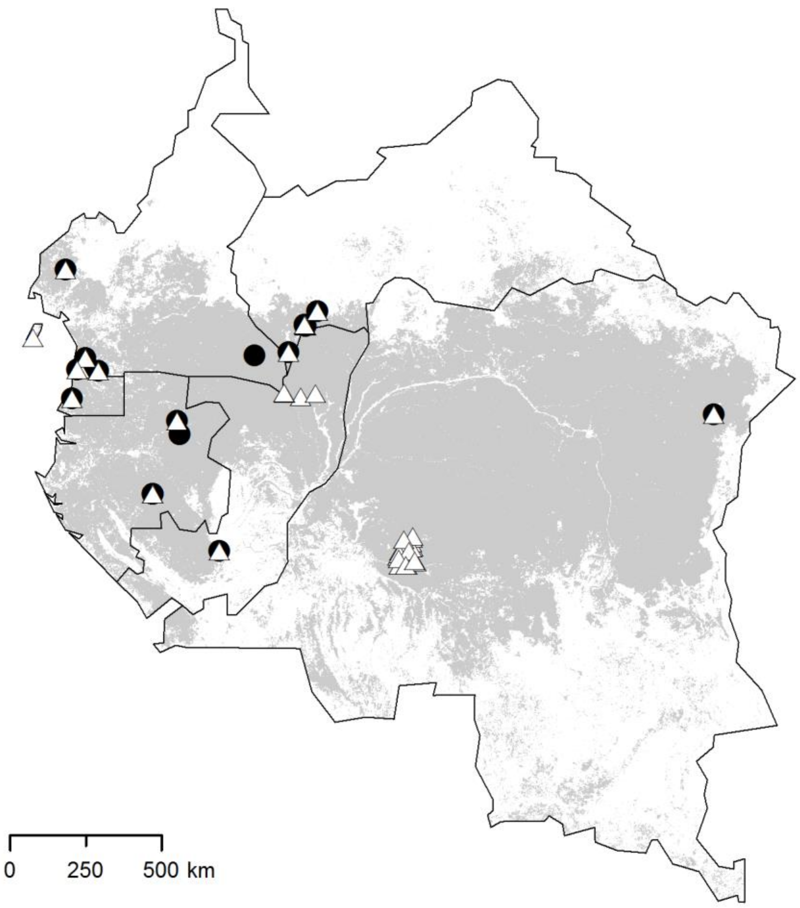

Figure S2. Studies with information on hunters and rural human population (white triangles) and hunter territory size (black circles) mapped on top of forest area (grey shading; Schepaschenko et al. 2015) in Central Africa.

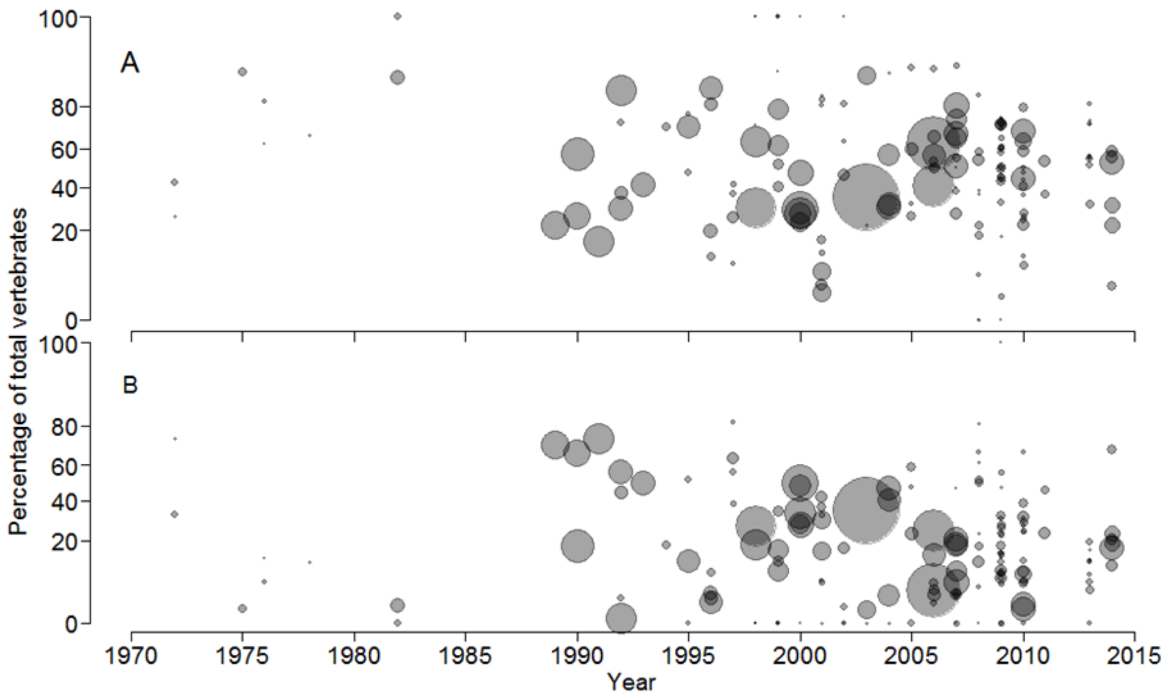

Figure S3. Trends in the percentage of vertebrates that were Cetartiodactyla (A) and Rodentia (B) in the catch over time across Africa. Samples shown as translucent points to show density of samples, and are scaled by total catch of individual vertebrates. There was no significant effect of year on the percentage of vertebrates that were Cetartiodactyla (χ5,6 = 2.56, p = 0.11) or Rodentia (χ5,6 = 0.11, p = 0.74).

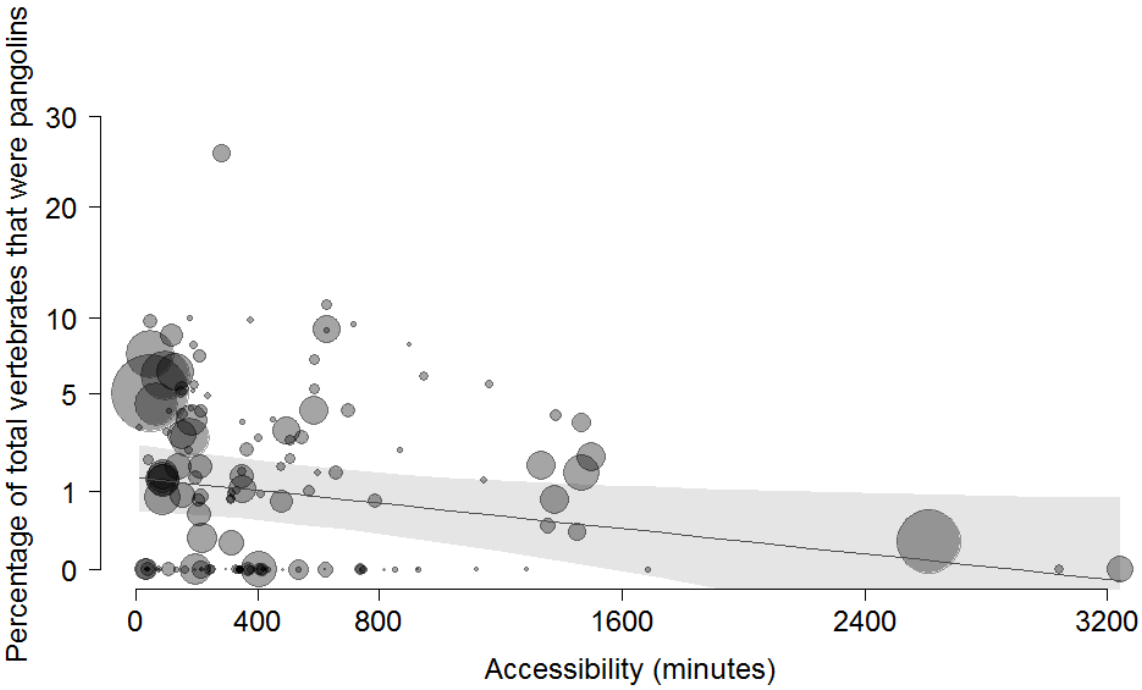

Figure S4. The percentage of vertebrates that were pangolins in the catch related to accessibility. Accessibility is the travel time (minutes) to the nearest major city with a human population ≤50,000 people (Nelson 2008). Samples shown as translucent points to show density of samples, and are scaled by total catch of individual vertebrates. Significant trend line (likelihood ratio test: $\chi^2$6,7 = 4.8, p = 0.028) and 95% CI (shading) fitted using a linear mixed effects model.

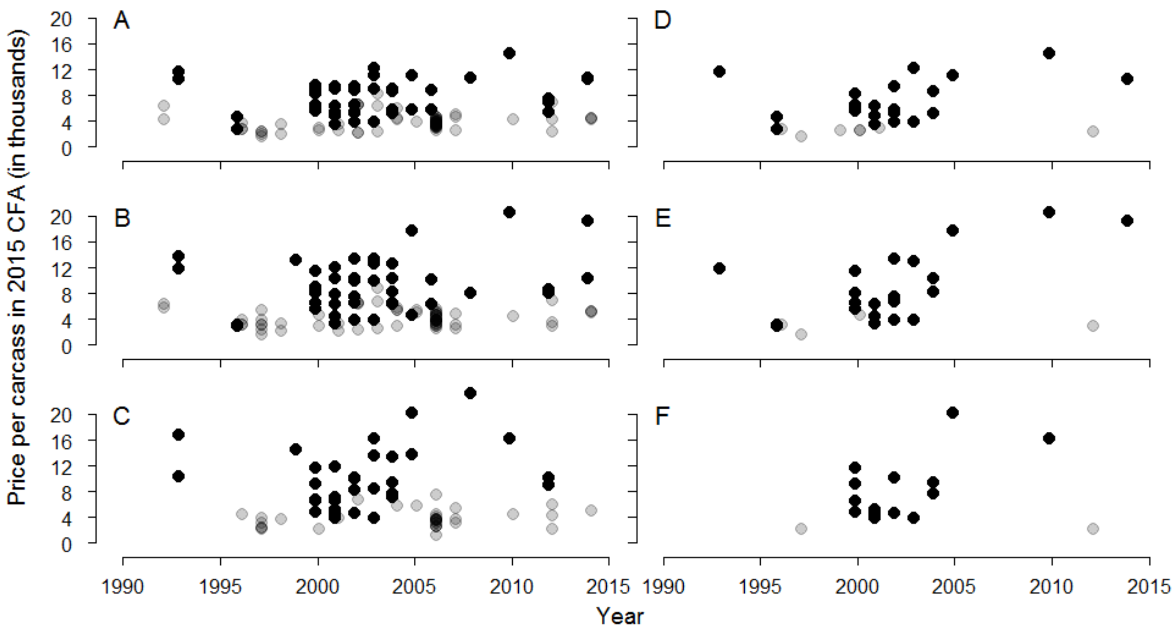

Figure S5. Trends in prices of blue duikers (A,D), brush-tailed porcupines (B,E), and cane rats (C,F) from studies that also contained data on arboreal pangolins (A-C) or giant ground pangolins (D-F) at urban (black points) and rural (grey points) markets. Prices are in 1000 Central African Francs (CFA) adjusted to 2015 prices using the Consumer Price Index (The World Bank 2017).

Table S1. Sources used in analyses and the countries in which data were collected. Crosses (X) indicate the analyses in which a data source was included.

Reference	Country	Hunting / Market	Price	Area-based estimate	Population -based estimates
Abernethy et al. 2010	Democratic Republic of Congo	X			X
Abernethy & Ndong Obiang 2010	Gabon		X		
Abugiche 2008	Cameroon	X	X	X	X
Allebone-webb 2009	Equatorial Guinea		X		
Ampolo & Bikouya 2008	Congo Republic	X			
Amubode 1995	Nigeria	X			
Anadu et al. 1988	Nigeria	X			
Blake 1993	Congo Republic	X			
Bobo et al. 2015	Cameroon	X			
Bolle 2001	Cameroon	X			
Carpaneto et al. 2007	Gabon		X		
CIFOR/CIRAD/FAO (Unpublished)	Congo Republic, DRC, Gabon	X	X	X	X
Coad 2007	Gabon	X	X	X	X
Colell et al. 1994	Equatorial Guinea	X			X
Cowlishaw et al. 2005	Ghana	X			
Cronin et al. 2015	Equatorial Guinea	X			
Dame Mouakoale 2012	Cameroon		X		
Dethier & Ghuirghi 2000	Central African Republic	X		X	X
Dounias 1993	Cameroon	X		X	X
East et al. 2005	Equatorial Guinea		X		
Eves & Ruggiero 2000	Congo Republic		X		
Fa & Yuste 2001	Equatorial Guinea	X			
Falconer 1992	Ghana	X			
Fargeot 2010	Central African Republic	X	X	X	X

Fimbel et al. 2000	Cameroon	X		X	
Foerster et al. 2012	Gabon		X		
Fusari & Carpaneto 2006	Mozambique	X			
Gandiwa et al. 2013	Zimbabwe	X			
Gill 2010	Equatorial Guinea	X	X	X	X
Greengrass 2011	Liberia	X			
Hayashi 2008	Cameroon	X			
Hennessey & Rogers 2008	Congo Republic	X			
Hitchcock et al. 1996	Botswana	X			
Hofer et al. 1996	Tanzania	X			
Holmern et al. 2002	Tanzania	X			
Ichikawa 1983	Democratic Republic of Congo	X		X	X
Jeffrey 1977	Liberia	X			
Kakeya 1976	Tanzania	X			
Kamgaing 2011	Cameroon	X	X		
Kitanishi 1995	Congo Republic	X			
Kümpel 2006	Equatorial Guinea	X	X		
Laurent 1992	Cameroon		X		
MacDonald et al. 2011	Cameroon		X		
Martin 1983	Nigeria	X			
Mbete et al. 2010	Congo Republic	X			
Mbete 2012	Congo Republic		X		
Meli et al. 2012	Cameroon		X		
Mockrin et al. 2011	Congo Republic	X			
Ngueguim 2001	Cameroon	X		X	X
Nguetsop 2001	Cameroon	X		X	X
Nielsen 2006	Tanzania	X			
Nielsen & Treue 2012	Tanzania	X			
Noss 1998	Central African Republic	X		X	X
Okiwelu et al. 2009	Nigeria	X			

Okiwelu et al. 2010	Nigeria				
Okorie & Ekechukwu 2004	Nigeria	X			
Okouyi Okouyi 2006	Gabon	X	X		
Olupot et al. 2009	Uganda	X			
Ondo née Ntyam 2001	Cameroon	X			
Ondo Obiang 2001	Cameroon	X	X	X	X
Osaki 1984	Botswana	X			
Pollard 1997	Cameroon		X		
Poulsen et al. 2009	Congo Republic		X		
Puit et al. 2004	Equatorial Guinea	X			
Rieu 2004	Central African Republic	X			
Rieu 2005	Central African Republic		X		
Schleicher 2010	Gabon	X			
Seino et al. 1995	Cameroon	X			
Solly 2003	Cameroon	X	X		
Steel 1994	Gabon	X	X		
Steel et al. 2008	Democratic Republic of Congo				
Swensson 2005	Ghana	X			
Tee et al. 2012	Nigeria	X			
Thibault & Blaney 2003	Gabon	X			
Tieguhong & Zwolinski 2009	Cameroon		X		
van Vliet 2008	Gabon	X		X	
Vanwijnsberghe 1996	Congo Republic		X		
Vath 2014	Nigeria	X			
Whitham 2009	Ghana	X			
Willcox & Nambu 2007	Cameroon		X		
Ntiamoa-Baidu 1998	Ghana	X			
Wilkie 1987	Democratic Republic of Congo	X			

Wilkie et al. 2000	Congo Republic	X			X
Wright & Priston 2010	Cameroon		X		
Yasouka 2006	Cameroon	X			
Zouya Mimbang 1998	Cameroon		X		

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