GENETICS, EVOLUTION
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Model-based approaches to understanding wild meat harvesting in Central Africa: uncertainty, yields and ecosystem impacts

A thesis submitted in partial fulfilment of the requirements for the degree of:

Doctor of Philosophy

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I, Tatsiana Barychka, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

The current levels of bushmeat harvesting, combined with other human-made pressures, are likely to drive many African species to extinction and disrupt ecological processes. However, reliably predicting what the appropriate harvesting levels might be is a challenge. Existing methods for assessing sustainability of harvesting rely heavily on species observational data, despite the widely-recognised limitations (such as geographical and taxonomic biases) of these data. In addition, population models can be employed; however, these necessitate parameter estimates which are often lacking. This thesis investigates new model-based approaches to overcoming these data and modelling limitations, in particular, high parameter uncertainty and simplistic population models which ignore many of ecological complexities (such as multi-trophic interactions).

The first two chapters investigate proportional and quota-based harvesting in single-species population models of duiker antelope, but extended to include (1) an explicit consideration of parameter uncertainty, which revealed a trade-off between yield and population survival probability not apparent when ignoring uncertainty; and (2) model-based adaptive harvesting, which was predicted to increase yields and survival, particularly when combined with parameter updating.

Chapters 3 and 4 employ the Madingley General Ecosystem Model, which can simulate a wide range of scenarios without any species-specific data. The Madingley Model predictions for duiker harvesting were similar to those from the single-species model, but the Madingley could also predict (1) wider ecosystem impacts of duiker harvesting (which were minimal); (2) yields and impacts for multiple species harvesting (both yields and impacts were greater than for duiker, with large reductions in target functional groups and increases in smaller-bodied animals); and (3) variation in yield and impacts among ecosystems (yields varied by a factor of ten; impacts varied quantitatively, but not qualitatively).

These findings highlight the potential value of model-based approaches for informing bushmeat harvesting policies, given existing limitations in data and systems understanding.

Impact Statement

This work advances new theoretical approaches for a more robust assessment of the sustainability of bushmeat harvesting. I develop a method for combining data on harvested species in a risk-based decision-making framework. The implementation of this methodology in bushmeat management could, by identifying the likelihood of desired yields for a given level of threat to species survival, help reduce the occurrence of animal extinctions while ensuring that meat yields are sustained at required levels. This work also identified the combination of harvesting policy and decision-makers' attitude to risk where field-based research could bring about the greatest improvements in yield and species survival probability. By comparing possible management strategies in silico, i.e. before money and time are spent in the field, this work highlighted the potential of model-based approaches for optimising management outcomes under the condition of limited operational resources – a line of academic enquiry that is often overlooked. Duiker antelope is the most heavily hunted species in sub-Saharan Africa contributing 34-95% of all bushmeat captured in the Congo Basin. This work also contains the most comprehensive list, to my knowledge, of population parameter estimates for three duiker *Cephalophus* spp. (*C.callipygus, C.dorsalis* and *C.monticola*), which could be used in further academic enquiry, and to inform harvesting decisions on the ground.

This was also the first attempt to investigate whether the novel General Ecosystem Madingley Model could produce adequate harvesting recommendations for animals currently hunted in sub-Saharan Africa. This investigation suggests the Madingley Model is robust enough to support decisions in harvesting, and to help fill-in the large data gaps (including extrapolating to under-sampled species) and the vital gaps in understanding of ecology, such as the relationships between climate and ecosystem-level responses to human-made perturbations. Although the Madingley Model is still in its infancy, with further validation and data, this work points towards exciting new opportunities for future uses of general ecosystem models, both in academia (e.g. to explore the effects of climate change on ecosystem functioning) and in industry (e.g. in fisheries and bushmeat management).

To better illustrate and communicate the impact of data limitations on the predictability of harvesting outcomes, I developed two interactive online applications: one for duiker antelope harvesting (https://tinyurl.com/duikerantelope) and another, following a collaboration with a scientist from the Brazilian National Marine Biodiversity Research Centre, for exploitation of blue sharks (http://tinyurl.com/blue-sharks). With further modifications, such as adding demand-side inputs, these interactive online applications could be used to inform management decisions.

I have presented my work to a wide audience, from UCL conferences, to broader national and international conferences (e.g. British Ecological Society Annual Meeting in 2018). During my visit to the University of Queensland, Australia, I presented some of my early Madingley results, which helped extend the knowledge of the Madingley Model further afield. I am currently writing a paper due for submission at the high-impact peer-reviewed journal of “PLOS One”, to disseminate my findings and to promote the use of model-based approaches in bushmeat research and management.

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Chapter 1 Introduction

The Bushmeat Problem

Present levels of wild animal harvesting are believed to be a major threat to survival for over half of the 178 species currently hunted in Central Africa (Abernethy *et al.*, 2013). Declining animal abundances and potential loss of species will detrimentally affect biological diversity and ecosystem integrity (Abernethy *et al.,* 2013; Hooper *et al.,* 2005), as well as the livelihoods and wellbeing of human population relying on meat from wild animals (or bushmeat) for cash income and additional protein (Nasi, Taber and Van Vliet, 2011; Golden *et al.,* 2011; Njiforti, 1996; Davies and Brown, 2008; Foerster *et al.,* 2011). The need to deal with these threats has been recognised nationally (Hurst, 2007) and internationally (*Aichi Target 4: Sustainable Consumption and Production and use of natural resources*; CBD, 2010). However, policy and conservation interventions in sub-Saharan Africa have had limited success, mainly due to the complex socioeconomic and political climate in the region (Bennett *et al.,* 2007; Davies and Brown, 2008), as well as the difficulty in reliably estimating sustainable harvest rates for bushmeat species (van Vliet and Nasi, 2008).

Bushmeat harvesting is an essential source of food and income for many poor rural communities in sub-Saharan Africa (Milner-Gulland and Bennett, 2003; Davies and Brown, 2008; Fa, Currie and Meeuwig, 2003). The demand for bushmeat is being spurred by rising human population (Fa, Currie and Meeuwig, 2003), rural poverty (Brashares, 2003; de Merode, Homewood and Cowlishaw, 2004), a lack of diversified employment opportunities in rural areas (Nielsen, Jacobsen and Thorsen, 2014), limited availability of affordable, alternative protein sources (Foerster *et al.,* 2011; Otte and Chilonda, 2002), opening up of remote areas due to logging, mining and agriculture (Rudel, 2013), increasing use of firearms for hunting (Coad *et al.,* 2013) and cultural preferences for bushmeat (Njiforti, 1996). Dependence on free meat from the forest is particularly strong for the rural poor, and without practical and affordable alternatives to bushmeat, political will to curb its consumption on both national and local levels is not strong (Brown, 2007).

Socioeconomic Factors

Success of any conservation or policy interventions aimed at managing bushmeat offtakes is predetermined by a good understanding of the formal and informal institutions that determine the behaviour within bushmeat communities (Hurst, 2007). Bushmeat harvesting is embedded within complex socioeconomic and political structures (such as relationships between local and regional market players, and between state actors at the local and regional levels). The importance of these socioeconomic structures for successful bushmeat interventions is slowly being recognised by organisations tasked with governance of bushmeat exploitation. Traditional activities aimed at reducing bushmeat exploitation (such as fences and fines) by excluding the people, who depend heavily on wildlife and forest plants for food, from use of these resources, without providing them with alternatives (Brandon and Wells, 1992), are being replaced with community-based initiatives, which aim to involve and benefit local communities (Nielsen, 2006; Hurst, 2007). However, even these initiatives generally fail to correctly account for the existing socioeconomic structures (Hurst, 2007). In addition, conservation interventions are often developed outside the national governance (often, by international non-governmental organisations), which further undermines the effectiveness of bushmeat-related interventions (Hurst, 2007; Bennett *et al.,* 2007; Brown, 2007).

Even if the right socioeconomic structures are in place (e.g. Vermeulen *et al.,* 2009; Vaughan and Long, 2007), there still remains an issue due to a poor ability to estimate sustainable yields (Milner-Gulland and Bennett, 2003). In fact, the remoteness and technical difficulty of many approaches removes them from the communities who should be involved in setting quotas and enforcing them. Such community exclusion further reinforces the weak governance and ineffective local actions.

The Data Limitation Problem

A key problem with current quantitative methods for assessing sustainability of harvesting in terrestrial ecosystems is the reliance on species monitoring data, such as estimates of population parameters (e.g. Robinson and Bennett, 2004), animal abundances (e.g. Van Vliet *et al.,* 2007) and harvest offtakes over time (e.g.

Albrechtsen *et al.,* 2007). Obtaining systematic and reliable biological estimates in tropical forests requires substantial time and resources which are rarely available (Coad *et al.,* 2013). As a result, the data is limited to a small share of total species present in a few locations visited during a short field season. Lack of well-resolved (spatially, temporally, taxonomically) data and biases in parameter estimation (geographical, observation, detection, reporting; van Strien, van Swaay and Termaat, 2013), combined with natural variability common in complex tropical ecosystems, make reliable assessments of sustainability of harvesting problematic (van Vliet and Nasi, 2008; Milner-Gulland and Akçakaya, 2001). Where available, empirical estimates are also associated with large margins of error due to spatial and temporal variation, differences in data collection techniques, observation error and differences in methods used to produce population estimates (van Vliet and Nasi, 2008).

To deal with scarcity of data and large variability in population estimates, a number of indices used to assess sustainability of harvesting and to predict species-specific sustainable harvest rates have been developed (e.g. Robinson and Redford’s Index; Robinson and Redford, 1991). These indices involve an estimation of sustainable levels of production of harvested populations (based on field estimates of populations’ density and rates of increase) which can then be compared with actual data on animal offtakes (Milner-Gulland and Akçakaya, 2001). Because of their relative simplicity and availability of parameter estimates, some of these indices, in particular Robinson and Redford method, are widely used in the field for assessing bushmeat harvesting sustainability (Milner-Gulland and Akçakaya, 2001). However, because of the data limitations described above, parameter estimates used in these indices could be widely inaccurate. But the extent of these potential inaccuracies is often ignored in estimates of sustainable harvest rates (Frederick and Peterman, 1995; Sainsbury, 1991).

Where the problem of uncertainty is recognised, it is recommended that the rates of bushmeat harvesting are adjusted downwards to account for the fact that offtake levels could be underestimated and/or population sizes could be overestimated, i.e. a precautionary approach to uncertainty is expected to be followed (Milner-Gulland and Akçakaya, 2001). However, demand for bushmeat in the tropics is on the rise as human population increases (Milner-Gulland and Bennett, 2003). An alternative to curtailing offtakes until more is known about the harvested species has been advanced and is known as adaptive management approach (Holling, 1978; Walters, 1986). The key elements of adaptive management: constant monitoring of system's responses to management, iterative adjustments of management strategies, and development and implementation of alternative strategies – have the potential to deliver sustainable harvesting in highly uncertain systems such as pertain to bushmeat (Keith *et al.,* 2011; Probert *et al.,* 2011; Chadès *et al.,* 2017). Importantly for bushmeat, adaptive management does not require cessation or curtailment of management activities; instead, management is implemented in the face of uncertainty and is used to collect data about the system and its responses to management at the appropriate spatio-temporal scale, reducing uncertainty about the system over time (Probert *et al.,* 2011; Walters 1986; McCarthy and Possingham 2007).

In recent years, there have been a number of successful international initiatives to combine and open-source scattered data on terrestrial animals (Taylor *et al.,* 2015; Hudson *et al.,* 2014; Santini, Isaac and Ficetola, 2018). Combining data from various sources (e.g. Living Planet Index, Loh and Wackernagel, 2004; the IUCN Red List, Mace and Lande, 1991) or different individual sites over time could be useful for assessing general trends in the absence of comprehensive indicators of exploitation (Tierney *et al.,* 2014; Ingram *et al.,* 2015). However, for many of the exploited species in sub-Saharan Africa, the data is still scarce or non-existent.

Recent advances in data collection such as camera trapping (Rowcliffe *et al.,* 2008), drone technology (Koh and Wich, 2012), mobile phone applications (Vatresia *et al.*, 2016), satellite imagery (Turner *et al.*, 2015), citizen science projects (Kwok, 2009; van Strien, van Swaay and Termaat, 2013; Isaac *et al.*, 2014; Barlow *et al.*, 2015; Kretser *et al.*, 2015; Parham, Berger-Wolf and Rubenstein, 2017), online databases (e.g. iRecord, https://www.brc.ac.uk/irecord/) and locally-based monitoring (Rist *et al.,* 2010) have the potential to fill-in some of these knowledge gaps. However, with limited conservation resources, this will un-doubtfully take some time, even for the most abundant and / or iconic species.

The Lack of Understanding Problem

In addition to the data limitation problem described above, the ability of bushmeat harvesting experts and conservationists to model harvesting dynamics is hampered by an imperfect understanding of the complex ecosystems and the ability to simulate them (Milner-Gulland and Bennett, 2003). Most models used in terrestrial harvesting leave out trophic interactions (such as predation and competition) and environmental conditions, i.e. they do not represent the natural variability observed in real systems that may influence longer-term sustainability. Furthermore, most estimates of sustainable bushmeat harvesting also assume harvesting which is constant over time, i.e. methods used to estimate sustainable harvest rates do not account for likely animal fluctuations or changes in demand over time. Models that attempt to account for multi-species interactions in harvesting are limited to fisheries management (Frank *et al.*, 2005), where these relationships are described more explicitly than in terrestrial ecosystems (Ingram *et al.,* 2015). A number of more sophisticated end-to-end modelling frameworks, which incorporate multi-trophic interactions, climate and nutrient flows, as well as the socioeconomic and ecosystem feedbacks, have been developed in marine harvesting (Fulton *et al.,* 2011; Christensen and Walters, 2004). These modelling frameworks (Ecopath with Ecosim, Christensen and Walters, 2004; Atlantis, Fulton *et al.*, 2011) have been used to develop complex multi-trophic models of marine ecosystems (about 130 Ecopath with Ecosim models have been published; Travers *et al.*, 2007). However, currently these models require an extensive knowledge of a modelled ecosystem (such as detailed knowledge of ecosystem structure and functioning). So their application is constrained to a few well-studied marine ecosystems, mainly in the developed world (e.g. Link, Fulton and Gamble, 2010).

A number of terrestrial ecosystem models combining the understanding of multi-trophic interactions and of biophysical systems (climate, nutrient flows, ecological processes) have been attempted (desert, Goodall, 1975; freshwater, Metzgar *et al.*, 2013); however, these were biome-specific, and none of these terrestrial models have been used for decision-making in practice (Patten, 2013).

This Thesis

In this thesis, I attempt to address some of the data and modelling limitations as pertain to bushmeat harvesting in sub-Saharan Africa, focusing on how new and emerging statistical, analytical and computational tools, along with data gathering technologies might contribute to better tools for managers and decision-makers.

In Chapter 2, I begin by introducing large parameter uncertainty to a simple single-species model of bushmeat harvesting, where uncertainty has been explicitly parameterised from empirical studies of three duiker *Cephalophus* species (*C. callipygus*, *C.dorsalis* and *C.monticola*). In this Chapter, I set out to examine if and how including parameter uncertainty (population growth rate and carrying capacity) and small environmental stochasticity might alter our view of sustainable harvesting for these heavily hunted, and comparatively well-studied, antelope species in sub-Saharan tropical forest.

In Chapter 3, I replace the simple constant harvesting used in Chapter 2 by a more sophisticated adaptive harvesting approach (Walters, 1986) (harvest rate changes between years depending on previous year’s harvesting outcome) applied to one of the three duiker species. I implement it for a number of harvesting strategies with and without uncertainty on population growth rate and carrying capacity. The aim is to identify, in silico, the conditions under which adaptive harvesting outperforms constant harvesting, and which of the adaptive harvesting strategies would be the most beneficial in terms of expected yields and duiker survival rate.

In Chapter 4, I step away from population biology and parameter-driven models; instead, I use the Madingley General Ecosystem Model (Harfoot *et al.,* 2014), hereafter called the Madingley Model, which uses fundamental ecological processes (primary production for autotrophs, and eating, metabolism, growth, reproduction, dispersal, and mortality for heterotrophs). The aim of this Chapter is to explore whether a complex ecosystem model such as the Madingley Model is sufficient to inform harvesting policies, and if so, what can it tell bushmeat harvesting practitioners about sustainable harvesting of bushmeat and about the potential effects of harvesting on ecological communities in a tropical forest ecosystem. I begin with the validation, comparing estimates of yield and survival probability for duiker-sized herbivores from the Madingley Model with the single-species model's estimates for duiker antelope harvesting. I then use the Madingley Model to explore multiple species harvesting dynamics and ecosystem-level impacts of harvesting (neither experiments are currently possible with any other method). Although the Madingley Model ignores organisms' taxonomic identity, unlike conventional population models, it can provide additional information about ecosystem-level impacts of harvesting, in data-deficient locations, under present and future levels of human-made perturbations (such as climate change).

In Chapter 5, I take the analysis outside of both particular species (as in Chapter 2 and 3) and specific ecosystems (as in Chapter 4) and use the Madingley to model harvesting across seven ecosystem types, focusing on the potential role of ecosystem structure and its capacity to support sustainable bushmeat harvesting (e.g. bushmeat yields and species survival rates), as modelled by the Madingley Model. Building upon Chapter 4, I explore variation in bushmeat yields and organisms resilience to harvesting in different ecosystem types, investigating how different levels of harvesting vary in their effects on structure and functioning in seven different ecosystem types.

This thesis aims to make theoretical advancements in the two problem areas of predictive modelling described above: data limitations and modelling limitations, which could inform practical conservation in bushmeat harvesting in sub-Saharan Africa. The single-species modelling approaches explored in Chapters 2 and 3 are very different from the general ecosystem modelling approach explored in Chapters 4 and 5. But these approaches are potentially complementary - a topic I return to in the Final Discussion.

Chapter 2 Optimal wild meat harvesting under parameter uncertainty using a single-species population model

Abstract

Reliably predicting sustainable exploitation levels for many tropical species subject to hunting remains a difficult task, largely because of the inherent uncertainty associated with estimating parameters related to both population dynamics and hunting pressure. Here, I investigate a modelling approach to support decisions in bushmeat management which explicitly considers parameter uncertainty. I apply the approach to duiker *Cephalophus* spp., assuming either a constant quota-based, or a constant proportional harvesting, strategy. Within each strategy, I evaluate different hunting levels in terms of both average yield and survival probability, over different time horizons, and under different attitudes to risk on the part of the decision maker (risk averse, risk taking, risk neutral). Under quota-based harvesting, which is widely used in practice, the optimum quota was sensitive to a trade-off between yield and extinction probability: the highest yield was returned by a quota that implied a 40% extinction risk, whereas limiting extinction risk to 10% reduced yield by 70-80%. The optimum quota was also sensitive to risk attitude. This sensitivity to harvesting decisions under quota-based management was due to high proportion of extinct populations under the condition of parameter uncertainty, particularly close to the optimum. By contrast, under proportional harvesting, there was no trade-off between yield and extinction probability, and the optimum proportion was not sensitive to risk attitude. The optimum proportion returned a yield greater than the maximum possible under quota-based harvesting, but with extinction risk below 10%. However, proportional harvesting is considered much harder to implement in practice. The analysis shows how an explicit consideration of all available information, including uncertainty, can, as part of a wider process involving multiple stakeholders, help inform harvesting policies.

2.1 Introduction

Many studies raise alarm over the present rate of wild meat harvesting as a major cause of population decline and extinction risk for many species (Fa *et al.,* 2016; Hoffmann *et al.,* 2010; Noss, 2000). With wild meat providing a major source of protein and household income to some of the world's poorest people (Barnes, 2002; de Merode, Homewood and Cowlishaw, 2004; Milner-Gulland and Bennett, 2003), both subsistence and commercial hunting in West and Central Africa are on the rise (Fa *et al.,* 2016; Milner-Gulland and Bennett, 2003; Ingram *et al.,* 2015). Bushmeat harvest across the Congo Basin alone is estimated to occur at more than six times the sustainable harvest rate (Fa *et al.,* 2016).

However, reliably estimating a sustainable harvest level remains problematic. Ecological systems are highly complex and the relevant biological data on mammals in tropical forests is scarce (Taylor *et al.,* 2015). Information is often collected during short field seasons (Payne, 1992; Wilkie and Finn, 1990; Noss, 1998), across different spatial scales and in different ecosystems (Schmidt, 1983; Noss, 1998), producing point estimates of population parameters and species abundances that vary considerably between studies (Milner-Gulland and Akçakaya, 2001; van Vliet and Nasi, 2008). As a result, traditional techniques such as monitoring offtakes and correlating them with changes in harvested species dynamics such as abundance and age structure (Leeuwenberg and Robinson, 2000; Milner-Gulland and Akçakaya, 2001) struggle to accurately assess the sustainability of harvesting. To address this problem, a number of sustainability indices have been developed ranging from the relatively simple Robinson and Redford's index (Redford and Robinson, 1991) to the more sophisticated Bayesian techniques used in fisheries (Meyer and Millar, 1999; McAllister and Ianelli, 1997). Instead of using time-series data on animal densities and offtakes, these indices require as inputs point estimates of populations' carrying capacity and rate of population growth. This allows an estimation of sustainable levels of production of harvested populations (Milner-Gulland and Akçakaya, 2001) which can then be compared with actual data on animal offtakes. However, once again, to be effective most sustainability indices require accurate estimates of population parameters (Milner-Gulland and Akçakaya, 2001). As these estimates vary considerably between studies (for example, Van Vliet and Nasi (2008) demonstrated a four times difference in estimates of population growth rates for *Cephalophus monticola* from two methods), true parameter values are unknown, and sustainable harvest levels are often based on point estimates, effectively ignoring any uncertainty (Frederick and Peterman, 1995; Sainsbury, 1991). As a result, the suggested sustainable harvest levels could differ substantially from the actual sustainable levels, but the extent of this mismatch is unknown. In response to this uncertainty, the general recommendation is to adjust harvest rates downwards to reduce chances of a human-caused mortality going above a limit that could lead to the depletion of the population (Wade, 1998). But without an explicit consideration of uncertainty there is no objective way to set the size of this adjustment (McCarthy and Possingham, 2007). Therefore, any downward adjustments can be described as educated guesswork.

In this study, I introduce a method for calculating sustainable harvesting levels based on an explicit treatment of parameter uncertainty in harvesting models. The success is evaluated in terms of extinction probability and yield, and the level of uncertainty of yield. I examine the results for two constant harvesting strategies (quota-based and proportional), for different attitudes to risk among managers (averse, neutral and taking), and over a number of harvesting time horizons.

I illustrate my method with a case study of duiker harvesting in sub-Saharan Africa. Duikers are widely harvested in Central Africa, contributing over 75% of the harvested bushmeat in Central African Republic and Cameroon (Ngnegueu and Fotso, 1996; Noss, 1998a). Compared to other bushmeat species (e.g. primates, pigs, rodents) duikers are relatively well-studied: there are multiple published estimates of population parameters (Fa *et al.,* 1995; Fitzgibbon, Mogaka and Fanshawe, 1995; Noss, 1998a; Noss, 2000). However, these estimates vary widely, implying that ignoring uncertainty could be highly misleading, and calling for a method that considers the uncertainty explicitly. Based on availability of data, I assumed that enough was known about the three widely hunted duiker *Cephalophus* species (Peters' *C. callipygus*, bay *C. dorsalis* and blue *C.monticola*) in order to combine the available data in a Bayesian model.

The socioeconomic reality of bushmeat harvesting is such that harvesting levels would rarely be set by any single quantitative algorithm. Combining different techniques, such as population modelling introduced here and trend analysis, could result in more reliable assessments of sustainability of bushmeat harvesting for data-deficient species. Importantly for bushmeat, the process should involve stakeholders at all scales: local people, resource extraction companies, local and state government authorities and scientists (Milner-Gulland and Bennett, 2003). I used duiker antelope *Cephalophus* spp. as my case study. However, in principle, the uncertainty- and risk-based method introduced here could be applied to any harvested species and could, as part of a wider process involving multiple stakeholders, help place bushmeat hunting on a more sustainable footing.

2.2 Methods

2.2.1 Field Data

Three *Cephalophus* species: Peters' duiker *C. callipygus,* bay duiker *C.dorsalis* and blue duiker *C. monticola* were selected based on availability of independent empirical estimates of population parameters (Table 2-1) and their relative share in wild meat supply (34-95% of all bushmeat captured in the Congo Basin; Wilkie and Carpenter, 1999) in sub-Saharan Africa. Candidate papers were identified using Google Scholar, Web of Science and a UCL library search engine (using search terms: bushmeat, wild meat, tropical, Africa), and by searching the cited references in the collected papers. The following selection criteria were used to prioritise studies from which data were gathered: (a) pertaining to the three duiker species*;* (b) meeting basic quality requirements, i.e. I discarded studies where the method for estimating parameters was not specified; and (c) containing primary data on two key parameters: intrinsic rate of population increase (the maximal growth rate) r_{max} and carrying capacity K, where K was the number of animals per kilometre squared estimated in unhunted sites.

The parameter estimates were combined into a duiker dataset (Appendix 2-1).

To quantify and incorporate parameter uncertainty stemming from differences in methods, population parameters were estimated using two popular models: Cole's (Cole, 1954) and Caughley and Krebs (Caughley and Krebs, 1983), see Appendix 2-2 for model descriptions. Where available, estimates of population growth were taken directly from the literature; alternatively I used one of the two models to estimate r_{max} based on information provided by the authors (such as body mass ranges for the three duiker species). In addition, as an independent test of whether the estimates of K were reasonable, the allometric estimates of population density for the three duikers were also calculated, based on the proposed relationship between population density and body mass for mammalian primary consumers described by Damuth (1981):

$$D = a(\log W) + b \qquad \textbf{Eq. 2-1}$$

where D is the population density, W is the duiker body mass in grams, $a = -0.75$ is the slope of the relationship and $b = 4.23$ is the estimated intercept. Because the estimates of D were used here for reference only (see Table 2-1), I assumed that K was equal to D.

2.2.2 Modelling population dynamics

2.2.2.1 Population model

I used the Beverton-Holt population model (Beverton and Holt, 1957).

$$N_{t+1} = \frac{r_t N_t}{1+[(r_t-1)/K]N_t} \qquad \textbf{Eq. 2-2}$$

where N_t is the population density (individuals per unit area: in this case, animals km^{-2}) at time t; N_{t+1} is the population density in the following time step; K is the equilibrium population size in the absence of harvesting; and $r = \exp(r_{max})$ is the density-independent intrinsic rate of natural increase (the balance of births and deaths) for year t.

The Beverton-Holt model has been widely used in the past to study the dynamics of harvested species (e.g. Barnes, 2002; Holden and Conrad, 2015); it is compensatory rather than over-compensatory (high density leads to a reduction in per capita reproduction but does not reduce the recruitment of the entire population; Kot, 2001) and is believed to be a good representation of intraspecies competition in ungulate populations that are not constrained by resources or habitat availability (Ruckstuhl and Neuhaus, 2000).

The year-to-year fluctuation in births and deaths (i.e. environmental stochasticity) was represented by varying r between years, as follows:

$$r_t \sim \mathbb{N}\{r, \sigma\} \qquad \textbf{Eq. 2-3}$$

where r_t was the value of r that applied in simulation year t, and σ was the standard deviation for r across all years. Following methods by Lande, Sæther and Engen (1997), I assumed a coefficient of variation of 0.10, implying $\sigma = 0.10 \times r$.

2.2.2.2 Model parameterisation: Prior belief

Parameters r_{max} and K were supplied to the Beverton-Holt population model with uncertainty on these parameters, as follows.

For each of the two parameters r_{max} and K in my population model, a prior distribution reflecting the belief about the likely distribution of values of the parameter based on my duiker dataset was drawn, i.e. I assumed that a true value of r_{max} applied to a given local population, but I assumed also that this value was unknown. Hence, I use a probability distribution for r_{max}, which reflects my degree of belief in the likely values based on field data. Unlike uniform distribution, normal distribution clusters most of observations around a central pea: 95% of observations fall within two standard deviations of the mean. By sampling parameter values for my prior belief from a normal distribution rather than a uniform, I assumed that values closer to the average of r_{max} and K in my duiker dataset were more probable than values more than two standard deviations away from the average.

This distribution was my prior for r_{max}, drawn from a log-normal distribution (n=1000) as follows:

$$\ln(r_{max}) \sim \mathbb{N}\{\hat{r}_{max}, \tilde{r}_{max}\} \qquad \textbf{Eq. 2-4}$$

where $\hat{r}_{max}$ is the mean of log-transformed values of r_{max} (Eq. 2-5) established from field data, and $\tilde{r}_{max}$ is the standard deviation of the log-transformed values of r_{max} (Eq. 2-6). A log-normal distribution was used instead of a normal distribution (also see Appendix 2-3 and 2-4) to constrain r_{max} and K to positive values. I assumed that the log-transformed values of the reported parameter values in my field data were independent samples from the distributions defined in Eq. 2-4. The simplest approach was then to set $\hat{r}_{max}$ and $\tilde{r}_{max}$ using the field data as follows:

$$\hat{r}_{max} = mean\{\ln(r_{max}^{data})\}$$ **Eq. 2-5**

$$\tilde{r}_{max} = sd\{\ln(r_{max}^{data})\}$$ **Eq. 2-6**

where r_{max}^{data} denotes the values of r_{max} reported in the data.

A small value of $\tilde{r}_{max}$ implied that based on field data, I was highly certain that the true value of r_{max} was very close to $\hat{r}_{max}$. A large value of $\tilde{r}_{max}$ implied that I was highly uncertain about the true value of r_{max}, such that it could lay a long way from $\hat{r}_{max}$. More precisely, the choice of $\tilde{r}_{max}$ implied that I was 95% certain that the true value of r_{max} was in the range $\exp\{ln(\hat{r}_{max}) - 1.96\tilde{r}_{max}\}$ and $\exp\{ln(\hat{r}_{max}) + 1.96\tilde{r}_{max}\}$.

Likewise, I drew a prior (n=1000) for K:

$$\ln(K) \sim \mathbb{N}\{\widehat{K}, \widetilde{K}\}$$ **Eq. 2-7**

where $\widehat{K}$ was the mean of K (defined using field data) and $\widetilde{K}$ was the standard deviation of the log-transformed values of K.

The sampled prior distributions for r_{max} and K, along with the empirical estimates (field data), are presented in Appendix 2-3.

In addition to analysis with parameter uncertainty, I ran simulations without parameter uncertainty (but with environmental stochasticity), to provide a baseline comparison. For simulations without parameter uncertainty, I used the average values of r_{max} and K only (i.e. $\hat{r}_{max}$ and $\widehat{K}$) based on field data for each duiker species, to parameterise the Beverton-Holt population model.

2.2.3 Applying harvesting

2.2.3.1 Harvesting Strategies

To implement a simple, reasonable harvesting strategy, I assumed that harvesting occurred at a constant rate: set as either a quota or at a proportional rate. That is, each year, a quota h or a proportion φ of the population was targeted, and this target did not vary among years (Eq. 2-8 and Eq. 2-9, respectively).

$$N_{t+1} = \frac{r_t N_t}{1+[(r_t-1)/K]N_t} - h \qquad \textbf{Eq. 2-8}$$

$$N_{t+1} = \frac{r_t N_t}{1+[(r_t-1)/K]N_t} - \varphi N_t \qquad \textbf{Eq. 2-9}$$

Note that the rate φ is an aggregate parameter of harvesting effort and could in practice be altered by changing the number of hunting days per year, the density of traps, the efficacy of traps used, the proportion of animals released after being trapped, the proportion of land set aside as reserve, and so on; h is simply the number of animals removed. Here, φ represents a proportion of the population being targeted.

Total population losses to harvesting, or yield (Y_t), at time t is the difference between the number of animals at time t after reproduction at the end of year $t-1$ (Appendix 2-4 Eq. 2-13), and the higher of 0 and the number of surviving animals after target quota/proportion has been applied (Appendix 2-4 Eq. 2-14 and Eq. 2-15).

2.2.3.2 Simulation Experiment

I simulated quota-based and proportional harvesting over 100-, 50-, 20- and 5-year harvest periods for each duiker species. Based on model estimates, I assessed average yields, survival probability, and the uncertainty in both yield and survival, over these different timescales.

For proportional harvesting, I examined values of φ from 0 (no harvest) to 0.90 in discrete steps of 0.05, giving 19 different values of φ. For quota-based harvesting, the ranges of target quotas h for each species were found experimentally, by running harvesting simulations with increasingly high upper limit on h ($0 \leq h \leq 13$) and examining summary statistics (mean yield, median yield and mean survival probability) from harvesting each species for 50 years. The upper harvest rate limits beyond which there were no further changes in summary statistics were used for each species. The duration of harvesting (50 years) was based on preliminary analysis: I found that using short timeframes (5-10 years) resulted in upper limits of h which appeared unrealistic and imprudent (high-risk). Using timeframes >50 years did not significantly affect the outcome of the experiment. This resulted in target quota ranges of between: 0 and 3.5 animals km^{-2} year^{-1} for Peters' duiker, 0 and 1.5 animals km^{-2} year^{-1} for bay duiker, and 0 and 10 animals km^{-2} year^{-1} for blue duiker. I included zero-rate harvesting in both proportional and quota-based harvesting simulations to create a baseline scenario. The initial population size N_0 was set randomly, by drawing from a uniform between $0.20K$ and $0.80K$.

For each of the combinations of timescale (100, 50, 20 and 5 years) and harvest rate, I carried out an ensemble of 1000 simulations. Harvesting was applied from year 1 onwards (no harvesting took place in year 0). The ensemble size was based on preliminary analysis involving comparing summary statistics and visualising results for smaller (100 simulations and 500 simulations) and larger (10000 simulations) sample sizes. For each simulation within each ensemble, I drew a value for each parameter at random from the prior. From each of the ensembles, I report a mean, median, and 1st and 3rd quartiles for the yield, and calculate the probability of population survival for the harvesting period.

Survival probability was equal to the proportion of simulations without extinction. Extinction was defined as the population density dropping below 0.1 animals km^{-2} at any point during the simulation, based on lower end of density estimates collected in areas of high harvesting intensity (Lahm, 1993; Hart, 2000). A response of 1 was assigned to a year where population size N_t was equal to or was above a threshold of 0.1 animals km^{-2}; zero (0) was assigned to a year (and all the following years) where population size dipped below the viability threshold (I set N_t to zero, i.e. quasi-extinction). Responses were then averaged to give an estimate of survival probability at each harvest rate with 95% confidence intervals over 100-, 50-, 20- and 5-year harvests. A detailed description of my method is presented in Appendix 2-4.

2.2.4 Decision Framework

Two measures of harvesting success were used in my decision framework: expected meat yield and probability of species survival. The choice of harvesting strategy was motivated by maximising expected meat yield over the duration of harvesting horizon. The optimum harvesting strategy was the strategy that maximised yield subject to a survival probability constraint.

With reference to maximising meat yields under parameter uncertainty, in order to seek optimum hunting levels given the highly variable model outputs, I needed to consider the decision maker's attitude to risk. Using the decision-making framework of Canessa *et al.* (2016), I assumed that a risk-neutral decision maker would seek to achieve “the best average outcome”. The most obvious here was to select the policy with the greatest average yield, but I found it more informative to select the policy with the greatest median, due to the skewed nature of the distributions. By contrast, a risk-averse decision maker would opt for “the best worst outcome”. For this purpose, the selected policy was defined as the policy that returned the greatest value for the 1st quartile on the average yield. Finally, a “risk seeking” decision maker would focus on the “the best best outcome”. For this purpose, the selected policy was defined to be that which returned the greatest value for the 3rd quartile on the average yield.

With reference to species survival probability, I used a minimum survival threshold of 90% of population (based on the IUCN guidelines for identifying threatened populations; Mace and Lande, 1991) over the duration of harvesting horizon as a benchmark. Harvesting rates that could drive over 10% of population to extinction (see 2.2.3.2 for my definition of extinction) on average over 100-, 50-, 20- and 5-year harvests were deemed unsustainable.

All simulations were run in R version 3.5.1 (R Core Team, 2018). Results are reported with one standard deviation.

2.2.5 Framework Summary

The summary work flow is presented in Figure 2-1. The observed values for r_{max} and K (Appendix 2-1) are used to estimate the mean ($\hat{r}_{max}$, $\widehat{K}$) and the corresponding uncertainty ($\tilde{r}_{max}$ and $\widetilde{K}$) for each of these population parameters; these become 'Prior Belief' (Figure 2-1). I then use this Prior Belief about the true population parameters to inform the harvest model that also includes yearly changes in environmental conditions ('Yearly Environmental Stochasticity', Figure 2-1), to estimate yields and survival probability for the three duiker species using two constant harvesting strategies under parameter uncertainty. These predictions can then be used by bushmeat practitioners ('Stakeholder Groups', Figure 2-1) to guide their choice of harvest rate (subject to attitude to risk) and their expectations of harvesting outcomes.

The method assumes only two prerequisites: a model formulation that is believed to be appropriate for simulating the dynamics of population size and yield through time, given harvesting; and explicit prior beliefs, based on field data, on the parameters of that model. The method could be applied wherever these prerequisites are available. Given the prerequisites, the method uses ensemble modelling to estimate the probability distributions on population extinction, and yield, for different harvesting levels calculated over different time periods. These distributions can then be fed into a risk-based decision making process, to help set actual harvesting levels. In common with all methods employing ecological modelling (e.g. Phillips *et al.,* 2006; Bousquet *et al*., 2008; Wäber and Dolman, 2015), the method ignores many key ecological complexities that may affect populations and yield in reality.

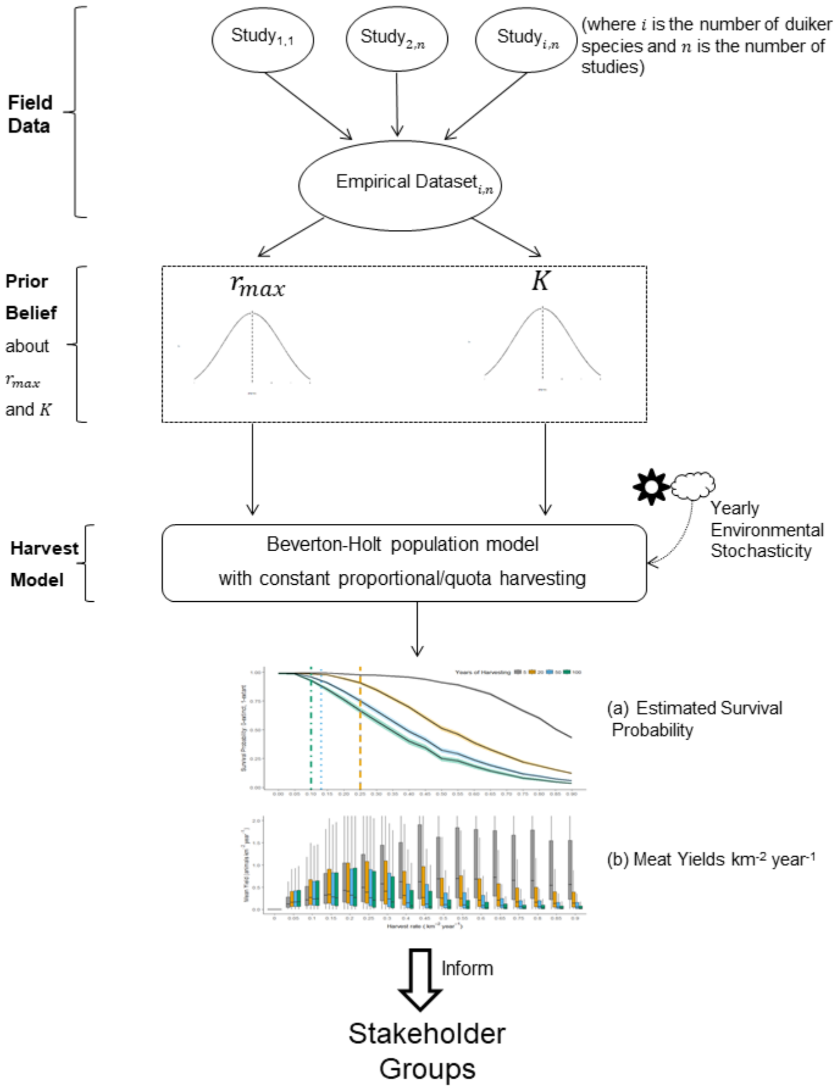


Figure 2-1 The method of combining field estimates of population parameters from independent studies into a parameter dataset, building parameter distributions based on this data (with uncertainty, centred on the mean), and feeding these parameter distributions (Prior belief) into the harvest model (the Beverton-Holt model with proportional/quota-based harvesting), to estimate expected yields and survival probability at different harvest rates under parameter uncertainty.

2.3 Results

2.3.1 Duiker dataset

I identified and assessed twenty six potential sources of primary data on population parameters r_{max} and K, including two PhD thesis (Payne, 1992; Lahm, 1993).

Parameter estimates from the thirteen studies that met my selection criteria were combined into a dataset of carrying capacity, K and intrinsic rate of natural increase, r_{max} for Peters' duiker *C.callipygus*, bay duiker *C. dorsalis* and blue duiker *C.monticola* (see Table 2-1 for sample sizes). Appendix 2-1 gives the observed values for r_{max} and K.

The spatial distribution of studies is presented in Figure 2-2.

Geographically, the studies were concentrated in five main research areas: the Ituri Forest (Democratic Republic of Congo); Makolou (north-eastern Gabon); Bioko and Rio Muno (Cameroon); Dzanga-Sangha and Dzanga-Ndoki National Parks, and Bayanga and Moussapoula (Central African Republic). Data varied greatly within the areas. The areas were between 160 kilometres and 3500 kilometres apart and that was at least 100 times the size of known duiker ranges (Payne, 1992). The east-west spread of samples in my dataset may explain some of the variation in parameter values (due to habitat and environmental differences). Overall, Peters' duiker was the most difficult to find data on. Most estimates of carrying capacity dated from the late 1970s-80s, with the latest estimates in 2000 (Hart, 2000; Noss, 2000).

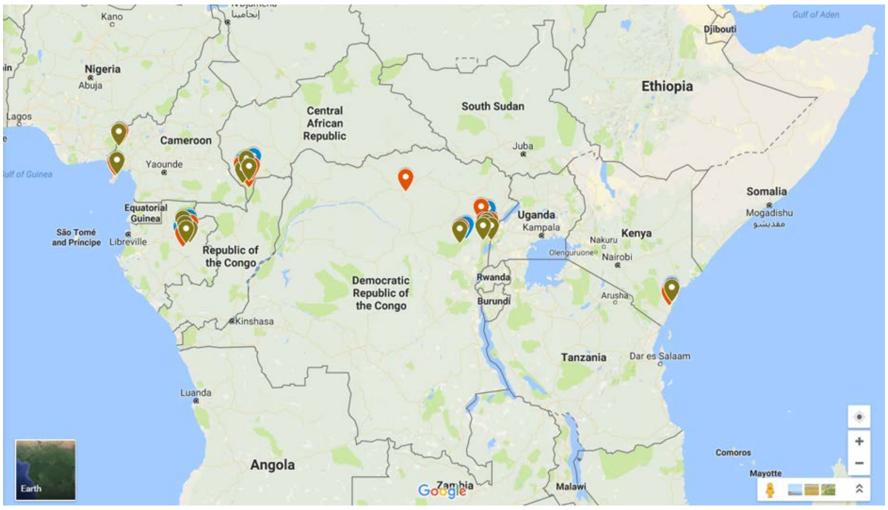


Figure 2-2 Geographic locations of field studies of Peters' duiker *C. callipygus* (blue pins), bay duiker *C. dorsalis* (red pins) and blue duiker *C. monticola* (green pins) included in my duiker dataset (Appendix 2-1).

The mean values for parameters r_{max} and K (μ_{rmax} and μ_K), and the variability of estimates (standard deviations, s_{rmax} and s_K) along with average body masses and sample sizes for each of the three duiker species in my dataset are given in Table 2-1.

Table 2-1 Mean parameter values (± 1 standard deviation, $\mu \pm s$), sample sizes, n, and body mass estimates (± 1 standard deviation) for three duiker *Cephalophus* species: Peters' *C. callipygus*, bay *C. dorsalis* and blue *C. monticola*, based on field data.

Species	**Body Mass ($\mu \pm s$)**	r_{max}			K			
		n	μ_{rmax}	s_{rmax}	n	μ_K	s_K	**Allometric[1]**
Peters'	16.22 ($\pm$2.60)	5	0.44	0.14	4	9.70	3.62	11.82
Bay	17.99 ($\pm$2.83)	6	0.39	0.14	6	5.43	2.55	10.96
Blue	4.62 ($\pm$0.55)	7	0.58	0.27	7	39.46	26.72	30.31

[1] density $D = a(\log W) + b$ (Eq. 2-1), where W is the duiker body mass in grams, $a = -0.75$ is the slope of the relationship and $b = 4.23$ is the estimated intercept (Damuth 1981)

2.3.2 Estimated Responses to Harvesting: without parameter uncertainty

Without considering parameter uncertainty, the choice of optimum harvesting was comparatively easy because the harvesting strategy that maximised yield also resulted in a 100% survival probability. Figure 2-3 gives an example for Peters' duiker without parameter uncertainty and with environmental stochasticity.

The same pattern holds for the other two duiker species (Appendix 2-5).

2.3.3 Estimated Responses to Harvesting: with parameter uncertainty

For all three species, the models predicted that average yield peaked at intermediate harvesting levels, whereas the probability of population survival declined steadily with increasing harvesting level. Figure 2-4 gives an example for Peters' duiker.

For a given harvest rate up to the optimum, median yield under parameter uncertainty (Figure 2-4) was comparable to the expected meat yield without parameter uncertainty (Figure 2-3); however, survival probability appeared higher in analyses without parameter uncertainty than with parameter uncertainty.

With parameter uncertainty for a given species, harvesting approach, and harvesting level, there tended to be a large amount of uncertainty in the predictions, most notably for average yield, where standard deviations were often greater than the mean. The estimated yields for a given harvesting level were often highly right-skewed, with most predictions for each ensemble returning yields somewhat below the mean, and a small number of simulations returning yields much greater than the mean. As a result of the uncertainty and the skew, the harvesting level that maximized the median yield, was often very different to the levels maximizing the 1st or 3rd quartiles. This in turn implies that attitude to risk will have a substantial impact on the choice of harvesting level.

Against these similarities, there were important differences according to species, harvesting method, and time horizon, as discussed below.

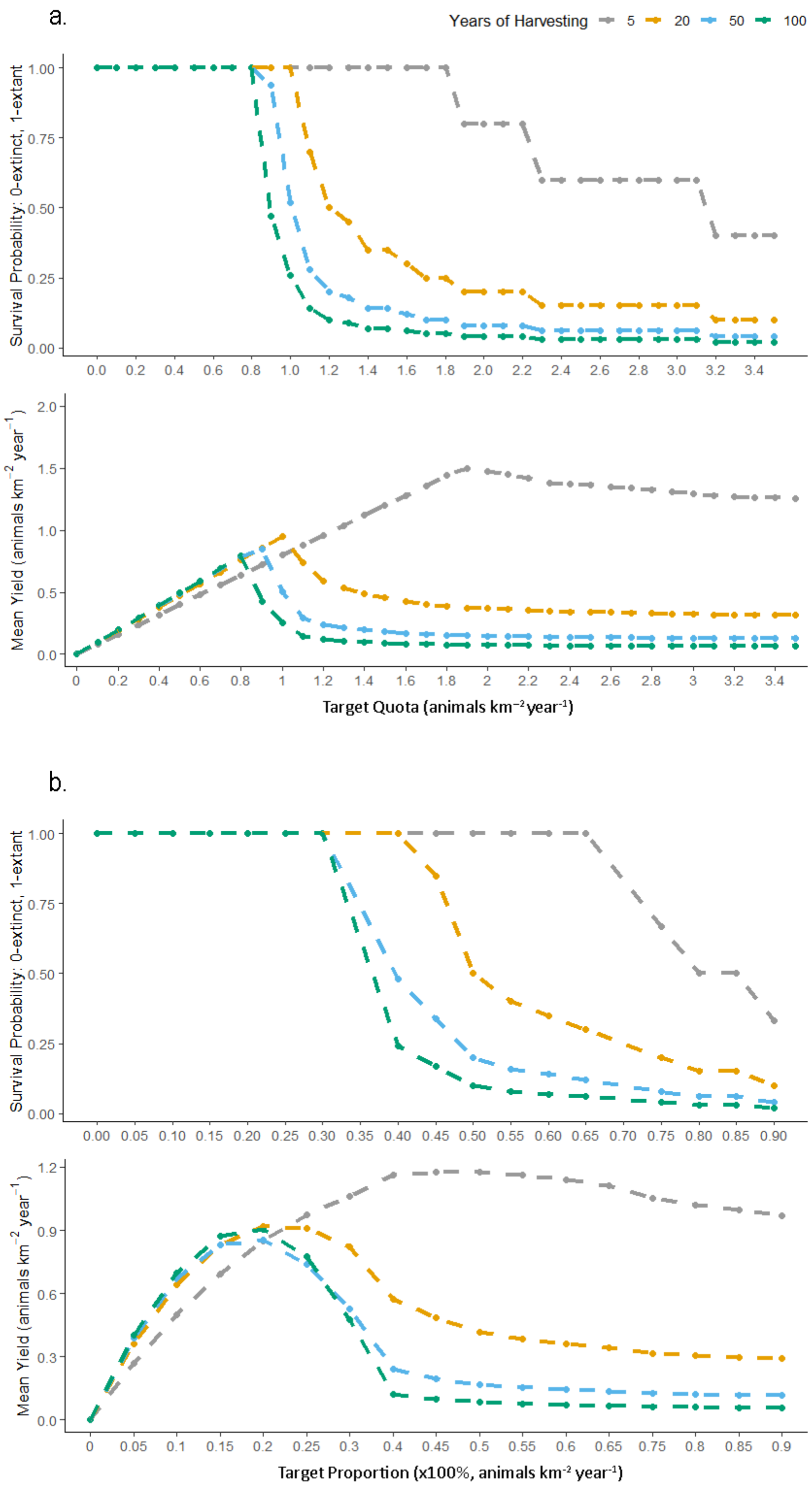


Figure 2-3 Survival probability and average yields for Peters' duiker *C.callipygus* without parameter uncertainty and with environmental stochasticity, under (a.) constant quota-based and (b.) proportional harvesting over 5 (grey), 20 (orange), 50 (blue) and 100 (green) years of harvesting.

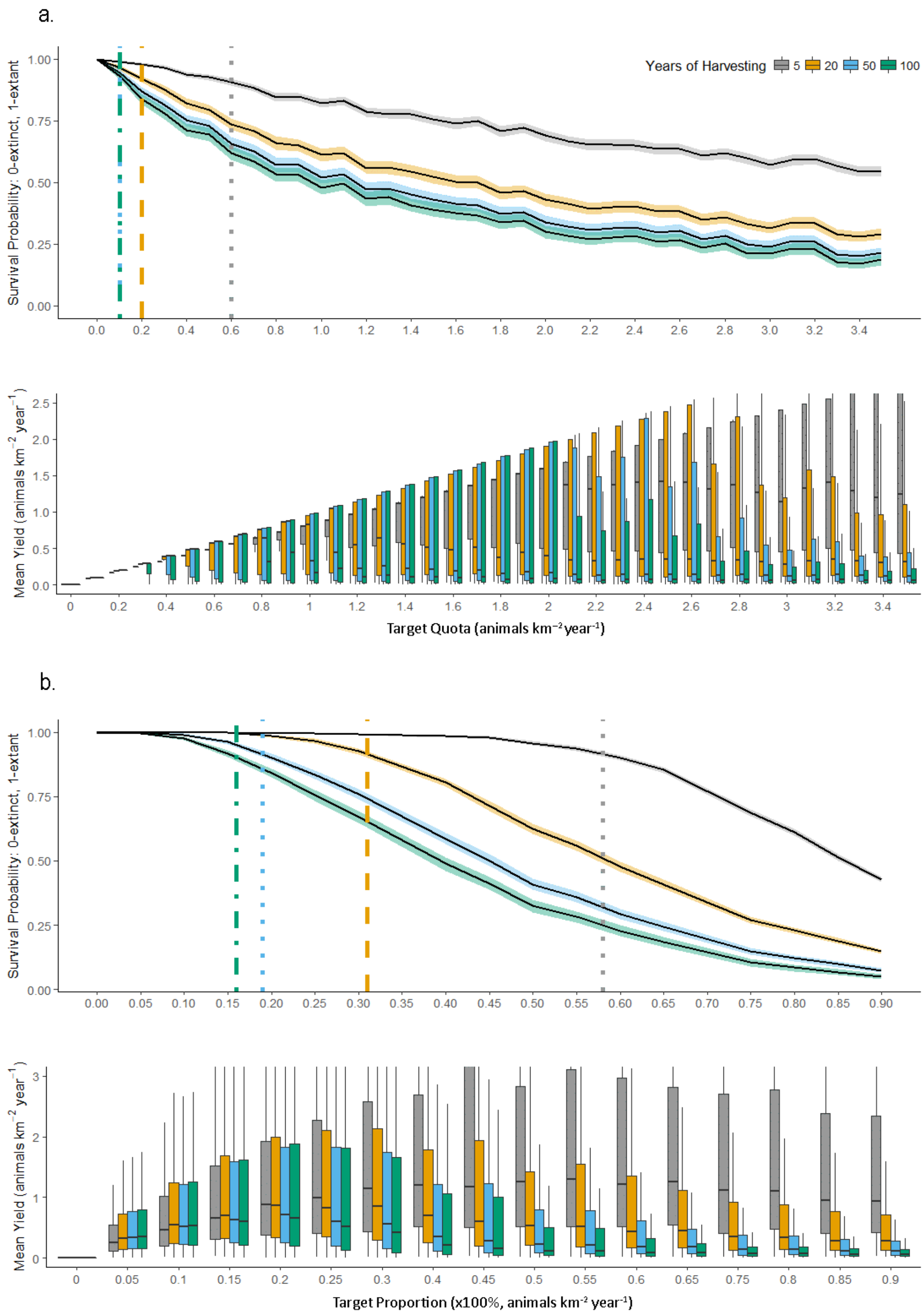


Figure 2-4 Survival probability (with 95% confidence intervals) and average yields for Peters' duiker *C.callipygus* with parameter uncertainty and environmental stochasticity, under (a.) constant quota-based and (b.) proportional harvesting over 5 years (grey), 20 years (orange), 50 years (blue) and 100 years (green). Dotted vertical lines represent harvest rates above which harvesting was expected to drive over 10% of duiker species to extinction over the duration of harvesting horizon.

2.3.4 Peters' duiker: quota-based harvesting

For Peters' duiker over a 100 year time horizon, and adopting a risk-neutral approach, I estimated a maximum yield of 0.69 (s=0.32) animals km^{-2} year^{-1} under quota-based harvesting (Figure 2-5a). However, the harvesting level carried a population survival of only 0.59 (i.e. on average, only 59% of population survived). This contrasts with the no uncertainty case, where the maximum yield of 0.79 animals km^{-2} year^{-1} was associated with a survival of 1 over 5-100 years (Figure 2-3). Imposing the 90% minimum survival threshold (Figure 2-5b,d) under parameter uncertainty, resulted in a lower quota (0.10 animals km^{-2} year^{-1} rather than 0.70 animals km^{-2} year^{-1}) and a lower median yield (0.10 animals km^{-2} year^{-1}, s =0.02, rather than 0.69 animals km^{-2} year^{-1}, s=0.32): an 86% reduction in median yield compared to the maximum.

Under parameter uncertainty, the optimum harvesting level, yield, and survival, were all affected by the attitude to risk. Without the minimum survival threshold, shifting from a risk-neutral position (maximizing the median) to risk-averse position (maximizing the 1st quartile) resulted in a much lower target quota (0.70 animals km^{-2} year^{-1} to 0.20 animals km^{-2} year^{-1}) but higher survival probability (0.59 to 0.84). As expected, the risk-averse position returned a lower median yield (0.20 animals km^{-2} year^{-1}, s=0.07, rather than 0.69 animals km^{-2} year^{-1}, s=0.32), but a higher 1st quartile (0.20 animals km^{-2} year^{-1} rather than 0.03 animals km^{-2} year^{-1}). By contrast, adopting a risk-taking position (maximizing the 3rd quartile) with no survival constraint (Figure 2-5a) resulted in a higher target quota (2 animals km^{-2} year^{-1}), lower survival (0.30), lower median yield (0.08 animals km^{-2} year^{-1}, s=0.84), but greater 3rd quartile (1.98 animals km^{-2} year^{-1}). Due to the highly skewed nature of the yield predictions, the risk-taking position returned the greatest mean yield – but the great majority of simulations in the ensemble were substantially below this mean value.

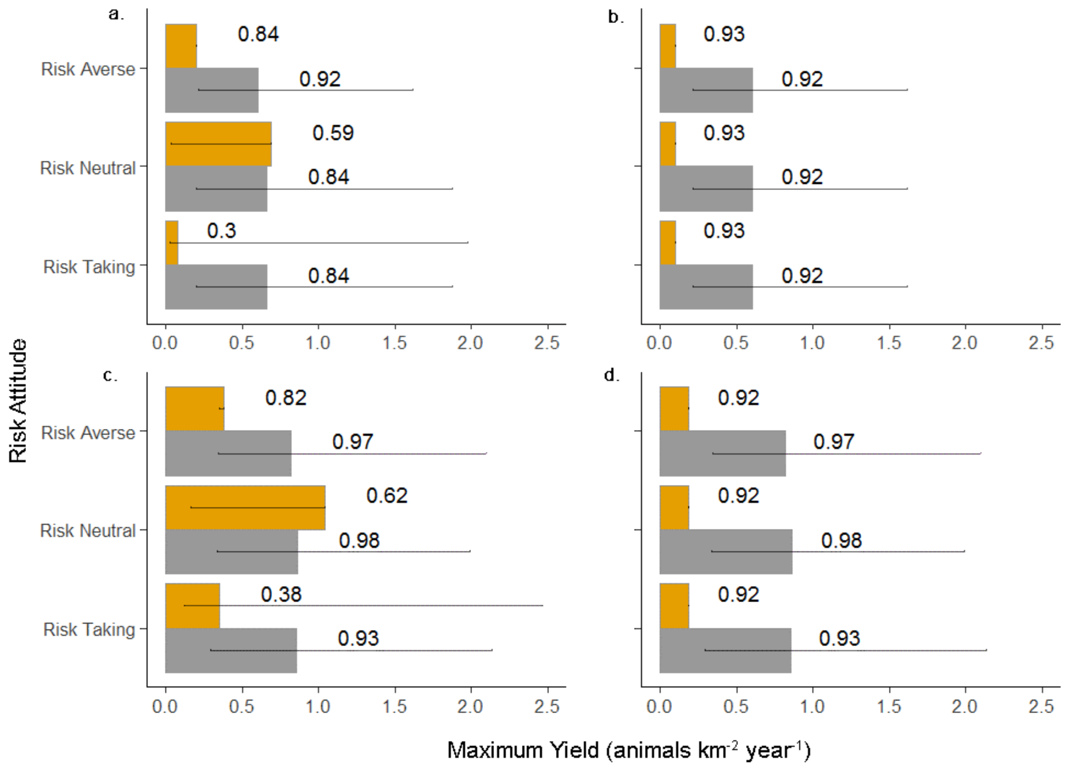


Figure 2-5 Maximum median yields (with interquartile ranges) and associated survival probabilities (next to the bars) for constant quota-based (in orange) and proportional (in grey) harvesting of Peters' duiker over 100 years (a, b) and over 20 years (c, d) for different attitudes to risk: averse, neutral and taking, with an option to adopt the 90% minimum survival threshold (b, d).

The choice of time horizon had quantitative, but not qualitative, effects. Over shorter time horizons (Figure 2-5c,d), the optimum harvesting levels were higher, and the trade-off between yield and survival was less severe (i.e. the same yield could be achieved with greater survival; or the same survival could be achieved with a greater yield). Yields expected from quota-based harvesting over 20 years were on average 106% higher than the same yields over 100 years, ranging from 0.19 (s=0.04) (Figure 2-5d), to 1.05 (s=0.43) animals km^{-2} year^{-1} under a risk-neutral strategy (Figure 2-5c).

2.3.5 Bay and blue duikers: quota-based harvesting

The estimates for quota-based harvesting for bay and blue duiker were qualitatively similar to those for Peters' duiker, but there were important quantitative differences (Appendix 2-5, Appendix 2-6, Figure 2-6, Figure 2-7). For the same time horizon, risk attitude, with or without the minimum survival threshold, and with and without parameter uncertainty, bay duiker had a lower maximum sustainable yield, and blue had a higher yield, compared to Peters' and bay duiker. For risk-neutral harvesting over 100 years, with no extinction threshold, the yields (Figure 2-5a, Figure 2-6a, and Figure 2-7a, in orange) were 0.69 animals km^{-2} year^{-1} (s=0.32) (Peters'), 0.35 (s=0.16) animals km^{-2} year^{-1} (bay), and 3.47 (s=1.65) animals km^{-2} year^{-1} (blue). Analysis that did not consider uncertainty returned very similar yields to the uncertainty case. However, with parameter uncertainty at the upper end of harvesting pressure (target quotas of 0.3-0.45 animals km^{2} year^{-1} for bay, and 3.5 animals km^{2} year^{-1} for blue duiker), the risk of extinction was estimated at about 40-45% for both bay and blue duiker over 100 years (Appendix 2-6.1a, Appendix 2-6.2a), compared to 100% survival probability estimated without considering uncertainty (Appendix 2-5.1a, Appendix 2-5.2a).

The threshold at which harvesting decreased survival was lower for bay duiker, than for Peters' and blue duiker: 0.05 bay duiker km^{-2} year^{-1} (or 1 bay duiker per 20 km^{2} year^{-1}), compared to 0.25 blue duiker km^{-2} year^{-1} (or 1 per 4 km^{2} year^{-1}) over 100 years (under risk-neutral harvesting). Harvesting conservatively (i.e. risk-averse approach) at 0.10 bay duiker km^{-2} year^{-1} and at 0.75 blue duiker km^{-2} year^{-1} yielded 0.10 (s=0.04) and 0.75 (s=0.28) animals km^{-2} year^{-1}, respectively (Figure 2-6a, Figure 2-7a). For blue duiker, the more conservative risk-averse harvesting resulted in a 79% reduction in yield compared to the maximum, with an increase in survival probability to 81% under quota-based policy. The optimum yields increased only marginally over the 20-year time horizon, to 0.43 (s=0.18) and to 3.80 (s=1.67) animals km^{-2} year^{-1} for bay and blue duiker, respectively (Figure 2-6c and Figure 2-7c).

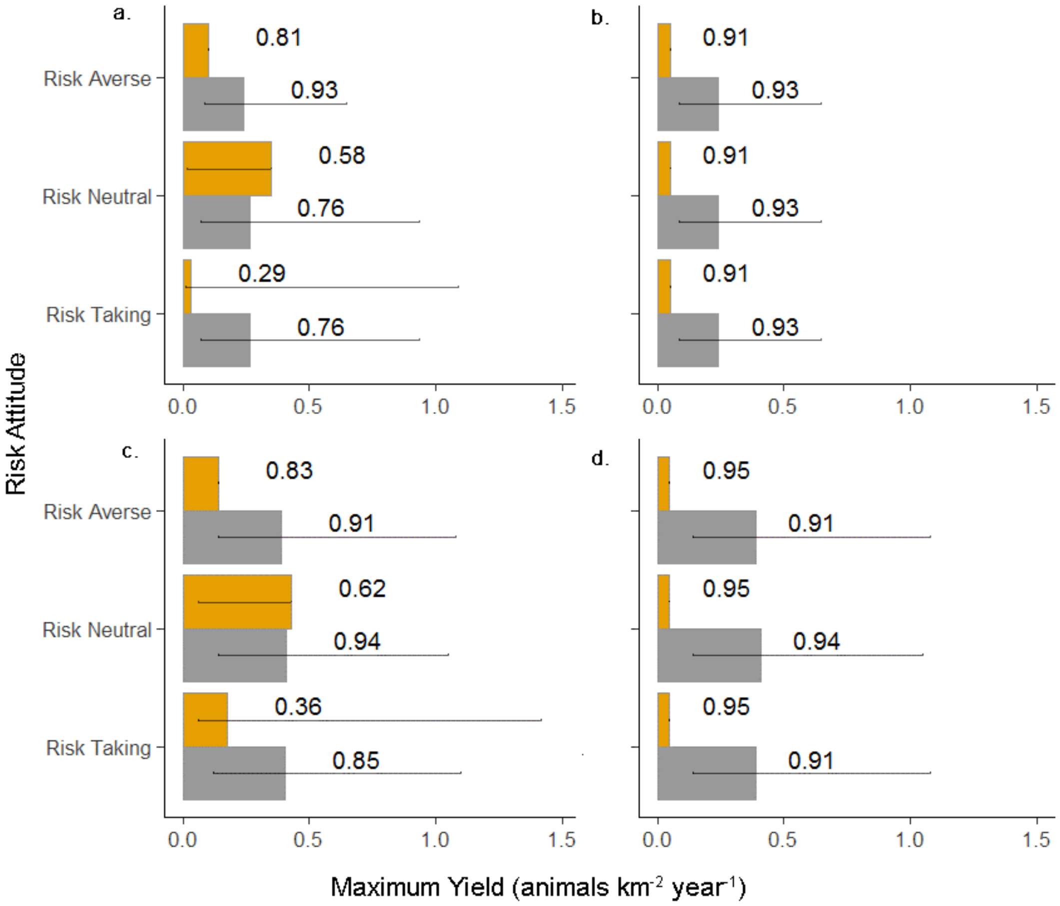


Figure 2-6 Maximum median yields (with interquartile ranges) and associated survival probabilities (next to the bars) for constant quota-based (in orange) and proportional (in grey) harvesting of bay duiker *C.dorsalis* over 100 years (a, b) and over 20 years (c, d) for different attitudes to risk: averse, neutral and taking, with an option to adopt the 90% minimum survival threshold (b,d).

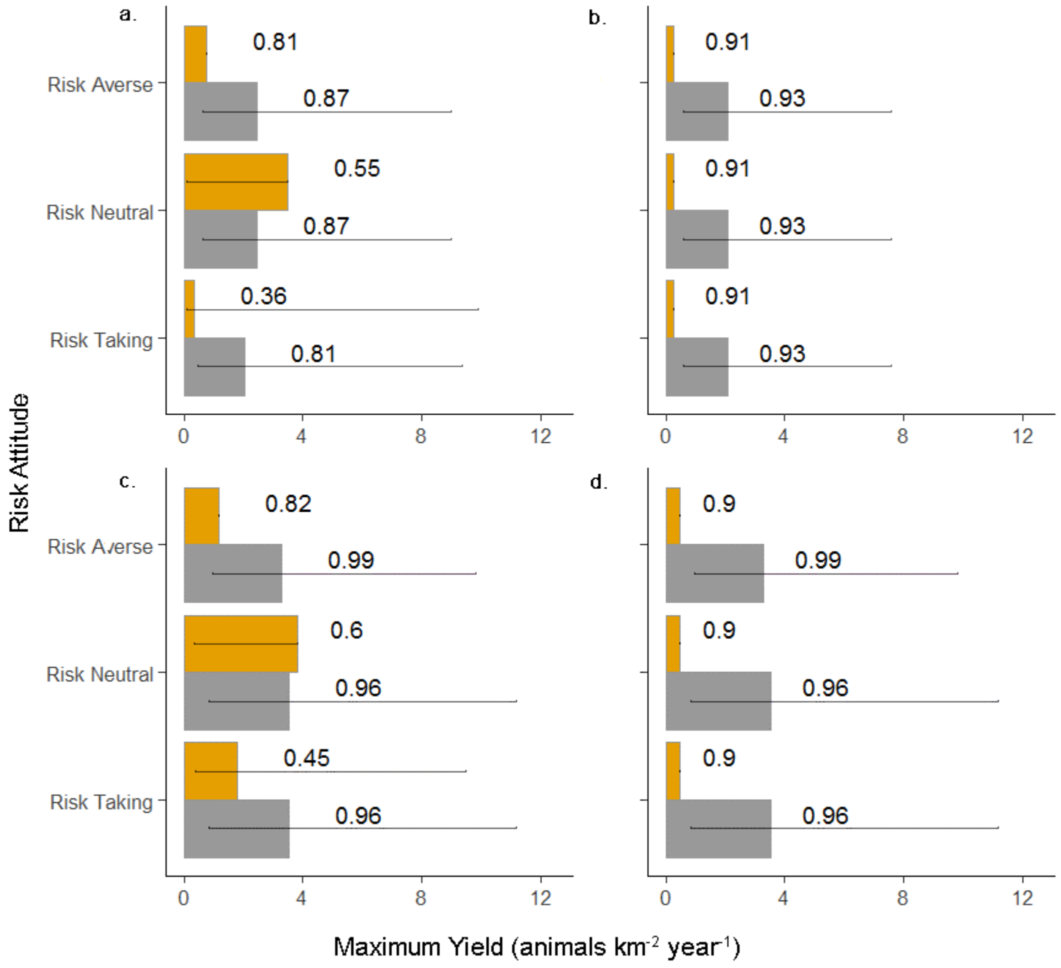


Figure 2-7 Maximum median yields (with interquartile ranges) and associated survival probabilities (next to the bars) for constant quota-based (in orange) and proportional (in grey) harvesting of blue duiker *C.monticola* over 100 years (a, b) and over 20 years (c, d) for different attitudes to risk: averse, neutral and taking, with an option to adopt the 90% minimum survival threshold (b,d).

Under parameter uncertainty, meeting the 90% minimum survival threshold led to an 85%-93% reduction in expected yields for quota-based harvesting compared to the maximum: to 0.05 (s=0.01) bay duiker km^{-2} year^{-1} (Figure 2-6b), and to 0.25 (s=0.06) blue duiker km^{-2} year^{-1} (Figure 2-7b) over 100 years.

The uncertainty on predictions was greatest for blue duiker (Appendix 2-6.2), resulting in an even larger impact of attitude to risk, compared to other duiker species in my study. With high short-term meat yields at harvest rates well above sustainable (for example, at $h \geq 10$), yields from blue duiker may remain high in the short term despite overharvesting. The prediction for population survival vs harvesting level was also closer to linear under quota-based harvesting (Appendix 2-6.2a). This further complicates decision making, because with a relationship closer to linear, the exact choice of a threshold for a survival constraint has a larger impact on the quota and yield. For example, the most risk-seeking decision-maker targeting around 10 blue duiker km^{-2} year^{-1} could cause an extinction risk of 60% of blue duiker over 100 years (Appendix 2-6.2a). The corresponding increase in harvesting profitability was mainly in the 3rd interquartile range and would motivate a risk-taking decision maker hoping to achieve the highest possible return.

2.3.6 Proportional harvesting

Predictions for proportional harvesting shared three key features with the predictions for quota-based harvesting: (1) yields peaked at intermediate harvesting levels; (2) population survival declined with increased harvesting; (3) considering parameter uncertainty resulted in substantial uncertainty on estimates, especially for yields. However, the declines in survival probability and average yields after the optimum were noticeably more gradual under proportional harvesting than under quota-based harvesting.

Furthermore, estimates for proportional harvesting under parameter uncertainty showed two important qualitative differences. First, the 1st quartile, median, and 3rd quartile tended to travel together, all peaking at the same, or a similar, harvesting level. This meant that the choice of optimum harvesting rate, and hence the average yield and survival, was relatively insensitive to attitude to risk. Second, the population survival returned by a risk-neutral position tended to be greater than, or close to, the 90% survival threshold. This meant that the choice of whether or not to impose a survival constraint also had little effect on the harvesting policy or yield.

A naïve comparison across all species and risk attitudes, shows that proportional harvesting is theoretically superior to quota harvesting in all cases and in all ways. There was no combination of species and risk attitude for which quota-based harvesting returned a greater yield, and where quota-based harvesting returned a similar yield, the survival was substantially lower. This comparison is naïve however, because proportional harvesting is considered much harder to carry out in practice (see Discussion).

Once again, there were important quantitative (but not qualitative) differences among the three species for proportional harvesting.

2.3.6.1 Proportional harvesting: Peters' duiker

For Peters' duiker under proportional harvesting, both risk-neutral and risk-taking strategies peaked at a harvest rate of 20% of annual population over 100 years (Figure 2-4b), yielding 0.66 (s=4.35) Peters' duiker km^{-2} year^{-1} on average with expected survival probability of 0.84 (s=0.30) (Figure 2-5a, grey bars). This contrasts with the no uncertainty case (Figure 2-3) where, under optimum harvesting, both average yields and survival probability were noticeably higher (estimated 0.91 animals km^{-2} year^{-1} and 1, respectively).

If survival probability was the priority, under the condition of parameter uncertainty, reducing target rate from 20% (risk-neutral) to 15% (risk-averse) of annual population km^{-2} reduced expected yields by less than 0.1 duikers km^{-2} year^{-1} while increasing expected survival by 8%. On average, yields were 32% higher over 20 years compared to over 100 years under proportional harvesting.

2.3.6.2 Proportional harvesting: bay and blue duiker

The optimum yields were noticeably lower for bay than for Peters' duiker: 0.27 (s=3.38) animals km^{-2} year^{-1} under risk-neutral proportional harvesting (Figure 2-6a, in grey), increasing only marginally over the 20-year time horizon, to 0.40 (s=3.24) animals km^{-2} year^{-1} (Figure 2-6c, grey bars). The threshold at which harvesting decreased survival was also lower, with rates as low as 10% of annual population showing a statistically significant effect (Appendix 2-6.1b). Compared to analysis with parameter uncertainty, the optimum yield (0.41 animals km^{-2} year^{-1}), the associated survival probability (1) and the harvesting threshold that reduced survival probability below 1 (25% of annual population) were all higher in analysis without parameter uncertainty.

Under parameter uncertainty, harvesting conservatively (i.e., risk-averse approach) at 10% of annual population yielded 0.24 (s=2.28) bay duikers km^{-2} year^{-1} (Figure 2-6a). At these low rates, extinctions were comparatively rare and yields increased in the long term suggesting that population was growing despite harvesting. Proportional strategies were more sensitive to risk for bay than for Peters' duiker; however, still less so than quota-based.

The optimum yields were significantly higher for blue duiker than for Peters' and bay duiker (Figure 2-7), reflecting higher densities and population growth rates. Under a proportional harvesting strategy, the estimated yields were maximised at a harvest rate of 20-25% of blue duiker annually with little difference between risk approaches in terms of survival (Figure 2-7, grey bars), and yields varying between 2.44 (s=55.25) and 3.5 (s=56.63) animals km^{-2} year^{-1} depending on harvesting horizon. Under parameter uncertainty, extracting 20% of annual population resulted in an average survival probability of between 0.87 and 0.99. Without considering uncertainty, harvesting up to 40% of annual population returned survival probability of 1.

2.4 Discussion

My analysis demonstrates significant potential benefits of incorporating parameter uncertainty into model-based analyses of sustainable bushmeat yields. All such model-based analyses (e.g. Milner-Gulland and Akçakaya, 2001; Barnes, 2002; van Vliet and Nasi, 2008) can only ever form part of the complex decision process that eventually leads to harvesting practice on the ground (Nasi *et al.,* 2012; Nasi *et al.,* 2011; Willis *et al.,* 2013; Milner-Gulland and Bennett, 2003). However, the incorporation of uncertainty does reveal some key features that may inform the stakeholders that influence harvesting. In particular, for quota-based harvesting, parameter uncertainty causes an important trade-off between yield and survival, and causes highly uncertain and skewed outcomes for any given policy; whereas uncertainty makes the idea of proportional harvesting all the more attractive compared to quota-based harvesting.

The trade-off between yield and survival is absent, or much reduced, in analysis ignoring uncertainty, where the choice of optimum harvesting may appear simple because harvesting that maximises yield also maximises survival probability. To understand why, consider that the uncertainty-based analysis deals with an ensemble of model simulations, which can be thought of as a set of populations with different parameters. An analysis ignoring uncertainty effectively deals with just one of these populations, in which case the policy that maximizes yield needs to keep the population extant for most of the harvesting period. In contrast, in the presence of uncertainty, a policy can maximize overall yield by setting a quota that harvests effectively from the most productive populations, at the cost of sending the less productive populations extinct. This is also true for proportional harvesting; however under proportional harvesting, only a share of animals is ever extracted, and this share is proportionally lower in less productive populations than in more productive populations (see below). This means that even when harvest rates are set too high (for example, due to imperfect knowledge of a local population), under proportional harvesting a share of population survives whereas every animal might be extracted under quota-based harvesting. However, if overharvesting continues, under proportional harvesting, as well as under quota-based, populations eventually become unviable (represented here by the 0.1 animals km^{-2} extinction threshold) and a local extinction follows.

However in reality, our knowledge of species is not perfect (Milner-Gulland and Akçakaya, 2001; van Vliet and Nasi, 2008), as demonstrated here for my duiker antelope species. In addition, animal populations are subject to demographic and environmental variability (Bousquet *et al.,* 2008; Lande 1998; Lande *et al.,* 1995; Holden and Conrad, 2015). Lack of species data, as well as natural variability, are major sources of uncertainty about real-life populations and their responses to harvesting (van Vliet and Nasi, 2008). Considering parameter uncertainty for quota-based harvesting (the policy that is more often used in practice; Mockrin and Redford, 2011) revealed a stark trade-off between yield and survival for all three species. Those policies that maximized yield resulted in low survival rates (0.59, 0.58 and 0.55 for Peters', bay and blue duiker, respectively), whereas policies constrained by a survival requirement, resulted in much lower yields.

For a given harvesting policy, I also found highly variable, skewed outcomes in terms of yield. For the optimum yield, the standard deviation on yield was often over 100% of the mean (e.g. for blue duiker, yield = 3.5 animals km^{-2} year^{-1} and standard deviation = 56.63), and this for a set of species that were chosen specifically because they were relatively well studied (e.g. Payne, 1992; Mockrin, 2010; Van Vliet *et al.,* 2007; Schmidt, 1983). As a result of the uncertainty in yield, the apparent best policy was highly dependent on attitude to risk (e.g. Figure 2-5, especially for quota-based in orange). The importance of the uncertainty in yield also depends in part on scale. If the parameter variation varies at fine scales, then stakeholders can expect to gain yields that average over the distributions. However, if the parameters vary coarsely, then the analysis implies that a given stakeholder may receive a yield that is very different from the average. The skewed nature of the distributions implies further that for every stakeholder lucky enough to gain substantially more than the average, there would be many receiving substantially less – a situation of few winners and many losers. This observation could be potentially important in weighing up the economic implications of harvesting at local or regional scales.

Finally, my analysis showed that proportional harvesting was much more robust to uncertainty than was quota-based harvesting (Beddington and May, 1977; Lande *et al.,* 1995). Based on likely ranges for the duikers' reproduction rates and population densities (Appendix 2-3), proportional harvesting showed a reduced trade-off between yield and survival, returning a greater survival for a given average yield. Moreover, the apparent best policy was insensitive to risk attitude; estimated yields were maximised at the same harvest rate regardless of decision makers' risk attitude, time horizon, or willingness to adopt the 90% minimum survival threshold, so there was less incentive for greedy, risk-taking decisions. In part, the superiority of proportional harvesting can be understood as follows. If a population equilibrates to a steady population density, then a proportional harvest corresponds to a quota. For example, taking 10% per year from a population of 500, implies a quota of 50. However, as outlined above, the uncertainty-based analysis deals with an ensemble of populations. In this case, proportional harvesting naturally sets higher effort level for the more productive populations that tend to equilibrate to greater population densities, and vice versa (Beddington and May, 1977; Engen *et al.,* 1997) . Thus, proportional harvesting can return higher yields overall, whilst keeping more of the vulnerable populations extant (Lande, Sæther and Engen, 1997). The analysis shows that proportional harvesting is not perfect in this regard (the policy that maximises yield still results in some extinctions), but, in this theoretical analysis, it clearly outperforms quota-based harvesting. However, it is important to recognise that despite its obvious benefits proportional harvesting is currently not feasible in Central Africa (to begin with, it requires knowledge of population densities; Mockrin and Redford, 2011). Yields similar to proportional harvesting were possible under risk-neutral quota-based harvesting; however, at targets close to the optimum, there was an over 40% chance of extinction (Figure 2-5, Figure 2-6 and Figure 2-7). For the three duiker species under quota-based management, a risk-averse harvesting strategy appeared to be the most prudent, the trade-off being a 70-80% loss in harvesting productivity. Whether, when and how the potential, theoretical benefits of proportional harvesting can be translated into benefits for real bushmeat harvesting remains to be seen.

According to my model, blue duiker was the most high-yielding species (yields as high as 3.5 animals km^{-2} year^{-1}, s=1.65), followed by Peters' duiker (up to 0.69 (s=0.32)) and bay duiker (0.35 (s=0.16)). Out of the three species, bay duiker was particularly sensitive to harvesting, with recommended target offtakes as low as 1 duiker per 20 km^{2} year^{-1}. The recommended target quotas were noticeably higher over a shorter time horizon (5-20 years). For example, for Peters' duiker, the short-term (5 years; grey boxplots in Figure 2-4a) vs long-term (100 years; green boxplots in Figure 2-4a) target quota rates increased nearly three-fold: from 0.6 animals km^{-2} year^{-1} to 2 animals km^{-2} year^{-1}. However, if a 5-year harvesting horizon was used to set harvest targets, long-term species survival probability dropped to around 25% (Figure 2-4a).

Under proportional harvesting, the recommended harvest rates of 10%-16% annually were consistent across species, and were more precise and higher on average than the sustainable harvest rates (suggested by Noss, 1998a) of 1.2%-12.8%, 1.6%-12.8% and 2.3%-17.2% for Peters', bay and blue duiker, respectively. According to my model, the least conservative policy estimate of 13.5% by Noss (1998b) was too risky for bay but not for Peters' and blue duiker. My modelled estimates at the maximum yield (Table 2-2) were higher than sustainable offtakes calculated by Noss (2000) using Robinson and Redford formula, and Payne's (1992) estimates in Korup National Park, Cameroon (Table 2-2); the differences in the 3rd quartile (the best possible outcome) are particularly noticeable. Larger predicted ranges for meat yields in my model (particularly in the 3rd quartile) may be explained by the fact that unlike most studies (e.g. Hart, 2000; Noss, 1998; Van Vliet *et al.,* 2007) I used range estimates of K to parameterise the harvesting system. These estimates of carrying capacity were quite variable, for example, ranging from 10.2 blue duikers km^{-2} in the Ituri Forest, north-eastern Democratic Republic of Congo (Fa *et al.,* 1995) to around 70 blue duikers km^{-2} in north-eastern Gabon estimated by Feer (1993). The reasons for this discrepancy could be manifold: different measuring techniques (Schmidt, 1983), observation error (Wäber and Dolman, 2015; Dennis *et al.,* 2006; Field *et al.,* 2005), or indeed, a spatial gradient as suggested by Peres (2000) in his comparison of hunted and unhunted sites across the Amazonian rain forest making cross-habitat generalisations about the optimum harvesting rates more difficult. Unfortunately, my sample sizes were not sufficient to explore this in more detail.

I realise that my model is a simplification of real-life processes. Firstly, harvesting rates are not constant and are adjusted between years to reflect changes in perceived yields (Fryxell *et al.,* 2010). However, by examining survival and yields over different timeframes, this work presents a novel and a useful perspective on wild meat harvesting under uncertainty, using risk management framework for decision making in a simple and systematic way. Secondly, using a relatively simplistic analytical model such as the Beverton-Holt model provides certain advantages over stochastic simulation studies for particular species (Bordet and Rivest 2014; Canessa *et al.,* 2016; Jonzén *et al.,* 2002), such as more generalizable, robust conclusions that capture the most salient population dynamic features useful for exploring system sensitivity to different parameter values and guiding more detailed simulation studies of particular situations (Fryxell *et al.,* 2010; Lande, Sæther and Engen 1997). Other population models could easily be used instead of the Beverton-Holt model (Probert *et al.,* 2011), and employing different models would allow model uncertainty (ignored here) to be addressed. More sophisticated harvesting policies such as threshold harvesting policies (Engen, Lande and Sæther, 1997; Lande, Sæther and Engen, 1997), or no-take reserves are sometimes feasible (Vermeulen *et al.,* 2009; Vaughan and Long, 2007); however, in most cases and, certainly, in West and Central Africa, managers have relatively little control over resource users and harvest intensity (Fryxell *et al.,* 2010).

Table 2-2 Modelled meat yields (animals km^{-2} year^{-1}; for sustainable yields: survival probability≥0.90 over 100 years) for Peters' duiker *C.callipygus*, bay duiker *C.dorsalis* and blue duiker *C.monticola*, compared to sustainable meat yield estimates by Noss (2000) and Payne (1992).

Species	**Sustainable meat yields (animals km^{-2} year^{-1})**			**Maximum meat yields (animals km^{-2} year^{-1})**
	My model	**Noss (2000)**	**Payne (1992)**	**My model**
Peters'	0.1-1.3	0.07-0.08	-	0.1-3.75
Bay	0.05-0.6	0.02-0.1	0.16-0.33	0.25-1.3
Blue	0.1-2.4	0.85-1.27	2.38-4.18	0.05-6.3

Here, I developed a relatively simple model-based approach for informing decisions in bushmeat harvesting under high parameter uncertainty. The need to translate theoretical research into practical solutions which can facilitate decision-making in conservation has been widely recognised (Schonewald-Cox, 1988; Knight *et al.,* 2009; Hall and Fleishman, 2010) and a diverse range of tools is now available, in particular in marine conservation (Christensen and Walters, 2004; Link, Fulton and Gamble, 2010) and in spatial planning and prioritisation (Ball *et al.*, 2009; Pressey *et al.*, 2009). Recognising the need to make my modelling approach more accessible to bushmeat practitioners, I also built an online interactive application (using R Shiny package, R

Core Team (2018)) using my modelling approach. A screen shot of my online application is presented in Appendix 2-7. Originally, my online application was envisaged as a management tool that could be used for comparing outcomes of various management strategies under parameter uncertainty. At the moment the tool is not yet fit for purpose; however, it can be used to help understand the underlying structure that generates particular predictions, by varying parameter values, level of uncertainty and the duration of harvesting horizon for one of my study species (Peters' duiker *C.callipygus*). Practical implementations of conservation actions based on applications of modelling techniques are still relatively rare (though see Link, Fulton and Gamble, 2010). With further improvements, more sophisticated interactive decision-support tools can be developed, ideally with input from bushmeat practitioners.

Although my model could not eliminate uncertainty, by handling it in a systematic and transparent way (Johnson and Gillingham, 2004; Ruckelshaus *et al.,* 2013), it helped identify the impacts of uncertain parameters on decision-making (Frederick and Peterman, 1995; Canessa *et al.,* 2016), laying out boundaries for sustainable harvesting. The framework was applied to duiker *Cephalophus* spp*.,* but it can potentially be used to estimate sustainable harvest rates for any data-deficient exploited species. It is obviously preferable to use data to set prior belief wherever possible (Rout *et al.,* 2017; Canessa *et al.,* 2015). However, in the absence of any data, it is still possible to define priors on parameters based on expert judgement (Johnson and Gillingham, 2004). Such priors could still be used with my method, and I would argue that doing so would be better than not using modelling at all, or using modelling but ignoring uncertainty.

I demonstrated that quota-based harvesting strategy could be high-yielding; however, to make it sustainable, particularly in the long term, parameter uncertainty needs to be reduced. The alternative: to use a precautionary approach for setting harvest rates (described in Annex II of the UN Straddling Stocks Agreement as management approach 'intended to constrain harvesting within safe biological limits'), resulted in yield losses – an undesirable outcome given that bushmeat is an essential source of protein and additional income for many of the poorest people in

West and Central Africa (Njiforti, 1996; Wilkie and Carpenter, 1999; de Merode, Homewood and Cowlishaw, 2004; Fa *et al.,* 2014). In the next Chapter, I will explore, in silico, potential benefits of reducing parameter uncertainty over time. I will measure improvements in bushmeat yields, species survival probability and predictability of bushmeat yields for a number of harvesting strategies, using the adaptive management framework.

Appendices

Appendix 2-1 Duiker dataset used to estimate intrinsic rate of natural increase, r_{max} and carrying capacity, K. Population growth rates were estimated using Caughley and Krebs (C&K) (Caughley and Krebs, 1983) or Cole's (C) (Cole, 1954) method (see Appendix 2.2).

Species	r_{max}	K, Ind. Km^{-2}	Length of study	Location	Method
C.callipygus[1]	0.6$^{C\&K}$	-	2 months	Mossapoula, Central African Republic	76 net hunts, N=24
C.callipygus[2]	0.07-0.3^{C}	-	-	Bayanga, Central African Republic	N=36, some parameters are from literature or personal communications
C.callipygus[3]	0.5$^{C\&K}$	13.3-15.5	-	Near Makolou, Gabon	Study site=80ha; home ranges used to estimate density
C.callipygus[4]	-	7±1.8 ($\mu \pm se$)	March 1981 - May 1983	Kapituri, near Epulu, Ituri Forest, Democratic Republic of Congo	25 net drive counts

C.callipygus[5]	0.29[C]	-	-	-	From data in captivity
C.callipygus[7]	0.51[C&K]	6.7	March 1988 - December 1990	Near Makolou, Gabon	12 surveys, N=7
C.callipygus[11]	-	10.7	-	-	-
C.dorsalis[1]	0.55[C&K]	-	2 months	Mossapoula, Central African Republic	76 net hunts, N=40
C.dorsalis[2]	0.05-0.3[C]	-	-	Bayanga, Central African Republic	N=7, some parameters are from literature or personal communications
C.dorsalis[3]	0.51[C&K]	7.5-8.7	-	Near Makolou, Gabon	Study site=80ha; home ranges used to estimate density
C.dorsalis[4]	-	7±1.8 $(\mu \pm se)$	March 1981 - May 1983	Kapituri, near Epulu, Ituri Forest, Democratic Republic of Congo	25 net drive counts

C.dorsalis[5]	0.29[C]	-	-	-	From data in captivity
C.dorsalis[7]	0.49[C&K]	5.8	March 1988 - December 1990	Near Makolou, Gabon	12 surveys, N=8
C.dorsalis[8]	0.2[C]	-	12 months	Bioko and Rio Muno, Equatorial Guinea	Reproduction estimates derived from Payne (1992), age of last reproduction substituted by max recorded longevity
C.dorsalis[9]	-	1.9 (SD=1.41)	6 months	Lenda, Ituri Forest, Democratic Republic of Congo	40 net drive counts
C.dorsalis[9]	-	2.7 (SD=1.41)	4 months	Edoro, Ituri Forest, Democratic Republic of Congo	40 net drive counts
C.dorsalis[11]	-	7.1	-	-	-
C.monticola[1]	0.87[C&K]	-	2 months	Mossapoula, Central	76 net hunts, N=440

				African Republic	
C.monticola[2]	$0.12\text{-}0.3^{C}$	-	-	Bayanga, Central African Republic	N=38, some parameters are from literature or personal communications
C.monticola[4]	-	13.6±1.6 $(\mu \pm se)$	March 1981 - May 1983	Kapituri, near Epulu, Ituri Forest, Democratic Republic of Congo	25 net drive counts
C.monticola[5]	0.29^{C}	-	-		From data in captivity
C.monticola[6]	0.39^{C}	-	4 months	-	Reproduction estimates from literature
C.monticola[7]	$0.87^{C\&K}$	30.8	March 1988 - December 1990	Near Makolou, Gabon	12 surveys, N=44
C.monticola[8]	0.49^{C}	-	12 months	Bioko and Rio Muno, Equatorial Guinea	Reproduction estimates derived from Payne (1992), age of last reproduction

					substituted by max
C.monticola[9]	-	20.6 (SD=3.73)	4 months	Edoro, Ituri Forest, Zaire	40 net drive counts
C.monticola[9]	-	10.2 (SD=3.62)	6 months	Lenda, Ituri Forest, Zaire	40 net drive counts
C.monticola[10]	-	62-78	16 months (in 1971, 1972, 1973 and 1975)	Near Makolou, Gabon	74 ha, capture-recapture
C.monticola[11]		70			-
C.monticola[12]	0.85[C&K]	-	28 months between 1980 and 1984	Nera Makolou, Gabon	Capture-recapture
C.monticola[13]	-	61	March 1983	Ituri Forest, Congo-Zaire	500x4m line transects

[1]Noss (1998a); [2]Noss (1998b); [3]Feer (1988); [4]Koster and Hart (1988); [5]Noss (2000); [6]Fitzgibbon, Mogaka and Fanshawe (1995); [7]Lahm (1993); [8]Fa *et al.,* (1995); [9]Hart (2000); [10]DuBost (1980), [11]Feer (1996) quoted in Van Vliet and Nasi (2008), [12]DuBost (1979); [13]Wilkie and Finn (1990)

Appendix 2-2 Intrinsic rate of natural increase $\mathbf{r_{max}}$: Cole's and Caughley and Krebs formulae.

The intrinsic rate of natural increase in studies in my dataset was estimated using either Cole's (Cole, 1954), or Caughley and Krebs (Caughley and Krebs 1983) formula.

Following Cole's formula, intrinsic rate of natural increase r_{max} was estimated using:

$$1 = e^{-r_{max}} + be^{-r_{max}a} - be^{-r_{max}(w+1)} \qquad \textbf{Eq. 2-10}$$

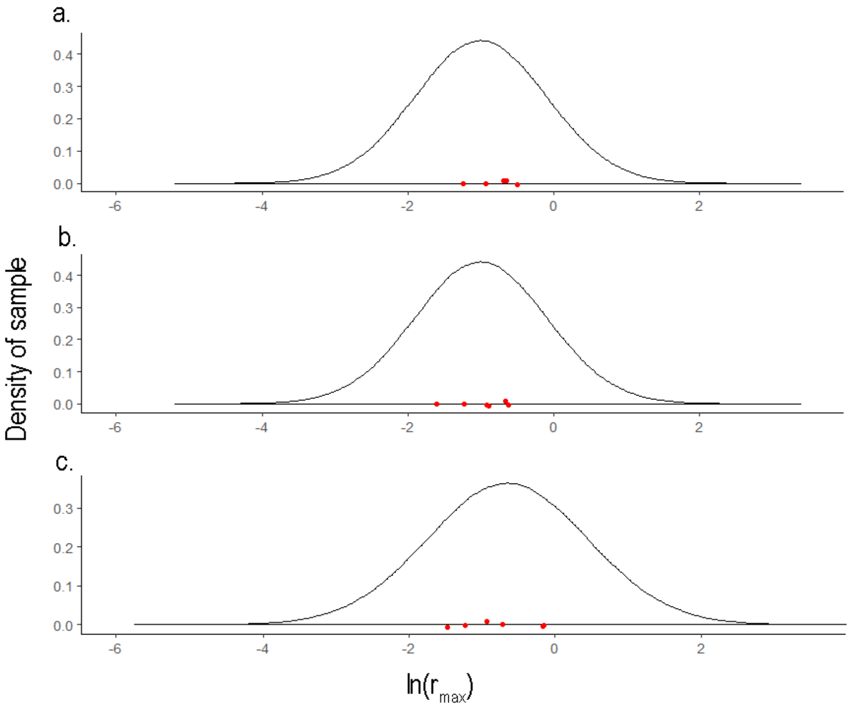
where a is the age at first reproduction, b is the annual birth rate of female offspring and w – age at last reproduction. Main criticisms of Cole's formula is that mortality before the age of last reproduction (w) is assumed to be zero for both adults and juveniles. In addition, because the population information is unknown for some of duiker species, the same values for reproduction parameters have been often used for blue *C. monticola*, red (*C. callipygus*, *C. dorsalis, C. nigrifrons, C. leucogaster, C. ogylbi*) or yellow *C. sylvicultor* duikers (van Vliet and Nasi 2008).

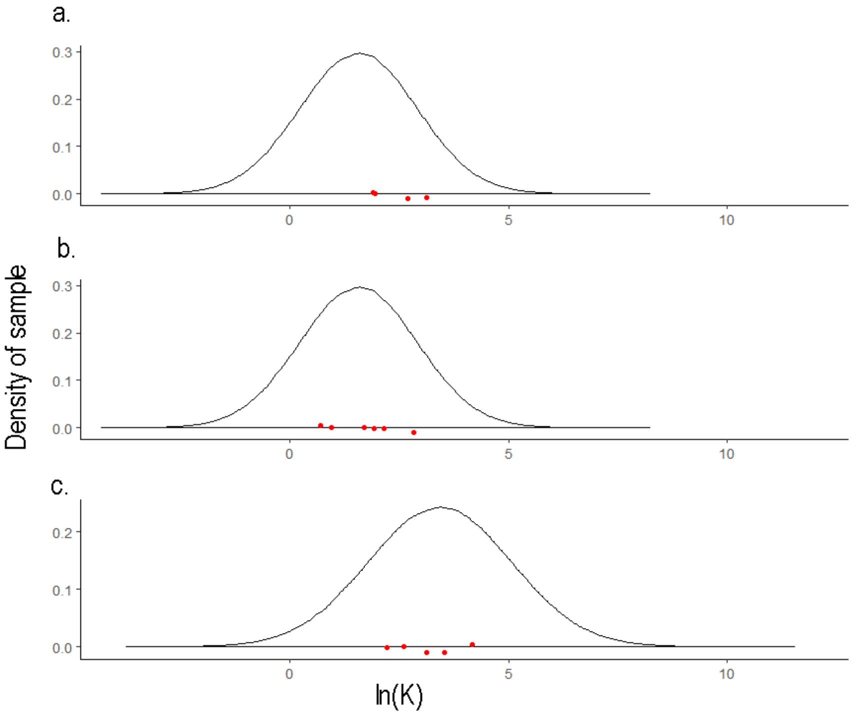
Because of poor knowledge of duiker mortality and fecundity (van Vliet and Nasi, 2008), some authors (Feer, 1988; Andrew J Noss, 1998; Dethier and Ghuirghi, 2000) use Caughley and Kreb's formula to estimate r_{max}:

$$r_{max} = 1.5P^{(-0.36)} \qquad \textbf{Eq. 2-11}$$

which only relies on assumptions about P - the mean population weight in kg. To take account of the age structure of the population, some studies used the percentage of mean weight of an adult duiker. Noss (1998b) used the actual weight of carcasses sold on markers.

Appendix 2-3 Sample densities for population growth rate, r_{max} , and carrying capacity, K, used to inform my harvesting models (i.e., Prior belief) as a result of sampling from a log-normal distribution (see 2.2.2.2), for a.) *C.callipygus;* b.) *C. dorsalis*; and c.) *C.monticola.* Field data is represented by red dots with sample sizes as follows: a.) $n_{r_{max}} = 5$; $n_K = 4$; b.) $n_{r_{max}} = 6$; $n_K = 6$; and c.) $n_{r_{max}} = 7$; $n_K = 7$.





Appendix 2-4 Detailed instructions for executing my method.

Yields from harvesting are estimated as follows:

$$Y(\varphi, N) = q \times \varphi \times N$$

$$Y(h) = h \qquad \textbf{Eq. 2-12}$$

where N is the population size (follows the Beverton-Holt model, see below), φ and h are the harvest rates and q is the catchability coefficient measuring the efficiency of each unit of hunting effort (equal to 1 for the purposes of this study).

I assume that animals are harvested at the end of each time step. The Beverton-Holt model has no age structure, and so the model assumes implicitly that every animal, including the newborns, can be extracted.

Using the Beverton-Holt model, the number of animals $N_t^{pre-harvest}$ at time t before harvesting is applied:

$$N_t^{pre-harvest} = \frac{r_t \times N_{t-1}^{post-harvest}}{(1+\frac{r_{t-1}}{K}) \times N_{t-1}^{post-harvest}} \qquad \textbf{Eq. 2-13}$$

where $N_{t-1}^{post-harvest}$ is the number of animals that survived harvesting in the previous time step, and r_t is the intrinsic rate of natural increase at time t, sampled from a log-normal distribution as described by Eq. 2-4.

Total losses to harvesting, or yield (Y_t) at time t:

$$Y_t = N_t^{pre-harvest} - N_t^{post-harvest} \qquad \textbf{Eq. 2-14}$$

If every animal in the population has been extracted in the previous time step (i.e., no animals remain), the number of animals at time t, $N_t^{pre-harvest}$ reverts to *0*.

Under the constant proportional harvesting policy, the yield Y_t depends upon the number of animals present at time t, and the harvest rate, φ. Under the constant quota-based policy, the yield Y_t depends upon the target quota, h only. The number of animals $N_t^{post-harvest}$ that remain in the population after harvesting at time t, is the higher of 0 (no animals survive to the next time step) and the number of animals after a proportion φ or target quota h of animals has been extracted.

$$N_t^{post-harvest} = \max(0, N_t^{pre-harvest} - \varphi \times N_t^{pre-harvest})$$

Eq. 2-15

$$N_t^{post-harvest} = \max(0, N_t^{pre-harvest} - h)$$

To examine the impact of harvesting intensity, I carry out different m-year simulations (100-, 50-, 20-and 5-year), each with a different harvest rate φ or h. I calculate yield Y_t as an average of m time steps. The rate of harvesting remains constant throughout the harvesting period of m time steps.

Each simulation has the same harvest rate(φ or h) but is subject to different parameter values, with additional variability introduced by stochastic growth rates (due to environmental stochasticity, see Eq. 2-3). Environmental stochasticity was present in simulations without parameter uncertainty and with parameter uncertainty. From a technical perspective, the differences between simulations for a given harvest rate result from selecting different population parameter samples (r_{max}, K, r, D) from a random number generator.

I use discrete time formulation rather than continuous: as long as there are no substantial fluctuations in population dynamics within a year, population growth per year is assumed to be a reasonable approximation. Similarly, I consider harvesting a set number of animals per year (rather than continuously) a reasonable approximation of the real-life processes.

Dealing with low sample sizes using chi-squared (χ^2) distribution

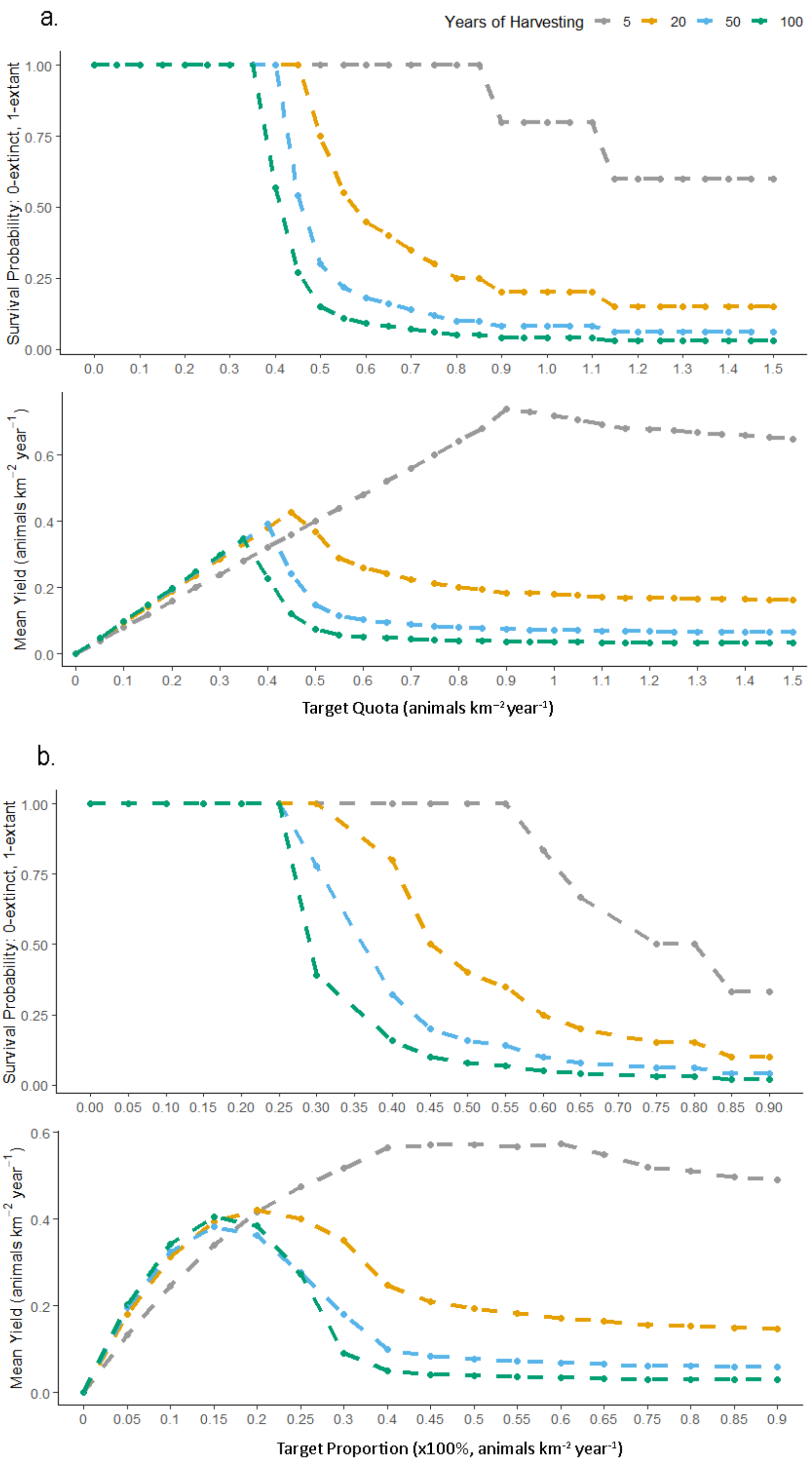
Because of the low number of estimates ($4 \leq n \leq 7$) for parameters in my dataset (i.e. observed parameter estimates), I was less confident that I was able to capture the true parameter values. To ensure that I included less likely harvesting scenarios I used the chi-squared distribution (χ^2) to estimate confidence intervals for standard deviations based on sample standard deviations (i.e. the observed standard deviations that informed the parameter distributions). I constructed the confidence intervals for the standard deviation using the χ^2-squared distribution at 95% confidence level with $n-1$ degrees of freedom:

$$\sqrt{\frac{(n-1)s^2}{\chi^2_{\alpha/2}}} \leq \sigma \leq \sqrt{\frac{(n-1)s^2}{\chi^2_{1-\alpha/2}}}\ , \qquad \textbf{Eq. 2-16}$$

where s is the sample standard deviation for each duiker species in our dataset, α is the significance level (=0.05) and χ^2 is the critical value found from the table of χ^2 values. For example, for Peters' duiker ($n = 5$) the $\chi^2_{0.025,4} = 0.484$ and the confidence intervals for standard deviation of $\ln(r_{max})$ are $0.179 \leq \ln(\sigma) \leq 0.86$. I use the upper tail (the higher value) as an estimate of standard deviation.

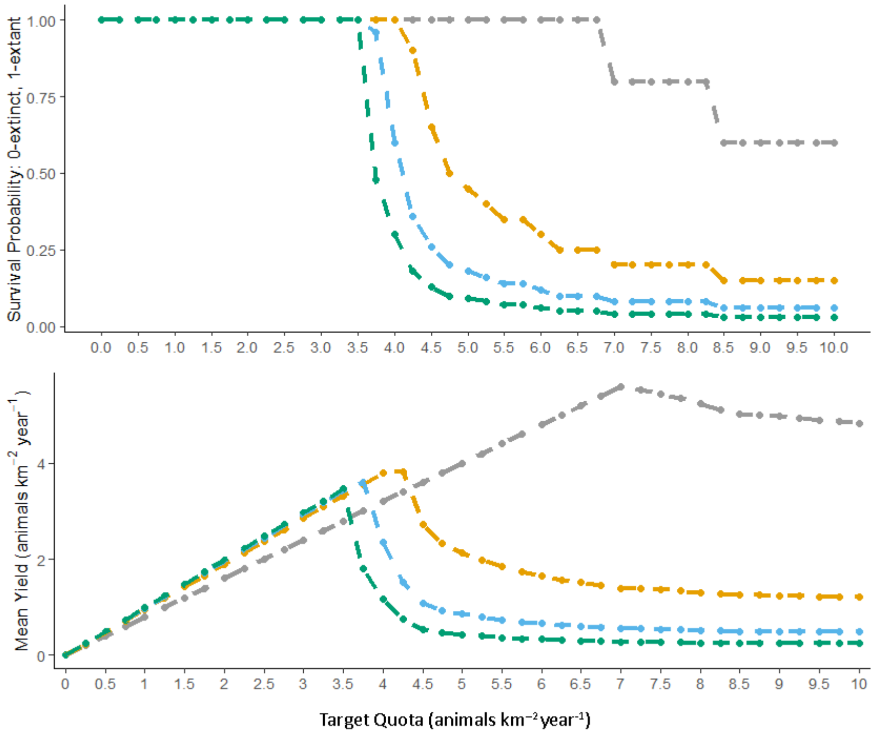
Appendix 2-5 Survival probability and average yields for bay duiker *C.dorsalis* (2-5.1) and blue duiker *C.monticola* (2-5.2) without parameter uncertainty and with environmental stochasticity, under (a.) constant quota-based and (b.) proportional harvesting over 5 (grey), 20 (orange), 50 (blue) and 100 (green) years of harvesting.

2-5.1. Bay duiker

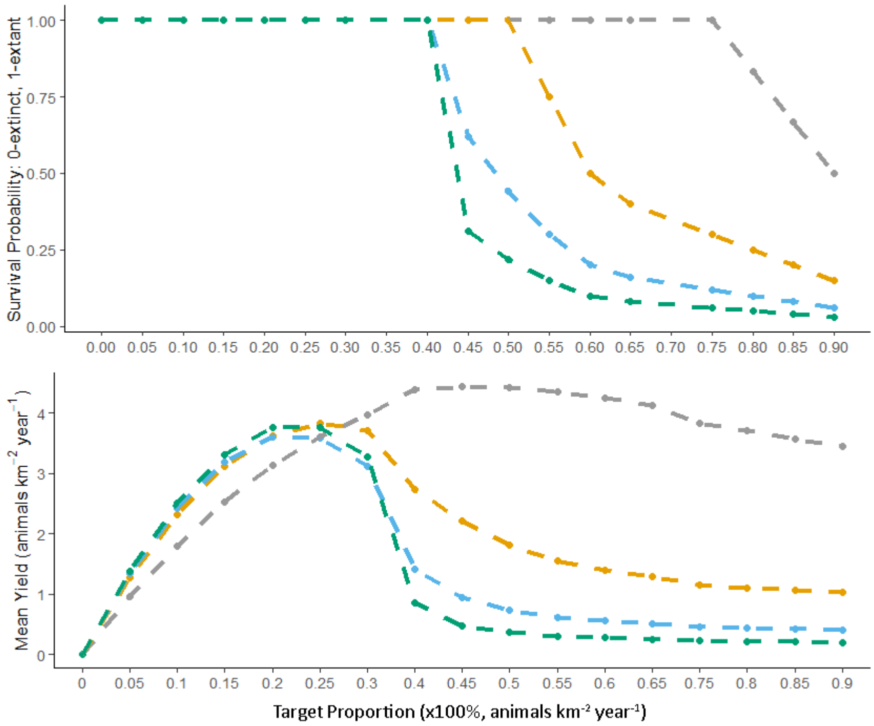


2-5.2. Blue duiker

a.

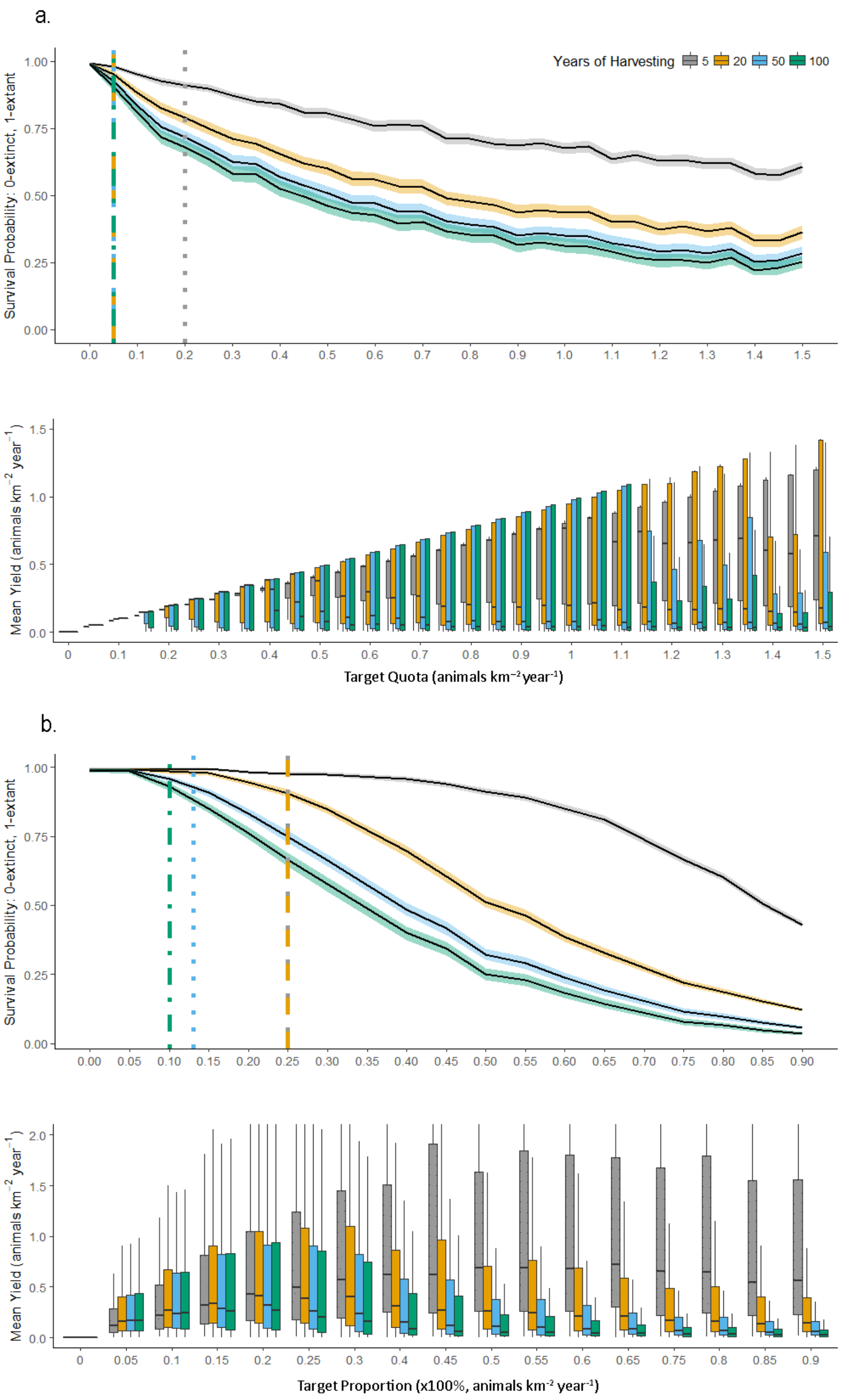


b.



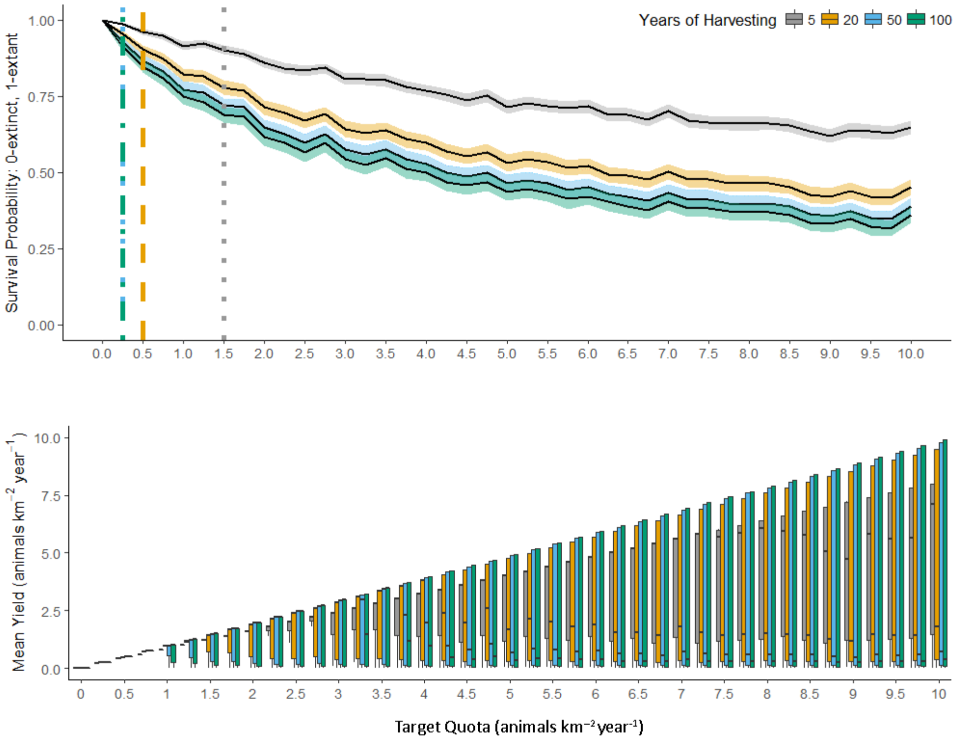
Appendix 2-6 Survival probability (with 95% confidence intervals) and estimated yields with parameter uncertainty and environmental stochasticity for bay duiker *C.dorsalis* (2-6.1) and blue duiker *C.monticola* (2-6.2) under (a.) constant quota-based and (b.) proportional harvesting over four time horizons (5, 20, 50 and 100 years). Dotted vertical lines represent harvest rates above which harvesting is expected to drive over 10% of duiker species to extinction over the harvesting horizon.

2-6.1. Bay duiker

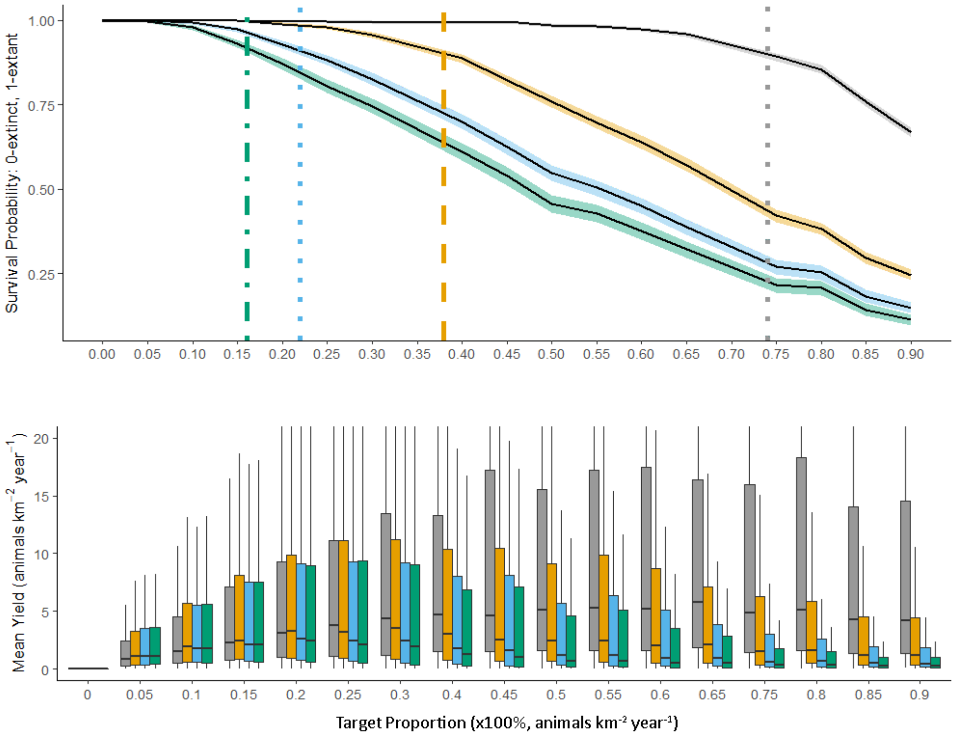


2-6.2. Blue duiker

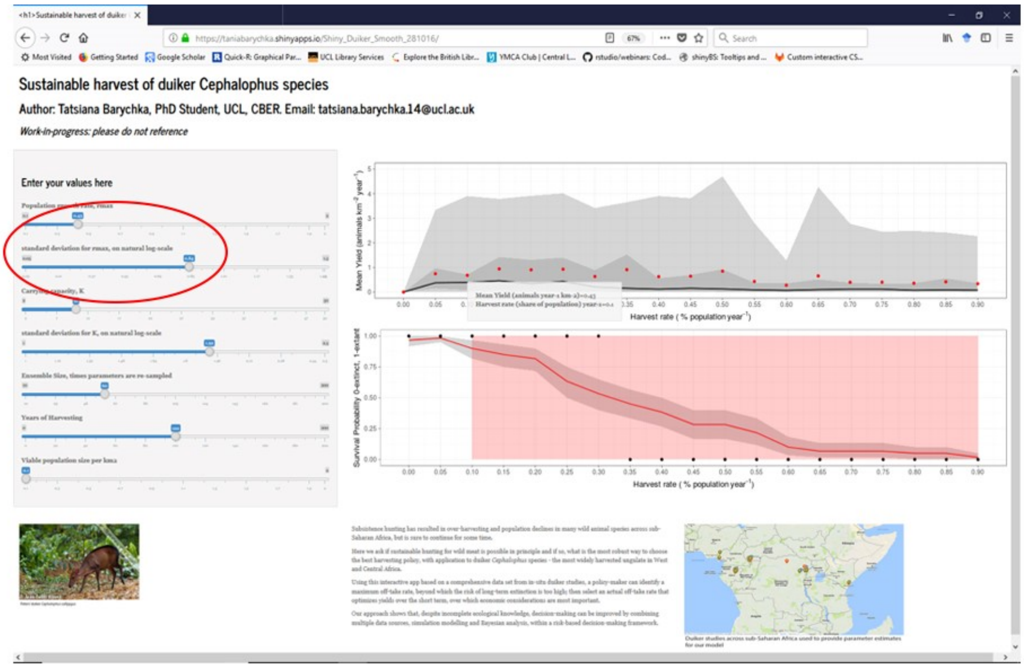
a.



b.



Appendix 2-7 A screenshot of my interactive online application built to support decision-making in bushmeat harvesting (for Peters' duiker *Cephalophus callipygus*). Users can adjust population parameter values r_{max} and K (as highlighted by red ovals) via sliders in the grey box on the left. The output includes average yields and survival probability, and is updated automatically after changes in input parameter values. The red area on the plots indicates harvest rates that could drive over 10% of animal population to extinction over the duration of harvesting horizon (also user-defined). The app is hosted at http://tinyurl.com/duikerantelope.



Sustainable harvest of duiker Cephalophus species

Author: Tatsiana Barychka, PhD Student, UCL, CBER. Email: tatsiana.barychka.14@ucl.ac.uk

Work-in-progress: please do not reference

Enter your values here

Population growth rate, rmax

standard deviation for rmax, on natural log-scale

Carrying capacity, K

standard deviation for K, on natural log-scale

Ensemble Size, times parameters are re-sampled

Years of Harvesting

Viable population size per km2

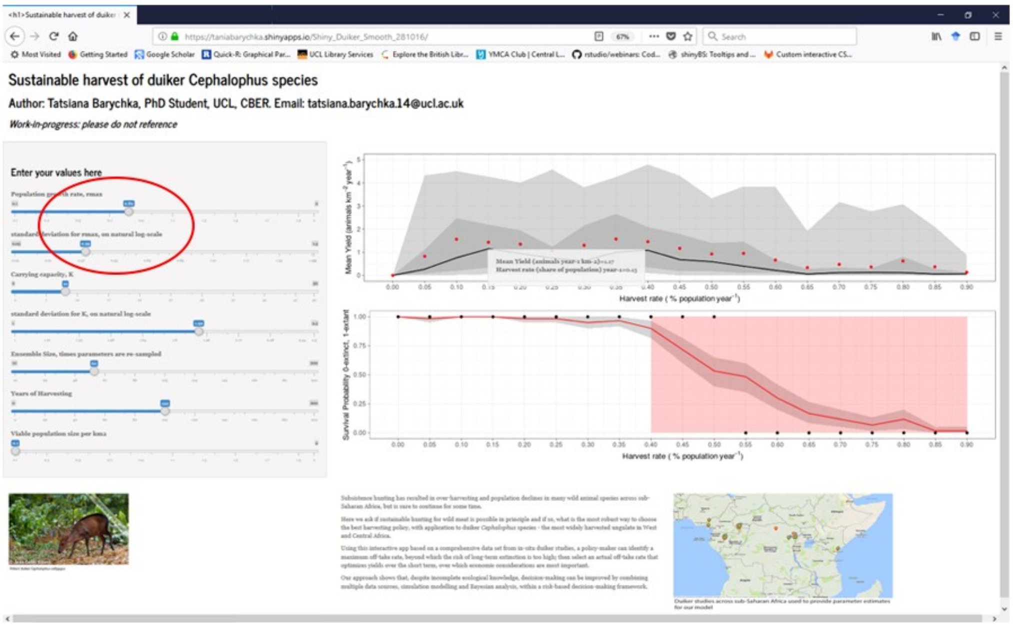
Subsistence hunting has resulted in over-harvesting and population declines in many wild animal species across sub-Saharan Africa, but is sure to continue for some time.

Here we ask if sustainable hunting for wild meat is possible in principle and if so, what is the most robust way to choose the best harvesting policy, with application to duiker *Cephalophus* species - the most widely harvested ungulate in West and Central Africa.

Using this interactive app based on a comprehensive data set from in-situ duiker studies, a policy-maker can identify a maximum off-take rate, beyond which the risk of long-term extinction is too high; then select an actual off-take rate that optimizes yields over the short term, over which economic considerations are most important.

Our approach shows that, despite incomplete ecological knowledge, decision-making can be improved by combining multiple data sources, simulation modelling and Bayesian analysis, within a risk-based decision-making framework.

Duiker studies across sub-Saharan Africa used to provide parameter estimates for our model



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Duiker studies across sub-Saharan Africa used to provide parameter estimates for our model

Chapter 3 Quantifying the value added from adaptive harvesting using a single-species population model

Abstract

It has been suggested that the long-term profitability of wild animal harvesting could be improved by using an adaptive management approach. An adaptive approach adjusts harvesting levels guided by some form of monitoring of the system's response. However, identifying conditions where additional monitoring would increase the profitability of wild meat harvesting is hard in practice. Here, I simulate the potential benefits of twenty different adaptive management strategies, differing in whether or not they consider uncertainty, their attitude to risk, whether or not the parameter estimates used to guide the choice of harvest rate are updated based on field data, and in whether they employ quota-based or proportional harvesting. I use changes in population density as a measure of systems' response to harvesting. The outcomes for these twenty strategies were simulated using real-life population parameter estimates, including parameter variability, for Peters' duiker *Cephalophus callipygus* - a species that is subject to bushmeat harvesting. For quota-based harvesting, the analysis predicts that adaptive harvesting could increase yields by 125%. Parameter updating conferred greater benefits than considering uncertainty, but considering uncertainty still helped. Although proportional harvesting outperformed quota-based in terms of duiker survival probability and yield (67%-139% higher yield), it appeared that if properly informed, quota-based harvesting could nonetheless be nearly as productive as non-adaptive proportional harvesting, without jeopardising species survival. Since proportional harvesting is considered to be rarely feasible in practice, this finding could have important implications for resource management.

3.1 Introduction

In Chapter 2 I focused on parameter uncertainty and how it affected the predictability of sustainable levels of harvesting of duiker *Cephalophus* spp. To quantify uncertainty surrounding predictions of sustainable harvest, I assembled multiple independent empirical estimates of population growth rate and carrying capacity for *C.callipygus, C.dorsalis* and *C.monticola* from across sub-Saharan Africa. The high variability of my assembled estimates could be attributed to a number of sources, from natural variation (demographic, spatial) (Lande, 1998), to imperfect observations of the system (Isaac *et al.*, 2014), to methods used to estimate parameter values (Parma, 1998). I was able to make recommendations for the optimal duiker harvesting based on estimated yields and survival probability using two conventional constant harvesting policies: quota-based and proportional harvesting. However, the uncertainty on expected yields was high, and keeping populations viable under high parameter uncertainty called for recommendations that were relatively conservative (risk-averse) because of a higher probability of extinction under medium-to-high levels of harvesting. The downside of this precautionary approach to harvesting was, of course, a potential loss of yield.

In reality, most natural systems are under increasing pressure to deliver resources: bushmeat, timber, fish, to the growing and often very poor and marginalised populations (Barnes, 2002; de Merode, Homewood and Cowlishaw, 2004; Milner-Gulland and Bennett, 2003). A common-sense alternative to restricting offtakes until more is known about the species was proposed by Holling (1978) and Walters (1986), and is known as adaptive management approach. The key elements of adaptive management - development and implementation of alternative management strategies, constant monitoring of system's responses and iterative modification of these management strategies – can, in theory, deliver sustainable resource use in highly uncertain systems (Keith *et al.,* 2011; Probert *et al.,* 2011). Crucially for bushmeat hunting this approach to resource management does not entail cessation or curtailment of activities; instead, management is implemented in the face of uncertainty and is used as an experiment, to gain information about the system and its responses to management at the appropriate spatio-temporal scale (Probert *et al.,* 2011; Walters, 1986; McCarthy, Armstrong and Runge, 2012). The approach is particularly suitable for dealing with parameter uncertainty (Chadès *et al.,* 2017) such as that observed in my duiker dataset.

In real-life systems, improvements in management outcomes are expected to flow from both expansion in knowledge of the system and the iterative adjustments of management policies as new understanding emerges (Chadès *et al.,* 2017; Wilgen and Biggs, 2011). However, the extent and the apportionment of these potential improvements to these different drivers is difficult to quantify in the field. Knowing if and where data gathering may add the most value to harvesting is crucial given ongoing conservation resource constraints (Rout *et al.*, 2018).

Here, I seek to quantify the potential benefits of both expansion in knowledge of the system (parameter updating) and the iterative adjustments of management policies applied in all 'adaptive' scenarios, using a simulated system which has been parameterised with real-life estimates of population growth rates and carrying capacities for Peters' duiker *C.callipygus* (Chapter 2). My focus is on improvements in both harvest yields and survival probability which I expect to result from monitoring the population's reponse to havesting (I used population density), and from gradual increase in knowledge of relevant population parameters (Rasch, 1989; Williams, 1996a). I compare these potential improvements for two conventional harvesting policies (quota-based and proportional), two levels of uncertainty (with and without uncertainty), two levels of parameter re-sampling (with and without parameter updating) and for three different attitudes to risk (average, neutral and averse; Pascual *et al.,* 2017). Quota-based harvesting involves targeting a quota of population (i.e. number of animals which could be below or equal to all animals present), while proportional harvesting involves targeting a proportion of animals present (Case, 2000; Rockwood and Witt, 2006).

In this Chapter I remove the unrealistic constraint of constant harvesting and progress to a harvesting strategy that adjusts the harvest rates on a yearly basis in response to information about the population. I use modelled animal densities, and estimates of populations' growth rates and carying capacities sampled from plausible population parameter ranges (Chapter 2). In real life, improvements in knowledge of the system could come from collecting estimates of animal densities at the beginning and the end of harvesting season (Williams, 1996b), and performing additional studies of animals' life histories (Elmberg *et al.*, 2006). To start addressing the question of the added value of information, I simulate a process where uncertainty is gradually reduced as more parameter estimates are obtained from a simulated ecosystem. The process of evaluating and choosing the best harvest rate is iterative; actions (to harvest or not to harvest) are combined into management strategies (rules that define how to harvest and at what rate), using a simulation to enact these strategies and to generate a stream of indicators (yields and survival probabilities), and using the objective of yield maximisation to choose among the time streams of indicators (Holling, 1978).

Exploratory modelling has been advocated as an important first step of the adaptive management process (Holling, 1978): not as a means to make precise quantitative predictions but as means to clarify management problems, identify important knowledge gaps and screen out policies that are likely to be ineffective (Keith *et al.,* 2011; Walters, 2007). Here, I explore potential benefits of reducing uncertainty using what might be described as a 'virtual ecology' approach (Hilborn and Mangel, 1997; Zurell *et al.,* 2010; Milner-Gulland and Shea, 2017). This approach creates a simulation of the interaction between duiker populations and decision makers who are guided by their own simulation models of those populations. This allows me to test different management strategies and quantify improvements in yields and species survival achieved by applying these alternative strategies.

Quota-based management is more common in real life (Mockrin and Redford, 2011); therefore, identifying benefits of gathering extra data (animal densities, number of newborns) under a realistic scenario of parameter uncertainty may be of practical interest for resource management. I expect more benefits in terms of meat yields and animal survival from combining adaptive management with quota-based than with proportional harvesting where only a share of (possibly declining) population is ever targeted.

3.2 Methods

3.2.1 Definitions

Harvesting policy. I implement two harvesting policies: quota-based harvesting and proportional harvesting.

Harvest rate. A yearly harvest target set for local population c as either an absolute number of animals km^{-2} year^{-1} (for quota-based) or as a percentage of remaining population (for proportional harvesting). The optimum harvest rate is the rate of harvesting expected to result in achievement of the management goal. The choice of the optimum harvest rate is also dependent on management strategy.

Management goal. The goal is to maximise the expected yield for each site i (and by extension, the overall average yield for all i simulated sites). Given the effect of parameter uncertainty on variability of harvesting outcomes, optimum harvesting was considered within the constraint of survival probability.

Management strategy. A combination of harvesting policy (quota-based/proportional), parameter updating ('yes' - estimates of species reproduction rates and carrying capacity are supplied to the decision model yearly, 'no'- no new parameter estimates are sent to the decision model), inclusion of parameter uncertainty ('yes'- a range of plausible parameter estimates are supplied, 'no'- a single estimate (one for each parameter) is supplied) and decision maker's attitude to risk (risk-neutral, risk-averse, risk-average).

Species model. A simulation of the true population dynamics for each local site i.

Decision model. A simulation used by decision makers in order to set harvest rates for each site i in each year involving running a single-species (the Beverton-Holt; Beverton and Holt, 1957) population model and selecting the optimum harvest rate for a given management strategy. These rates go on to affect the dynamics of the species model for population i.

3.2.2 Framework

My adaptive harvesting system consists of two interacting models: a) 'the species model', a model that simulates the true population dynamics ($N_{t,i}$) for i independent locations ('sites') over time t (Figure 3-1 in green), and b) 'the decision model', a model used by decision makers to identify the optimum harvest rates $h_{t+1,i}$ to guide the decision-making process (Figure 3-1 in orange).

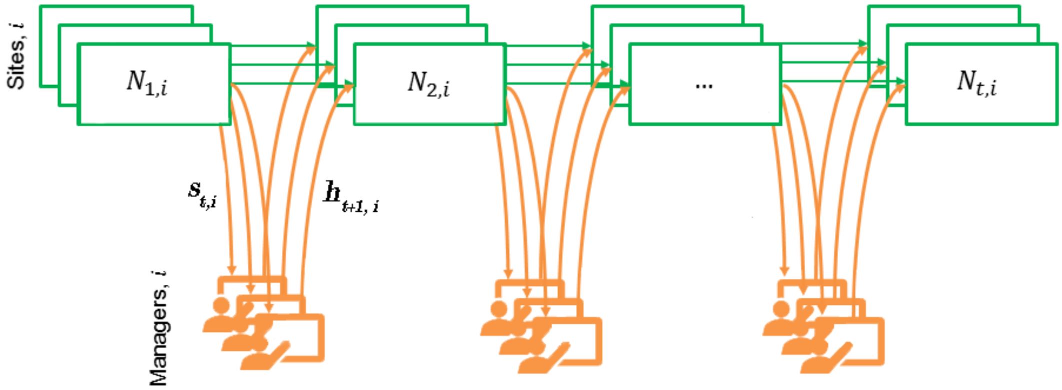


Figure 3-1 The two-model harvesting system: the species model (in green) simulates population dynamics ($\boldsymbol{N_{t,i}}$) for multiple sites $\boldsymbol{i}$ over time $\boldsymbol{t}$; the decision model (in orange) is used by decision makers to identify the optimum harvest rates $\boldsymbol{h_{t+1,i}}$ based on their knowledge of population growth rate, carrying capacity and population density in site $\boldsymbol{i}$ at time $\boldsymbol{t}$ ($\boldsymbol{s_{t,i}}$).

In the species model, the states of managed sites denoted with vector $s_{t,i}$, comprise of a finite set of local site-specific densities ($N_{t,i}$), population growth rates ($r_{t,i}^{true}$) and carrying capacities (K_i^{true}). I assume there exists a combination of population growth rate and carrying capacity that underlies true population dynamics for each site. Importantly, these parameters are not known to decision makers perfectly, but rather with different degrees of uncertainty. The exception is the theoretical 'perfect information' case which is included as a theoretical limit only. The decision model is a separate simulation model, used by decision makers to set harvest rates, based on the information available to the decision maker.

The interaction between the two models represents an iterative process where, in the decision model, a set of independent managers (one for each site i) interact with a set of independent local populations. Each year the managers first update their knowledge of the local species states ($s_{t,i}$) and second, react to this knowledge by running simulations of their decision models in order to choose the next set of harvest rates $h_{t+1,i}$. Depending on the management strategy, managers may improve their knowledge of the system by monitoring population densities, and by updating their estimates of population growth rates and carrying capacities.

The choice of the optimum harvest rate depends on the management strategy: a harvest rate at time t for a given system state is chosen from a finite pool of possible harvest rates h (quota, proportion) and is defined as an action that maximises expected yields over time t for a given risk-attitude (see 3.2.4.1.1). I assume that the chosen harvest rate is implemented in the next timestep. All simulations were run in R version 3.4.4 (R Core Team, 2018).

3.2.3 Model Formulations

3.2.3.1 Population Model

I use the Beverton-Holt population model (Beverton and Holt, 1957) to simulate population dynamics in both the species and the decision model, subject to either quota-based harvesting (Eq. 3-1) or proportional harvesting (Eq. 3-2):

$$N_{t+1,i} = \frac{r_{t,i}N_{t,i}}{1+[(r_{t,i}-1)/K_{t,i}]N_{t,i}} - q_{t,i} \text{ , where } \hat{Y}_{t,i} = q_{t,i} \qquad \textbf{Eq. 3-1}$$

$$N_{t+1,i} = \frac{r_{t,i}N_{t,i}}{1+[(r_{t,i}-1)/K_{t,i}]N_{t,i}} - \varphi_{t,i}N_{t,i} \text{ , where } \hat{Y}_{t,i} = \varphi_{t,i}N_{t,i} \qquad \textbf{Eq. 3-2}$$

where N_t is population density, K is carrying capacity and r is intrinsic growth rate and is equal to $e^{r_{max}}$ (Rockwood and Witt, 2006, p. 24), where r_{max} is the estimated maximal population growth rate in the absence of competition. The symbol $\hat{Y}_{t,i}$ denotes the yield achieved from site i in year t.

The total yield from all sites over the harvest horizon was calculated as:

$$\hat{Y} = \sum_{t=1}^{50} \sum_{i=1}^{100} \hat{Y}_{t,i} \qquad \textbf{Eq. 3-3}$$

where $\hat{Y}$ is the sum of expected yields $\hat{Y}_{t,i}$ from sites i (i in 1 to 100) over time t (50 years). I also calculate, for each of the ensembles, the median, and 1st and 3rd quartiles for the yield $Y_{t,i}$ over time, averaged across sites; and the fraction of populations that went extinct during the time course of the simulation, where extinction was defined as the density dropping below a threshold of 0.1 animals km^{-2}, based on the lower end of density estimates collected in areas of high harvesting intensity (same as Chapter 2; Hart, 2000; Lahm, 1993).

As in Chapter 2, population growth rates are subject to stochastic environmental variation in both models, as follows:

$$R_{t,i}^{(true)} \sim \mathbb{N}\{r_i^{(true)}, \sigma\} \qquad \textbf{Eq. 3-4}$$

where $R_{t,i}^{(true)}$is the value of r_i (or of r_i^{true}) that applies to site i in simulation year t and σ is the standard deviation for $r_i^{(true)}$ across all years, set at what I considered to be a reasonable value of 0.10 (Lande, Sæther and Engen, 1997), implying $\sigma = 0.10\, r_i^{(true)}$.

3.2.3.2 Parameters

Parameter estimates for Peters' duiker *C.callipygus* from a duiker dataset (Chapter 2 Appendix 2-1) were used as follows.

In the species model, i parameter ensembles $\{r_i^{true}, K_i^{true}\}$, one for each site, were drawn randomly from the prior distribution, defined as a log-Normal distribution:

$$\ln(r_i^{true}) \sim \mathbb{N}\{\ln(\hat{r}\,), \tilde{r}\}$$
$$\ln(K_i^{true}) \sim \mathbb{N}\{\ln(\widehat{K}), \widetilde{K}\} \qquad \textbf{Eq. 3-5}$$

where $\hat{r}$ and $\widehat{K}$ are the means of r and K, respectively; and $\tilde{r}$ and $\widetilde{K}$ are the standard deviations of the log-transformed values of r and K. For Peters' duiker, $\hat{r}$ = 0.44, $\tilde{r}$ = 0.14, $\widehat{K}$ = 9.70 and $\widetilde{K}$ =3.62 (Table 2-1). The resulting parameter ensembles were stored in a database consisting of one $\{r_i^{true}, K_i^{true}\}$ combination per site. In the species model, these underlying true population parameter values remained unchanged throughout the model run (see 3.2.2), with the addition of slight variation in growth rates between time steps due to environmental stochasticity (i.e. values for $R_{t,i}^{true}$ were re-drawn for individual time steps according to Eq. 3-4). Populations in each site were assumed to start at 50% of their respective carrying capacities (i.e. $N_{0,i} = 0.5 \times K_i^{true}$) to simplify programming and control the amount of uncertainty introduced into the models.

The parameters used in the decision model depended on the management strategy (see below).

3.2.3.3 Management Strategies

In total twenty management strategies were investigated. For each of quota-based harvesting and proportional harvesting, the strategies consisted of a theoretical best case (Perfect Information, Table 3-1; PI, Figure 3-3), a simple non-adaptive baseline (Global Rate, Table 3-1; GR, Figure 3-3) and eight adaptive strategies (Figure 3-2, Figure 3-3 and Table 3-1). Adaptive strategies differed from non-adaptive (Perfect Information and Global Rate) in that under the adaptive harvesting the decision model was supplied with an updated population density from the species model (Figure 3-1 and Table 3-1). Depending on whether the decision model was also supplied with the estimates of population growth rate and carrying capacity, the adaptive management strategies either included parameter updating (‘yes’, Figure 3-2, Figure 3-3; ‘P_+‘, Table 3-1) or did not include parameter updating (‘no’, Figure 3-2, Figure 3-3; ‘P_-‘, Table 3-1). The eight adaptive strategies consisted of two that ignored uncertainty (‘U_-‘, Figure 3-2, Figure 3-3 and Table 3-1), and six that considered uncertainty (‘U_+‘, Figure 3-2, Figure 3-3 and Table 3-1) with different attitudes to risk (average, averse and neutral; Figure 3-2, Figure 3-3 and Table 3-1). In this Chapter 3, I replaced risk-taking attitude with risk-average: a) risk-average harvesting resulted in harvest rates that were above risk-neutral but below risk-taking harvest rates; b) based on analysis in Chapter 2, risk-taking harvesting appeared imprudent (i.e. too risky) and therefore unlikely in practice.

Table 3-1 Parameterisation of the decision model: parameters were supplied with (+) or without (-) uncertainty (U) and updating (P). Each strategy was implemented for quota-based and proportional harvesting. Environmental stochasticity was included in the decision model by drawing a new value $R_{t,i}$ (Eq. 3-4) from a normal distribution centred on r_i (for Perfect Information and Global Rate) and on $r_{t,i}$ (for all adaptive management strategies) with standard deviation σ.

No.	Strategy	Population Parameter Inputs		Description
		Density	Growth Rate and Carrying Capacity	
1	Perfect Information (PI)	-	$r_i = r_i^{true}$ $K_i = K_i^{true}$	Explores a theoretical 'best case' scenario where the true population growth rates and carrying capacities for each site are known to decision makers, and therefore the optimal harvest rate can be identified with certainty.
2	Global Rate (GR)	-	$r_i = e^{\hat{r}_{max}}$ $K_i = \widehat{K}$	Uses the prior means on growth rate and carrying capacity for Peters' duiker ($\widehat{r_{max}} = 0.44$, $\widehat{K} = 9.70$) to estimate a single optimal harvest rate which is used for all sites. The method is the same as that described in Chapter 2. No parameter uncertainty was included.

3	$U_{-}P_{-}$	$N_{t,i}$	$r_i = e^{\hat{r}_{max}}$ $K_i = \widehat{K}$	In addition to global parameter estimates, the decision model is supplied a post-harvest site-specific population density $N_{t,i}$. The decision maker carries out a set of 50-year simulations of the decision model, each beginning at $N_{t,i}$, but with different harvest rates. The harvest rate returning the greatest mean yield from the decision model over the 50-year window is chosen as the harvest rate for the following year. The decision model simulations are all run at the prior means ($\widehat{r_{max}} = 0.44$, $\widehat{K} = 9.70$), thus ignoring uncertainty.
4	$U_{+}P_{-}$	$N_{t,i}$	$\ln(r_{t,i}) \sim \mathbb{N}(\ln(\hat{r}), \tilde{r})$ $\ln(K_{t,i}) \sim \mathbb{N}(\ln(\widehat{K}), \widetilde{K})$ -	As for $U_{-}P_{-}$, except that (1) the decision maker now incorporates parameter uncertainty by running, for each potential harvest rate, an ensemble of simulations, where for each member of the ensemble $r_{t,i}$ and $K_{t,i}$ are drawn from the prior; (2) because the decision model returns a distribution of yields for each potential harvest rate, then in order to select the harvest rate, the decision maker must define an

				attitude to risk. In a slight change from Chapter 2, I defined risk-neutral as maximizing the median yield, risk-average as maximizing the mean, and risk-averse as maximizing the 1st quartile on yields.
5	U_P_+	$N_{t,i}$	$\ln(r_{t,i}) = \frac{\sum \ln(r_{t,i}^{obs})}{t}$ $\ln(K_{t,i}) = \frac{\sum \ln(K_{t,i}^{obs})}{t}$ where $\ln(r_{t,i}^{obs}) \sim \mathbb{N}(\ln(r_{t,i}^{true}), \ln(\delta_r)^2)$ $\ln(K_{t,i}^{obs}) \sim \mathbb{N}(\ln(K_i^{true}), \ln(\delta_K)^2)$ with observation error $\delta_r = 1.1$ and $\delta_K = 3$	As for U_P_-, except that the decision maker updates their parameters as follows. A site-specific estimate of growth rate ($r_{t,i}^{obs}$) and carrying capacity ($K_{t,i}^{obs}$) (with observation error) are obtained from the species model on an annual basis, and are added to the decision-maker's database of parameters. The local parameter database is then used to update means on the local values of r and K. Through time, the parameters used in the decision model converge to the true local values, but the uncertainty in the parameters is ignored in the decision modelling. The harvest rate returning the greatest mean yield from the decision model over the 50-year window is chosen as the harvest rate for the following year.

6	U_+P_+	$N_{t,i}$	$\ln(r_{t,i}) \sim \mathbb{N}\,\{\ln(\bar{r}_{t,i}), \ln(\bar{\sigma}_{\bar{r}_{t,i}})^2\}$ $\ln(K_{t,i}) \sim \mathbb{N}\,\{\ln(\bar{K}_{t,i}),\ \ln(\bar{\sigma}_{\bar{K}_{t,i}})^2\}$ where $\ln(\bar{r}_{t,i}) = \frac{\sum \ln(r_{t,i}^{obs})}{t}$ $\ln(\bar{K}_{t,i}) = \frac{\sum \ln(K_{t,i}^{obs})}{t}$ $\ln(r_{t,i}^{obs}) \sim \mathbb{N}\{\ln(r_{t,i}^{true}), \ln(\delta_r)^2\}$ $\ln(K_{t,i}^{obs}) \sim \mathbb{N}\{\ln(K_i^{true}), \ln(\delta_K)^2\}$ with observation error $\delta_r = 1.1$ and $\delta_K = 3$ And $\ln(\,\bar{\sigma}_{\bar{r}_{t,i}}) = \frac{st.dev(\ln(\bar{r}_{t,i}))}{\sqrt{t}}$ $\ln(\,\bar{\sigma}_{\bar{K}_{t,i}}) = \frac{st.dev(\ln(\,\bar{K}_{t,i}))}{\sqrt{t}}$	Combines both parameter uncertainty and updating. Each year, and for each potential harvest rate, an ensemble of simulations is run (allowing uncertainty to be considered); where the parameters used for the ensemble are drawn from local means and standard deviations, updated as described for U_P_+. Through time, the means on parameters will converge on the true local values, whereas the standard deviations will decrease toward zero. The choice of harvest rate depends on attitude to risk.

The last four treatments in Table 3-1 are all adaptive, since they all use observed densities $N_{t,i}$ to inform the choice of optimal harvest rates $h_{t,i}$ for each year. However, strategy $U_{+}P_{+}$ is the most adaptive, since it: (a) uses observed densities $N_{t,i}$ to inform the choice of optimum harvest rates; and (b) explicitly incorporates uncertainty; which is (c) gradually reduced by improving site-specific knowledge. These three ideas lie at the heart of adaptive environmental management as described by Holling (1978).

3.2.4 Harvesting

3.2.4.1.1 The optimum harvest rate

For the non-adaptive harvesting, the optimum harvest rates were the rates expected to maximise average yields over the harvesting horizon.

For the adaptive harvesting, each ensemble $\{r_{t,i}, K_{t,i}, d_{t,i}\}$ was first paired with all possible harvest targets q / φ within their ranges ($0 \geq q \geq 3.5$ in steps of 0.10; $0 \geq \varphi \geq 0.95$ in steps of 0.05). The yield statistics were calculated for each $\{r_{t,i}, K_{t,i}, d_{t,i}\}$ and (q / φ) pair. Where uncertainty was not modelled (No. 1, 2, 3 and 5 in Table 3-1), a harvest rate that maximised the expected yield for site i and time t ($\hat{Y}_{t,i}$) was selected and implemented in the species model ($q_{t,i}$/ $\varphi_{t,i}$ in Eq. 3-1 and Eq. 3-2). Under parameter uncertainty (No. 4 and 6, Table 3-1), I used risk management framework to select the optimum harvest rate.

A risk attitude (risk-neutral, risk-average or risk-averse) was set at the beginning of each simulation run: I assumed it remained fixed for the duration of the harvesting period. For each ensemble $\{r_{t,i}, K_{t,i}, d_{t,i}\}$ paired with a harvest target h from q / φ possible ranges, the decision model predicted yield $\hat{Y}_{t,i}$. Because parameters were sampled with uncertainty, each given harvest rate resulted in a distribution of average yields. For a given risk attitude, the harvest rate that maximised meat yield (in the 1st quartile - for risk-averse harvesting; median - for risk-neutral harvesting; or average - for risk-average harvesting; Table 3-1, No. 4 and 6) was used as the optimum harvest rate in the species model.

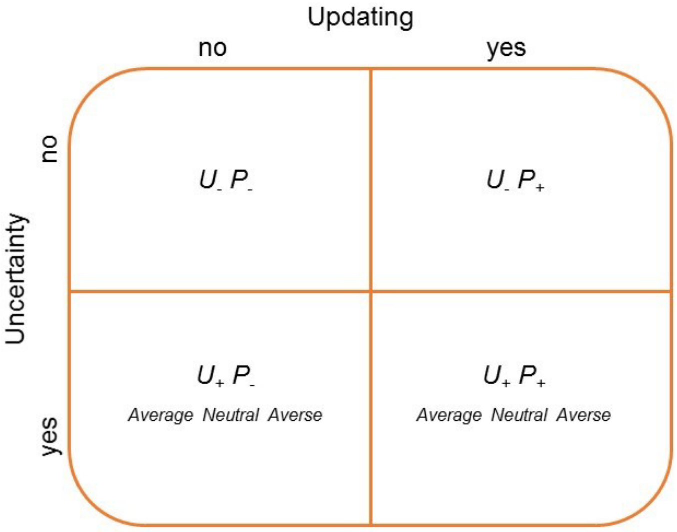


Figure 3-2 Adaptive harvesting with and without parameter uncertainty ($U_{+/-}$) and parameter updating ($P_{+/-}$); results were estimated for two harvesting policies (quota-based, proportional). For scenarions with uncertainty (U_{+}), results were estimated under three attitudes to risk: average, neutral and averse.

3.2.5 Site-specific analysis

For two individual sites that differed in whether their true parameter values (r_i^{true}, K_i^{true}) were above or below average (potentially, more or less productive sites, and therefore, more or less high-yielding), I examined meat yields and population densities for different strategies, to gain some understanding of the site-to-site variation in the benefits of adaptive harvesting, and also why some strategies performed better overall.

3.3 Results

3.3.1 Perfect Information vs Global Rate

A simple way to estimate the potential gain of adaptive harvesting is to compare the yields returned by the Global Rate strategy, with those returned by the Perfect Information strategy. For quota-based harvesting I found that Perfect Information returned yields that were 147% greater than Global Rate, with 95% confidence intervals of 142%-157% (Figure 3-3, grey triangle and diamond, respectively). This large difference indicates that adaptive strategies, which may get part-way to the Perfect Information case, could be highly useful. Similarly, for proportional harvesting, Perfect Information returned yields that were 35% (33%-36%) greater (Figure 3-3, orange triangle and diamond, respectively). Interestingly, the yield returned by Perfect Information with quota-based harvesting, was similar to that returned by Global Rate with proportional harvesting. In terms of species survival probability, Perfect Information returned survival probability of over 0.90 (mean of 0.92 (95% CI: 0.88-0.96) under quota-based, and mean of 0.99 (95% CI: 0.97-1) under proportional policy) (Figure 3-3, grey and orange triangles, respectively). This contrasts with average survival probability under Global Rate harvesting, of 0.50 (95% CI: 0.41-0.58) and 0.74 (95% CI: 0.65-0.83) for quota-based and proportional harvesting, respectively (Figure 3-3, grey and orange diamonds, respectively).

3.3.2 Adaptive vs Non-adaptive

For quota-based harvesting there was a clear overall tendency for adaptive strategies to outperform the Global Rate baseline (Figure 3-3, grey bars). Of the 8 adaptive strategies tested, 7 returned average yields that were significantly greater than the Global rate, sometimes by a wide margin; and the 8th ($U_+P_-\ Averse$) returned an average yield that was only just below Global Rate (as a result of harvest rates that were highly conservative - note higher survival probability under $U_+P_-\ Averse$ compared to the Global Rate). For proportional harvesting, the benefits of adaptive harvesting were much less pronounced (Figure 3-3, orange bars). All 8 adaptive strategies returned a mean yield above that of the Global Rate, a result which is unlikely by chance alone ($p<0.004$). However, the differences were not nearly as substantial as those seen for quota-based harvesting, and no single adaptive strategy returned an average yield that was significantly greater than Global Rate at $p \leq 0.05$ (Figure 3-3, note that red error bars on proportional strategies overlap with the mean returned by the Global Rate). Harvesting adaptively resulted in higher survival probability, compared to the Global Rate, for all but one ($U_+P_-\ Average$) adaptive harvesting strategy (quota-based or proportional).

3.3.3 Uncertainty vs Parameter Updating

For quota-based harvesting, parameter updating was much more beneficial than incorporating uncertainty. For example, the strategy for $U_{-}P_{+}$, which includes parameter updating but does not include any uncertainty, outperformed all strategies that did not include parameter updating (i.e. the P_{-} strategies). Moreover, once parameter updating was included in a strategy (the P_{+} strategies) there was clearly no additional effect of including uncertainty (Figure 3-3 right hand-side, grey bars). Without parameter updating (the P_{-} strategies) uncertainty may have helped in one case ($U_{+}P_{-}\ Average$ returned a greater mean than $U_{-}P_{-}$) although even here the difference was only marginally significant, and the strategy resulted in a marked reduction in survival compared to any other strategy (33% compared to the next lowest at 74%). Interestingly, including parameter updating resulted in yields that were very close to those returned from the Perfect Information case.

For proportional harvesting, parameter updating was also more important than incorporating uncertainty. Within the strategies not including parameter updating (the P_{-} strategies) there was no detectable difference in yield resulting from including uncertainty. The same was true within the strategies including parameter updating (the P_{+} strategies). In contrast, strategy for $U_{-}P_{+}$, which includes parameter updating but does not include any uncertainty, outperformed all strategies that did not include parameter updating (i.e. the P_{-} strategies).

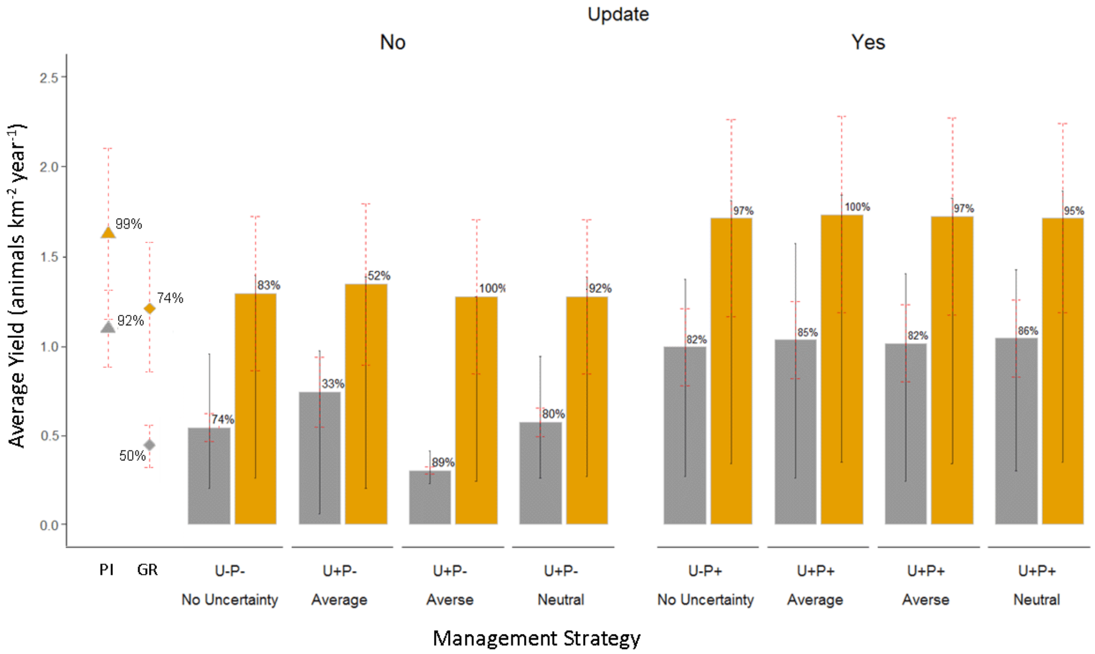


Figure 3-3 Average estimated yields from harvesting Peters' duiker from 100 simulated sites over 50 years, with and without updating population parameters (Yes/No) using quota-based (in grey) and proportional (in orange) harvesting. The grey error bars show ±2 standard deviations from the distribution of local yields, whereas the red error bars show ± 2 standard errors on the mean of that distribution. The theoretical best yields (Perfect Information, PI) are denoted by triangles (orange for proportional, grey for quota-based); the Global Rate (GR) yields from proportional and quota-based harvesting are denoted by orange and grey diamonds, respectively. Associated average species survival probabilities are reported next to average yields as percentages.

3.3.4 Risk Attitude

If implemented with parameter updating ('Update – Yes', Figure 3-3), adaptive harvesting was 125% (0.55 animals km^{-2} year^{-1}, 95% CI: -0.26-1.37, p=0.50) more high-yielding for quota-based strategies and 43% (0.51 animals km^{-2} year^{-1}, 95% CI: -0.31-1.32, p=0.63) more high-yielding for proportional harvesting than the non-adaptive Global Rate harvesting. Within harvesting policies with parameter updating, risk-attitude mattered little, with all risk-attitudes returning very similar yields and survival probability.

If parameter updating was not implemented (‘Update – No’, Figure 3-3), the relative increase in yield from adaptive management under quota-based harvesting ranged from 23% (0.1 animals km^{-2} year^{-1}; 95% CI: -0.40-0.60, p=0.98) under the ‘no-uncertainty’ strategy ($U_{-}P_{-}$), to 41% (0.30 animals km^{-2} year^{-1}, 95% CI:-0.71-1.31, p=1) under the risk-average strategy. These relative improvements in yield were more modest for proportional harvesting, ranging from 8% to 10% (0.1-0.14 animals km^{-2} year^{-1}).

Without parameter updating, the non-adaptive quota-based Global Rate outperformed risk-averse harvesting for the same policy by estimated 0.13 animals km^{-2} year^{-1} (95% CI: -1.14-0.88, p=1). The corresponding survival probabilities under the Global Rate harvesting were however relatively low: 0.50 (0.41-0.58) and 0.74 (0.65-0.83) for quota-based and proportional harvesting, respectively.

3.3.5 Quota-based vs Proportional Harvesting

Proportional harvesting outperformed quota-based by 0.73 animals km^{-2} year^{-1} (95% CI: 0.56-0.90, p=0), with the the highest difference between the policies (139% or 0.76 animals km^{-2} year^{-1}, 95% CI: 0.46-1.05, p=0.00) when no parameter updating was implemented (‘Update – No’, Figure 3-3).

Without parameter updating, the risk-average adaptive approach to harvesting (i.e. optimising for the mean average yield; $U_{+}P_{-}\ Average$, Figure 3-3) produced the highest expected yields: 0.74 animals km^{-2} year^{-1} (95% CI: 0.53-0.94) and 1.34 animals km^{-2} year^{-1} (95% CI: 0.88-1.79) for quota-based and proportional harvesting, respectively. For quota-based harvesting, the risk-neutral approach ($U_{+}P_{-}\ Neutral$, Figure 3-3) was the second best management strategy (0.57 animals km^{-2} year^{-1}, 95% CI: 0.50-0.64), closely followed by the harvesting strategy without parameter uncertainty ($U_{-}P_{-}$; 0.54 animals km^{-2} year^{-1}; 95% CI: 0.84-1.70) and the Global Rate non-adaptive strategy (0.44 animals km^{-2} year^{-1}, 95% CI: 0.36-0.51).

Both ‘no-uncertainty’ and risk-neutral strategies resulted in significant improvements in species survival compared to risk-average harvesting: from 0.33 (95% CI: 0.26-0.40) to 0.74 (95% CI: 0.67-0.81), and to 0.80 (95% CI: 0.73-0.87), respectively. Expected quota-based yields were at their lowest when survival probability was maximised and no parameter updating took place; here, proportional harvesting was over three times more high-yielding than quota-based harvesting, yielding an extra 0.96 animals km^{-2} year^{-1} (95% CI: 0.27-1.65, p=0.00).

For proportional harvesting without updating, the ‘no-uncertainty’ and the risk-neutral harvesting yielded on average 1.29 animals km^{-2} year^{-1} (95% CI: 0.87-1.72) and 1.27 animals km^{-2} year^{-1} (95% CI: 0.84-1.70), respectively, with the risk-averse being the lowest-yielding approach to harvest rate selection.

Under parameter updating (‘Update – Yes’, Figure 3-3) the difference between harvesting policies (quota-based vs proportional) was reduced to 0.7 animals km^{-2} year^{-1} (0.37-1.03, p=0) (or 69%), largely due to a 96% increase in quota-based yields. Expected yields did not differ significantly between policies at 95% confidence level (two standard errors overlap – see red dotted line in Figure 3-3) under parameter updating; however, I would expect proportional harvesting to be more high-yielding than quota-based.

The difference in estimated yields between adaptive quota-based harvesting with updating and adaptive proportional harvesting without updating was not significant (0.26 animals km^{-2} year^{-1}, 95% CI: 0.06-0.57; p=0.15) suggesting that quota-based harvesting could produce yields similar to proportional harvesting if parameter knowledge was improved as part of species management.

3.3.6 Site-specific Analysis

Since the results indicated strongly that parameter updating was beneficial whereas uncertainty was not, I report the results of the site-specific analysis for parameter updating only.

Sites with higher than average growth rate and/or carrying capacity ($\widehat{r_{max}} = 0.44$, $\widehat{K} = 9.70$ for Peters’ duiker, see Table 2-1) benefited more from parameter updating than sites with parameters close to or below the average. For example, in site 49 ($r_{max} = 1.33, K = 4.15$) adaptive quota-based harvesting with parameter updating yielded an extra 0.6 animals km^{-2} year^{-1} compared to adaptive harvesting without updating: an increase in yield of 45%, with no adverse impact on species survival probability (Figure 3-4e).

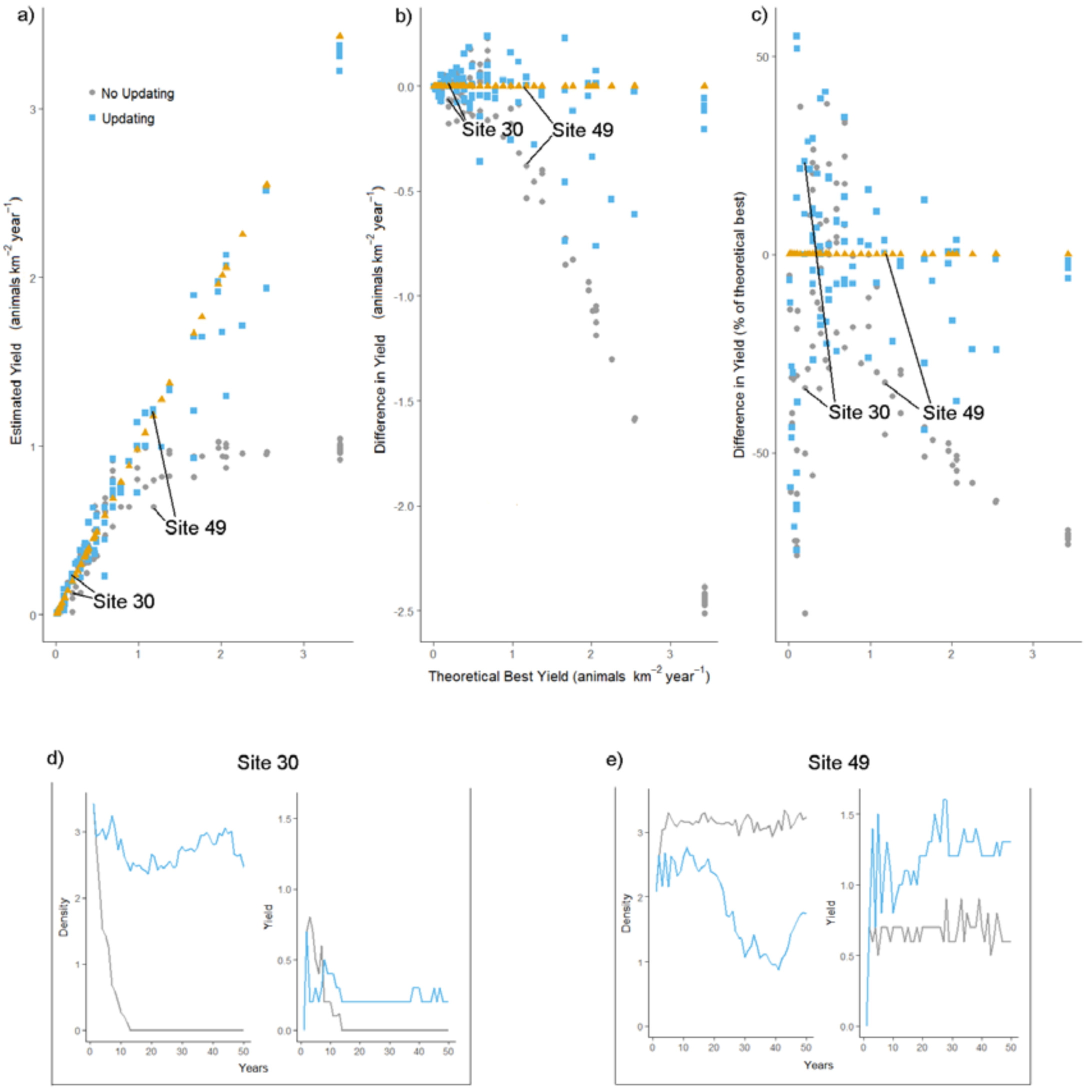


Figure 3-4 Estimated yields from applying adaptive approach under quota-based harvesting with (in blue) and without (in grey) parameter updating, versus a theoretical best (in orange) in (a); the corresponding difference in yields expressed as (b) number of animals km^{-2} year^{-1} and (c) a proportion of theoretical best, illustrated using density and yield time series for sites 30 (d) and 49 (e).

For sites with lower than average growth rates and/or carrying capacities (e.g. site 30: $r_{max} = 0.15, K = 6.84$, Figure 3-4d), 9% more harvesting trajectories (survival probability of 64% versus 73%) resulted in extinction under quota-based harvestingwithout parameter updating, compared to 2% more (survival probability of 96% versus 98%) in sites with population growth rate above the mean.

Under proportional harvesting, survival probability increased with parameter updating from 84% to 88% for populations with growth rate below the mean, and remained at 100% for sites with population growth rate above the mean. For quota-based harvesting, a minimum survival probability of 90% of species was maintained in 84% of sites with updating, compared to 65% of sites without updating. The average duration without extinction was also slightly higher: 43 versus 39 years, respectively. In sites with population parameters closer to their expectation, expected yields were close to their theoretical best (Appendix 3-1).

A decision tree based on my findings is presented in Appendix 3-2.

3.4 Discussion

A better understanding of species dynamics has often been quoted as one of the requirements for effective management: more population data such as time series of species densities and estimates of population parameters, would help discriminate between competing population models so that more precise management actions could be taken (Walters, 1986; Ingram *et al.,* 2015; Milner-Gulland and Bennett, 2003). However, such data are scarce, particularly in developing countries (Taylor *et al.*, 2015). With species surveys prohibitively expensive, time consuming and occasionally unfeasible (Coad *et al.*, 2013), I wanted to see if and when calls for more data were justified and what kind of information would be most useful (Lindenmayer and Possingham, 1996; Field, Tyre and Possingham, 2005; Tulloch *et al.*, 2013). Here, I implement a simulated model of adaptive management constrained by real-life parameter estimates for the commonly-hunted Peters' duiker *C.callipygus*. My aim was to identify situations, in silico, where extra monitoring (population density, parameter estimates) as part of the adaptive management framework could bring significant improvements in yield and species survival.

Monitoring how populations responded to harvesting was beneficial in terms of meat yield and species survival, particularly for the quota-based policy. However, to maximise these potential benefits of adaptive management, such as an up to 125% increase in yield under quota-based harvesting, decision makers would need to incorporate a regime of continuously improving parameter estimates. My results suggest that parameter updating contributed 96% and 35% to this potential increase in yield for quota-based and proportional harvesting, respectively. The expected increase in yield from parameter updating was very similar between the policies (0.45-0.5 animal km^{-2} year^{-1}) in absolute terms. Importantly, adaptive quota-based harvesting with parameter updating allowed the yield to be maximised while maintaining a viable duiker population (survival probability$\geq$0.9).

Although proportional harvesting outperformed quota-based on average (Figure 3-3), yields similar to those expected from proportional harvesting without updating, could be achieved by quota-based harvesting with parameter updating. Accurate and precise estimates of population densities are key to quantifying sustainable harvesting levels (Van Vliet *et al.*, 2015) both under quota-based and proportional harvesting. As quota-based remains the most commonly used harvesting strategy (Mockrin and Redford, 2011), these results are particularly pertinent: unless adaptive management is implemented, less profitable risk-averse harvesting might be necessary in order to maintain viable populations (Van Vliet *et al.*, 2015). Admittedly, estimates of population densities and reproduction rates are difficult to obtain in real life, particularly in sub-Saharan Africa (Abernethy *et al.,* 2013; Ingram *et al.,* 2015). Bushmeat market data (records of bushmeat sales) are often used as a proxy for hunted species densities and to assess sustainability of bushmeat harvesting (Noss, 1998; de Merode, Homewood and Cowlishaw, 2004; Cowlishaw, Mendelson and Rowcliffe, 2005; van Vliet *et al.*, 2012). Although market data provides a useful record of bushmeat sales (Taylor *et al.*, 2015), this data is heavily dependent on harvesting intensity (Noss, 1998), and levels of harvesting vary seasonally and by location (Lindsey *et al.,* 2013). The amount and the quality of species-level data (such as animal densities) is on the rise as new methods such as drones (Koh and Wich, 2012) and mobile phones (Tulloch *et al.,* 2013*;* Parham *et al.,* 2017*)*, which also record metadata that can be used as proxy for sampling effort (Isaac *et al.*, 2014), are used more widely for collecting species- and ecosystem-level data.

My results suggest that the most significant improvements will come from updating in sites with higher than average growth rates, i.e. more productive populations (Figure 3-4 and Appendix 3-1). Collecting additional data (Canessa *et al.*, 2015) was less profitable in unproductive populations; however, it led to noticeable improvements in probability of survival compared to uninformed harvesting: by 9% in sites with lower than average growth rates. This makes a strong case for better information in both highly productive (for Peters' duiker - above yields of 1 animal km^{-2} year^{-1}; Chapter 2) and less productive systems. Adaptive harvesting with parameter updating is essential if a minimum demand of 1.5 Peters' duiker km^{-2} year^{-1}, estimated based on wildlife consumption in sub-Saharan Africa (Fa, Currie and Meeuwig 2003), is to be satisfied. This minimum demand for Peters' duiker of 1.5 animals km^{-2} year^{-1} was met in 13 site years in total (0.3% of total site years) under quota-based harvesting without parameter updating, compared to 1272 site years (24% of total site years) with updating.

Detailed examination of estimated yields under parameter uncertainty with and without updating may have some interesting implications for decision making. In particular, for quota-based harvesting, introducing parameter uncertainty may lead to a reduction in harvesting profitability (Van Vliet *et al.*, 2015), particularly without updating parameter estimates. For example, if parameter updating is not feasible, it may be nearly as or even more high-yielding to put limited conservation resources towards updating animal density estimates and to not include uncertainty in the decision-making (Williams, 1996a; Van Vliet *et al.*, 2015), or even use the non-adaptive Global harvest rate.

My analysis in Chapter 2 suggested that including paramater uncertainty benefited the decision-making process, by exposing trade-offs between yield and species survival (Milner-Gulland and Shea, 2017), which were likely in reality given the general lack of population-level data (Van Vliet *et al.*, 2015), as well as other sources of uncertainty such as environmental stochasticity. This Chapter shows that, once harvesting adaptively (updating harvests each year, using a model initialized with population estimates taken from the field), the potential benefits of incorportating uncertainty into decision-making appear to be slight. The exact reasons for this are hard to diagnose; however, focussing on quota, there is a strong overall tendency for all of the adaptive harvests to reduce the quota for the next harvest, when the population estimate is low. This is likely to prevent most extinctions, and to reduce the tendency for overharvesting also.

Caveats and the next steps

Monitoring r and K: Here, I assume that year-to-year variability in observations of r_i results from environmental stochasticity and observation error, and year-to-year variability in observations of K_i comes from observation error only. Under these assumptions, parameter variability (but not the environmental stochasticity) will decline and tend towards the truth as more observations are collected from the species model. In real life, gathering parameters can generate very wide estimates due to stochastic variations in population demographics (Lande, Engen and Saether, 1995), environmental conditions (Lande, 1998; Jonzén *et al.*, 2002), sampling and modelling techniques (Gotelli and Colwell, 2001; Isaac *et al.*, 2014) so it may be near-impossible to home into the ‘true’ parameter estimates (even if they existed). More parameter estimates would need to be collected for the benefits of parameter updating to become apparent given natural variation in populations’ demographic rates. In addition, my assumption of starting densities at half carrying capacity may not hold for many overexploited populations, where population densities have been reduced by more than 50% due to hunting and other human-made pertrubations (Lahm, 1993; Hart, 2000). Lower-than-assumed starting population density would result in higher extinction rates and lower yields than currently modelled.

In practice, obtaining estimates of population parameters and densities in a systematic fashion is a big financial and logistical ask. Data on harvesting rates (hunting permits, fishing quotas) and the resulting yields is more obtainable, particularly in fisheries management. The next step for this work could be to use changes in bushmeat yields (which could be obtained from bushmeat market data or household surveys; Foerster *et al.*, 2011; Nielsen, Jacobsen and Thorsen, 2014; Taylor *et al.*, 2015) rather than densities to measure system's response to harvesting (though see above regarding variable effort).

Time Horizons: The duration of harvesting horizon is an ongoing concern for policy evaluation (Holling, 1978). Should the yields and survival probability be evaluated over a 5-year period or over 100 years? Here, yearly outputs were averaged (Beddington and May, 1977); however, one could argue that high yields today are more important than high yields in 50 years' time (Coad *et al.*, 2013; Lindsey *et al.*, 2013). The choice of time horizon and inter-temporal evaluation comes down to contrasting stakeholder objectives (e.g. yields vs long-term sustainability) and is a political, economic and even an ethical question (Holling, 1978).

I found that the duration of the evaluation period could have a strong impact on the realised sustainability of harvesting (Lande, 1998). If estimated over a short time horizon (5 years or less; results not shown here) yields and survival probability appeared higher than if estimated over longer time periods, because it could take overharvesting years to manifest through depressed population densities (Lande, 1998). This was particularly true for highly productive populations.

Some of the population trajectories I examined seemed to stabilise following 15-20 years of data collating (Figure 3-4d,e). It is possible that the value of additional parameter sampling is maximised at some intermediate level and diminishes thereafter. It would be interesting to quantify the relative value of updating estimates of population growth rate and carrying capacity, with a view that management and monitoring are pursued only to the extent that the reduction in parameter uncertainty improves management outcomes (McCarthy, Armstrong and Runge, 2012).

Local vs Regional View: In this study my aim was to examine potential benefits of parameter updating on average over 100 simulated sites. A more pertinent question may be to target improvements in yields on a local 'site' scale, i.e. to develop harvesting strategies aimed at ensuring that the minimum demand for bushmeat is met on a local scale (e.g. village, community) taking into consideration seasonal availability of alternative sources of protein and income (Brandon and Wells, 1992; Wilkie, Sidle and Boundzanga, 1992; Vermeulen *et al.*, 2009; Nasi, Billand and van Vliet, 2012).

Fixed management strategies: Here I assume that once selected, a harvesting policy (for example, risk-averse quota) is immutable throughout the harvesting period: this is known as passive adaptive management (Van Wilgen and Biggs, 2011; McCarthy, Armstrong and Runge, 2012). A more useful and realistic approach may be to allow the decision model to switch between management strategies to meet changing objectives such as shifts in demand for bushmeat or conservation priorities. It is also possible to incorporate experimenting in the decision process (active adaptive management; Chadès *et al.,* 2017; McCarthy, Armstrong and Runge, 2012) allowing the model to deviate from the optimum harvesting rate / strategy to help learn more about the system. Even though active adaptive management runs a higher risk of sub-optimal outcomes in the short term, this approach accelerates learning and promotes achievement of management goals in the long term (Probert *et al.,* 2011).

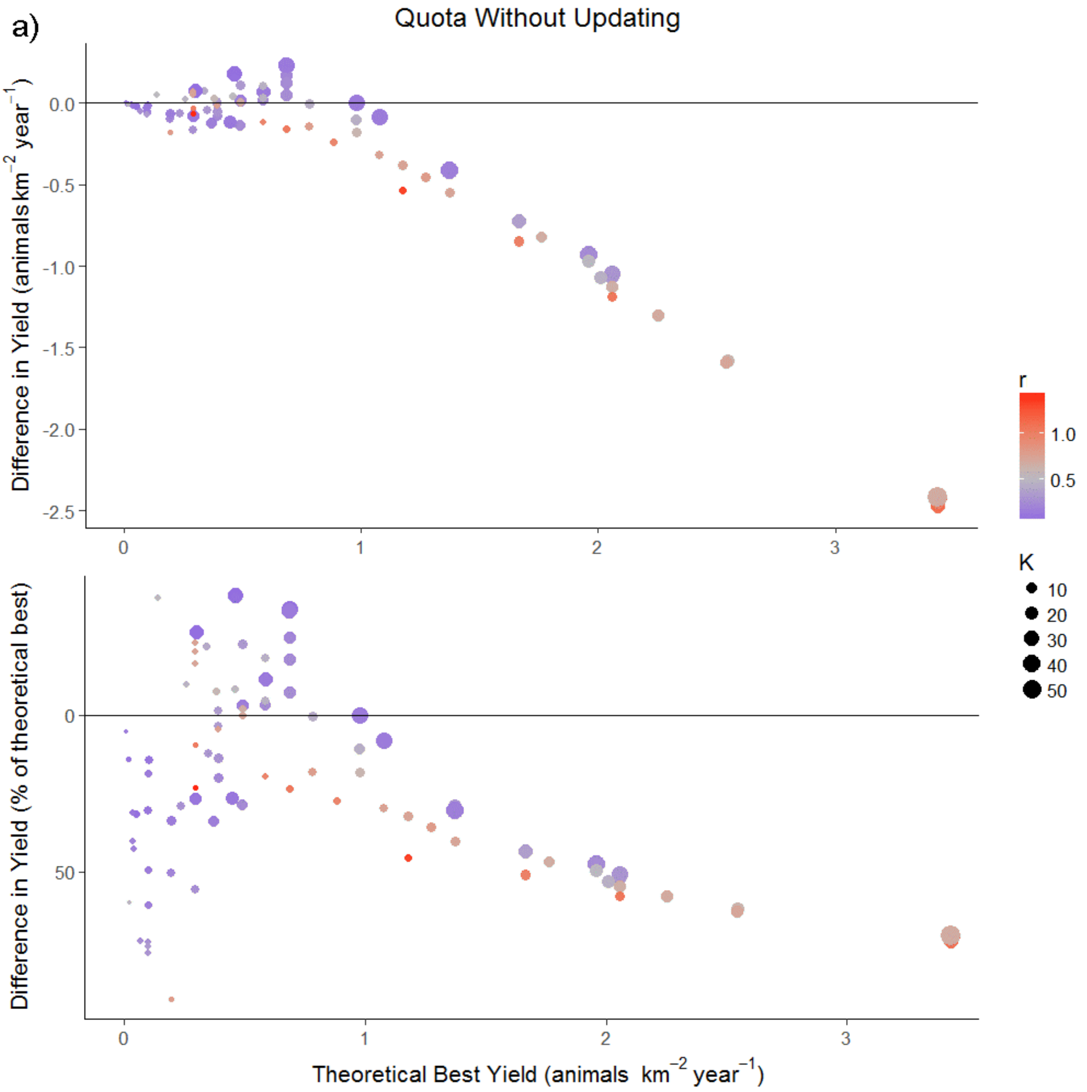
I used yield and survival probability as performance indicators. In real life, multiple socioeconomic and ecological indicators would be considered, and decision makers may have to select the most relevant for a given situation. Annual demand for bushmeat for a given location could be used as an input to the harvesting model, with optimum harvesting set to achieve a constant level of yield per annum which can meet that demand (i.e. without any very-low/no-yield years), rather than maximise yield overall, as I have done here.

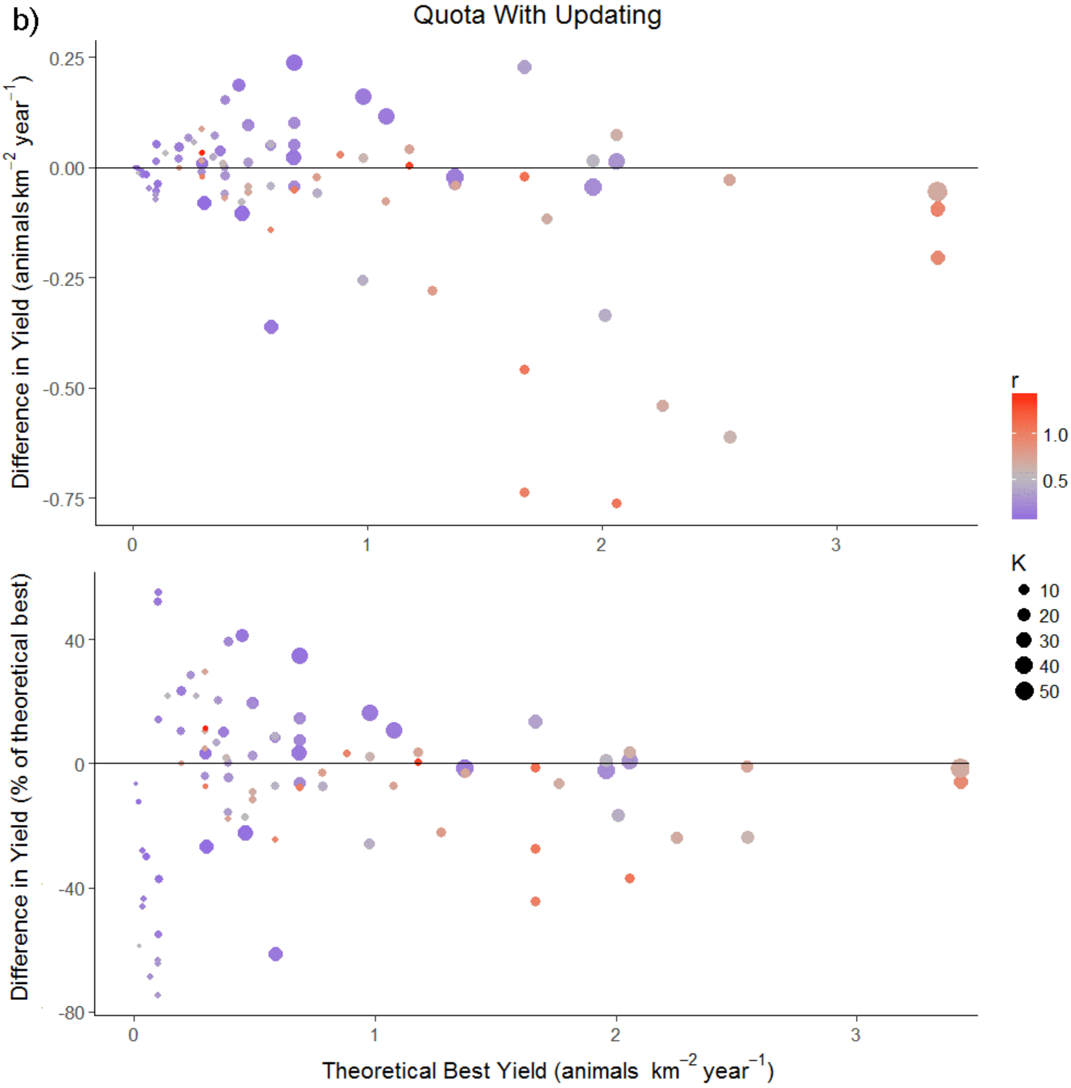
Single-species model and data limitations: A single-species model used here is useful for exploring systems dynamics and for identifying possibilities for more effective harvesting under parameter uncertainty (Holling, 1978; Walters, 2007; Keith *et al.*, 2011). The effectiveness of this model depends on the ability to reduce parameter uncertainty over time by re-surveying hunted populations (Williams, 1996b). However, continuous re-surveying is not currently feasible for the majority of harvested animals in sub-Saharan Africa (Coad *et al.*, 2013; Ingram *et al.*, 2015; Taylor *et al.*, 2015). In addition, single-species models are a simplification of complex ecological and environmental interactions that are likely to have a confounding impact (Nicholson *et al.*, 2009).

In Chapter 4, I will run a series of harvesting experiments to explore sustainability of bushmeat harvesting and ecosystem-level impacts of harvesting in African tropical forests, using a mechanistic model that bypasses the need for species-level data, and incorporates environmental impacts and multi-trophic interactions: the Madingley General Ecosystem Model (Harfoot *et al.*, 2014).

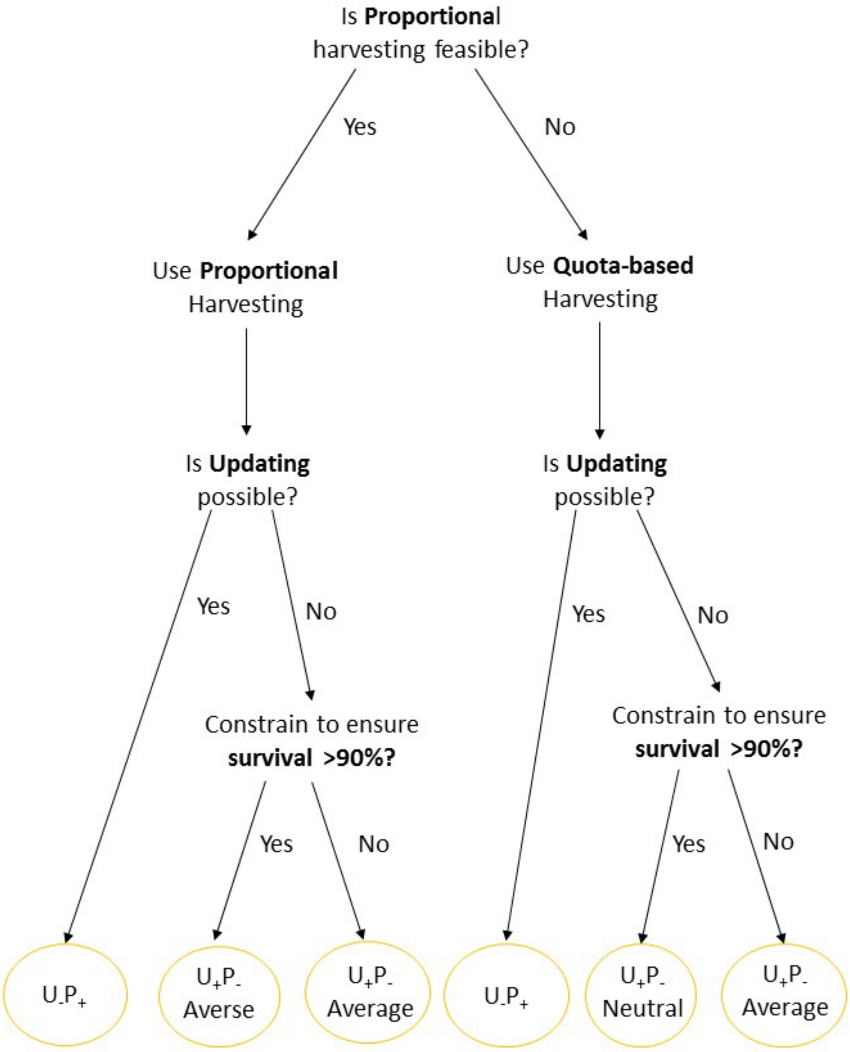
Appendices

Appendix 3-1 The absolute and proportional differences between the theoretical best yield (black horizontal line) and the predicted yields a) without and b) with parameter updating, with parameter uncertainty for quota-based harvesting. Each circle represents a modelled site i, with its relative productivity described by a combination of growth rate r_i and carrying capacity K_i. The average values for the parameters are $r_{max} = 0.42, K = 9.22$. Yields above the theoretical best were achieved by iteratively adjusting harvest rates based on the annual review of post-harvest animal densities.




b)
Quota With Updating
Difference in Yield (animals km^{-2} year^{-1})
0.25
0.00
-0.25
-0.50
-0.75
0
1
2
3
r
1.0
0.5
K
10
20
30
40
50
Difference in Yield (% of theoretical best)
40
0
-40
-80
0
1
2
3
Theoretical Best Yield (animals km^{-2} year^{-1})

Appendix 3-2 A summary decision tree based on my models' findings. In addition to harvesting policy (quota-based or proportional) and parameter updating (Yes/No), I included an option to impose a survival target of 90% of animal population (Constrain to ensure survival>90%: Yes/No).



Chapter 4 Yields, survival and whole-ecosystem impacts of bushmeat harvesting in a Central African tropical forest ecosystem: predictions from the Madingley General Ecosystem Model

Abstract

Traditional model-based approaches to harvesting wild meat often employ single-species models such as the Beverton-Holt model used in Chapters 2 and 3, which can only be employed where sufficient data is available, ignore key ecological complexities such as size structure, seasonality, multi-trophic interactions and evolution, as well as the reality that bushmeat hunters do not just focus on a single species but hunt multiple species within certain bounds of body mass and life history. Here, I employ the Madingley General Ecosystem Model, which suffers from none of these limitations, to examine yield, effort, species extinctions, and broader ecosystem impacts, for scenarios in which only duiker-sized herbivores are harvested, and scenarios where an ensemble of species are harvested. For harvesting duiker-sized herbivores (such as *Cephalophus callipygus* and *Cephalophus dorsalis*), the Madingley Model gave estimates for yield vs harvest rate, and extinction vs harvest rate, that were qualitatively and quantitatively similar to the estimates from the Beverton-Holt model, with both models estimating a maximum annual harvest rate of 20%-25% of duiker population per year. This match increased the degree of confidence with which I could examine other predictions, as follows. At medium and high levels of harvesting of duiker-sized herbivores only, the expected ecosystem-level impacts were minimal, with moderate reductions in the densities of the targeted functional groups, and limited (but statistically significant) effects on small-bodied herbivores and large-bodied carnivores. For ensemble harvesting (endothermic carnivores, omnivores and herbivores, 1-23kg in size), the model showed a much higher maximum harvest rate (65-70% population year^{-1}) and a corresponding yield of over 4500 kg km^{-2} year^{-1} (compared to around 150 kg km^{-2} year^{-1} estimated for the duiker-sized herbivores; and around 2700 kg km^{-2} year^{-1} reported for bushmeat in the Congo Basin). The ecosystem-level impacts of ensemble

harvesting were greater than for harvesting duiker-sized herbivores only (e.g. up to 1000% increases in small-bodied herbivores), but nonetheless limited to certain functional groups. The results suggest that general ecosystem models such as the Madingley Model could be used more widely to help estimate sustainable harvesting rates, bushmeat yields and broader ecosystem impacts, and to estimate how these might vary across different locations and target species.

4.1 Introduction

In Chapters 2 and 3, I explored the behaviour of a single-species model under fixed and adaptive harvesting, respectively. These experiments allowed for an initial assessment of the harvested population sensitivity to varying population parameters, level of perturbation and harvesting policies. However, single-species models are limited to studying the impacts of harvesting a single species, on that single species, and require species- or location-based data, or parameter estimates. By contrast, a holistic approach to bushmeat harvesting over whole regions will require methods that can estimate the impacts of harvesting multiple species, on both the target and the non-target species, over large regions where species- and location-specific data are not available. The Madingley General Ecosystem Model (Harfoot *et al.,* 2014), hereafter called the Madingley Model, can simulate the effects of many alternative harvesting scenarios, including multiple species harvesting, on all species in the ecosystem, without the need for any location- or species-specific data or parameters. It therefore offers an alternative to the traditional data-driven approaches explored in Chapters 2 and 3.

The modelling approaches currently used for assessing sustainability of bushmeat harvesting rely heavily on species monitoring data. These methods involve examining changes in animal abundances (e.g. Van Vliet *et al.,* 2007) and harvest offtakes over time (e.g. Albrechtsen *et al.,* 2007). Although declines in abundances of targeted species have been attributed to overharvesting in a number of Central African study sites, observational data is generally too limited (temporally, spatially) and/or too variable to identify an effective management strategy (Wilkie *et al.,* 2001; Linder, 2008; Gates, 1996). As discussed in Chapter 2, sustainability indices could also be used to estimate sustainable harvest rates (Robinson and Bennett, 2004). However, as demonstrated in Chapter 2, the effectiveness of this approach is also limited by the dearth of data.

In terms of the effects of harvesting on ecosystem structure and functioning, a number of studies reported increases in non-target species abundances (Peres and Dolman, 2000; Linder, 2008). Peres (2000) showed that species resilience to harvesting correlated with body size (large-bodied species were more sensitive to persistent harvesting) in the Amazonian tropical forests. However, bushmeat harvesting studies in tropical forests generally focus on impacts of harvesting on the target species.

New datasets including ones on global animal density (TetraDENSITY; Santini, Isaac, and Ficetola 2018), biodiversity (PREDICTS; Hudson *et al.,* 2017) and bushmeat harvesting (Offtake; Taylor *et al.,* 2015) have been developed, and new computational methods (e.g. Bayesian and Machine Learning) have been brought in to help make the most of this new data. However, despite these efforts, the extent (taxonomic, spatial, temporal) of species-level data in sub-Saharan Africa is still very limited. I.e., in the regions where bushmeat harvesting is of strongest concern (e.g. sub-Saharan Africa), there is no data at all available for the vast majority of the harvested species (Rodríguez *et al.,* 2007; Fa and Brown, 2009).

In practice, multiple species are targeted by hunters in tropical forests. To-date, optimising harvesting beyond a single-species approach has been studied in theory (Bhattacharya and Begum, 1996; Song and Chen, 2001) and attempted in fisheries management (Yodzis, 1994; Hutniczak, 2015), where multi-trophic relationships are better described than in terrestrial ecosystems. Attempts to combine the understanding of multi-trophic interactions, current knowledge of biophysical systems (climate, nutrient flows, ecological processes) and how humans interact with the system (offtake levels, monitoring, socioeconomic drivers of demand) resulted in a number of ecosystem models for separate biomes (Goodall, 1975; Travers *et al.*, 2007; Metzgar *et al.*, 2013); but none of the terrestrial ecosystem models have been used for decision-making in practice. More recently, sophisticated end-to-end marine ecosystem models, such as Atlantis (Fulton *et al.*, 2004, 2011) and Ecopath with Ecosim (EwE) (Christensen and Walters, 2004) have been developed and have now been applied to many marine ecosystems (for example, about 130 EwE models have been published; Travers *et al.,* 2007). However, deployment of these models required extensive data inputs such as place-specific biological parameters (e.g. production rate, diet composition) and stock assessment survey data for a number of selected functional groups (Link, Fulton and Gamble, 2010; Travers *et al.,* 2007). I.e. these modelling frameworks cannot be applied without extensive parameterisation and good knowledge of the system, by anybody without a reasonable modelling skill (Link, Fulton and Gamble, 2010).

To-date, the Madingley (Harfoot *et al.*, 2014) is the only mechanistic ecosystem model that can be applied to any ecosystem type (marine and terrestrial), at any spatial resolution level (although the effect of resolution on predictions has not been tested extensively) without additional parameterisation by a user: a truly General Ecosystem Model. It shares some important features with other ecosystem models such as aggregation into functional groups, inclusion of biophysical drivers (climate, net primary production) and reliance on ecological principles for emergent properties. However, unlike Atlantis for example, the aggregation is not species-specific: it takes place on a functional level. Ecosystem dynamics (animal and plant) emerge in the Madingley Model as a result of environmental inputs (such as air temperature and precipitation levels) working upon animals and plants, whose interactions between themselves and with the environment are based on fundamental concepts and processes derived from ecological theory. Importantly, all of these details mean that the model can simulate the ecosystem dynamics at any location, without the need for explicit parameterisation by a user. All that needs to be specified is the spatiotemporal location (latitude, longitude, time) because this is needed to look up the climate drivers; and any perturbations made to the system. Crucially for this Chapter, these perturbations could include harvesting of any combination of animals from the system.

On a functional group level, the Madingley Model has been shown to provide robust first order approximations of the dynamics of animal populations (Harfoot *et al.,* 2014). The model's outputs are spatially explicit and include whole-ecosystem metrics such as animal abundance, body mass and trophic indices, which could all be used as indicators of systems' sensitivity to perturbations. To date, the Madingley Model is the only, to my knowledge, simulated environment where such ecosystem-wide questions can be explored without specific and detailed parameterisation.

Here, I run a series of experiments in the Madingley Model to compare the estimates it provides of sustainable harvesting, to a species-level population model, the Beverton-Holt model, and then to explore the wider ecosystem consequences of different levels of wild meat extraction in the tropical forest ecosystem simulated in the Madingley Model. The experiment list is as follows: a) *Validation*. I begin by running the Madingley simulations for the case where I have the best knowledge already, i.e. harvesting duiker *Cephalophus* spp. (Chapters 2-3). I create a Madingley Model experiment that is as close as possible to those already run in previous chapters using the single-species model (Beverton-Holt), to allow comparison of the outputs. The single-species model is parameterised using population estimates for Peters' duiker *C.callipygus* and bay duiker *C.dorsalis* (Table 2-1), so qualitative and/or large (higher than first order) (Coe, Cumming and Phillipson, 1976) quantitative differences between the models' outputs would increase my level of scepticism about using the Madingley Model. On the other hand, good level of correspondence between the models would increase my level of confidence in examining the Madingley predictions that the single-species model cannot make. Hence I view this as a 'validation experiment'; b) *Duiker-like harvesting*. Here, I look closely at the yield, and the maximum harvest rate, for duikers as predicted by the Madingley Model, including reporting on the uncertainty in the yields. This much was possible using the single-species model. However, I also examine the impact of duiker-like harvesting on the structure of the whole ecosystem, something that is only possible with the Madingley Model. This allows me to assess whether and how apparently sustainable harvesting, could affect ecosystem structure, which might make me reconsider whether the harvesting is actually sustainable overall; and c) *Ensemble harvesting*. In reality, hunters take multiple species, something that could not be simulated in my single-species model due to lack of data, and lack of information on interactions between different species. I examine the maximum harvest rate, and maximum sustainable yield, returned by harvesting a mixture of species that is typical for this area. As before, I assess both the yield, and the expected ecosystem impacts.

I am interested in the model's estimates of sustainable harvesting in the tropical forest ecosystem, and the potential impacts of harvesting on ecosystem structure. I am ultimately interested in whether such approach, using ecosystem modelling, should be developed to be useable in practice, and if so what model features and ecosystem information would be needed in the case of bushmeat harvesting. On the other hand, ecosystem models of this generality are still relatively rare, uncertain, and their utility for studying bushmeat harvesting remains unproven.

4.2 Methods

4.2.1 Simulation Protocol

4.2.1.1 The Model

A schematic representation of the Madingley Model (with harvesting) is given in Figure 4-1, along with a representation of a single-species model (with harvesting). The Madingley Model: a) receives environmental data based on user-defined latitude and longitude: location-specific empirical data on air temperature, precipitation levels, number of frost days, seasonality of primary productivity and soil water availability; b) predicts ecosystem dynamics from environmental inputs, and animal and plant dynamics described in the model using a set of core biological and ecological processes (plant growth and mortality, and eating, metabolism, growth, reproduction, dispersal, and mortality for animals); and c) outputs estimates of biological characteristics of the emergent ecosystem (Harfoot *et al.,* 2014).

The Madingley Model represents the state of the animal part of the ecosystem in terms of the densities of individual animals with different functional traits. The densities change through time as individuals interact, in turn resulting in births, deaths, growth rates, and dispersal, with the interactions (e.g. predation) defined entirely in terms of those traits. Although the model is defined entirely in terms of interactions among individuals, the simulation uses a computational approximation (based around so-called cohorts) to allow for all interactions among all individuals to be simulated. The animal part of the ecosystem is ultimately fed by the vegetation, which is simulated using a simple stock and flow model, driven by climate, but affected by herbivory. For detailed description see Harfoot *et al.,* (2014).

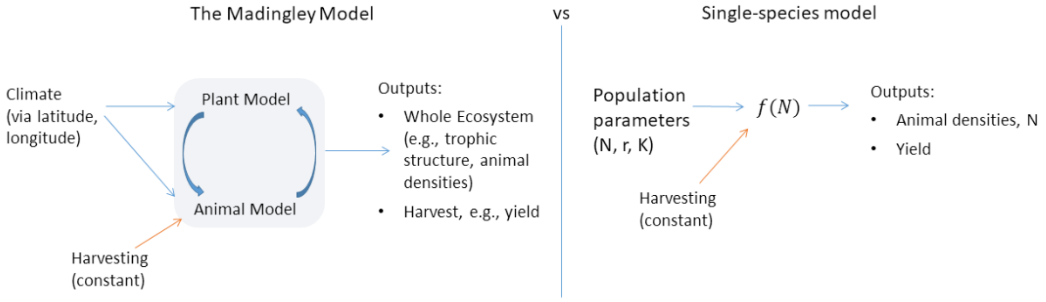


Figure 4-1 The Madingley Model's inputs, modelled processes and outputs, compared to a single-species model's inputs, processes and outputs.

4.2.1.2 Location

My experimental site was a simulated 1^0 x 1^0 geographic grid cell (111.32km x 110.57km) centred on 1°S, 15^0E; the coordinates were selected to fall within the known duiker range in the tropical forests of the Republic of Congo. For the purposes of this study, no inter-cell migration was modelled, i.e. no animals were allowed from outside the experimental area.

4.2.1.3 Target groups

I ran two harvesting simulation sets, herein referred to as duiker-like harvesting and ensemble harvesting (Table 4-1). For duiker-like harvesting, I simulated preferential harvesting of duiker antelope. I set up harvesting in the Madingley Model to target terrestrial herbivorous endotherms, described in the Madingley using the following categorical traits: 'Heterotroph - Herbivore - Terrestrial - Mobile - Iteroparous - Endotherm'. This definition was further narrowed using two continuous traits: adult body mass and juvenile body mass (Table 4-1) (Lahm, 1993; Noss, 1998). Under this definition, the target group for duiker-like harvesting included two out of the three duiker species examined in Chapter 2: Peters' duiker *Cephalophus callipygus* and bay duiker *Cephalophus dorsalis*. This excluded smaller-bodied herbivores (such as blue duiker *Cephalophus monticola*), but also other bushmeat species such as medium-sized herbivorous primates (such as *Piliocolobus badius*, mean weight = 7.75kg, mean density = 156.3 animals/km^2) and large rodents (such as *Thryonomys swinderianus*, mean weight=5.05kg; mean density=9.97 animals/km^2) (Fa, Ryan and Bell, 2005).

For ensemble harvesting, the definition of the target group was expanded to include two other functional groups: carnivores and omnivores, and broader body mass range than the duiker-like: adult body mass of 1-23kg, and above 100 gram as juveniles (Table 4-1) - to reflect animals present (Fa and Purvis, 1997) and exploited by hunters (Fa, Ryan and Bell, 2005) in the African tropical forest.

4.2.1.4 Harvesting

In the Madingley Model, a 1000-year 'burn-in' (no-harvesting) period was run (n=30) to produce estimates of ecosystem's equilibrium state in year 1000, including, for each functional group (carnivore/omnivore/herbivore): the number of surviving animal cohorts, animal abundances, biomass, and adult body masses. These estimates of ecosystem's equilibrium ecological community were output and were used as a starting point for subsequent harvesting simulations (i.e. the same 30 burn-in simulations were used as inputs for the subsequent harvesting simulations).

I used constant proportional harvesting policy, where each year a proportion (harvest rate φ, Table 4-1) of animals was targeted. I used proportional harvesting rather than quota-based to avoid defining quota targets, in particular, finding suitable quota ranges (in kilograms or in number of animals per km^{-2} year^{-1}) for multiple species which would require prior modelling of densities for both target groups (duiker-like and ensemble, Table 4-1). Using proportional harvesting was deemed adequate for the purposes of this analysis. In the future, realistic quota ranges could be identified from the literature or by consulting with bushmeat practitioners, applied in the Model and compared to harvesting outcomes on the ground.

Table 4-1 Summary of the two sets of harvesting experiments: a) harvesting duiker-like herbivores (13-21kg), and b) harvesting an ensemble of organisms: herbivores, omnivores and carnivores, with body mass of 1-23kg. I reduced the size of the steps for harvest rates of 0.25-0.60 for the duiker-like to examine the model's outputs and dynamics around the optimum harvest rates.

Title	**Target group**	**Madingley traits**	**Harvest rate, φ**	**Example species**	**Response metrics**
Duiker-like	Duiker-sized 13-21kg >100g as juveniles	Endothermic Herbivores	0.00-0.25 in steps of 0.05 & 0.25-0.60 in steps of 0.03 & 0.60-0.90 in steps of 0.10	Peters' duiker *Cephalophus callipygus*; Bay duiker *Cephalophus dorsalis*	Yields (animals km^{-2} year^{-1}); Survival Probability (over 30 years); Change in Ecosystem Structure*
Ensemble	Small and medium-sized 1-23kg >100g as juveniles	Endothermic Herbivores Omnivores Carnivores	0-0.30 in steps of 0.05 & 0.30-0.90 in steps of 0.10	African brush-tailed porcupine *Atherurus africanus*; Giant forest genet *Genetta victoriae*	Yields (kg km^{-2} year^{-1}); Probability of persistence (over 30 years); Change in Ecosystem Structure[1]

[1] expressed as increase/decrease in animal abundances

The harvest rate remained constant for the duration of harvesting period t (set at 30 years based on examining outputs' sensitivity to harvesting duration, results not shown here). Experiments were replicated 30 times at each harvest rate: I also tried a sample size of 100 for a selection of harvest rates; however, resulting dynamics did not differ significantly, and time needed to run the simulations was substantially higher. Harvesting took place once a year in month m set at 6: I simulated discrete harvesting (as opposed to continuous) to better approximate harvesting in the Beverton-Holt model (Chapter 2).

4.2.2 Output Metrics

4.2.2.1 Yields

Total yields and target animal densities were recorded. The total yield in year t was equal to $Y_{t,n} = \sum_1^c \sum_1^{n=30} y_{c,n}$, where $y_{c,n}$ was yield from harvesting cohort c in simulation n in month 6. The total density was $D_{m,n} = \sum d_{m,c,n}$, where $d_{m,c,n}$ was density for target cohort c in simulation n in month m.

4.2.2.2 Extinction

For harvesting duiker-like animals, I needed to assess the extinction of the target group. To do this, at each time step I recorded the total density of animals that matched the definition of duiker-like. The target animals were then defined as extinct (i.e. their survival recorded as zero) if the total density $D_{m,n}$ fell below 0.1 animals km^{-2} during a simulation run: this corresponded to approximately 99% reduction in density from average carrying capacity for Peters' duiker (Chapter 2).

For ensemble harvesting, I estimated probability of animal persistence using the percentage reduction in the total population density for the entire targeted group, compared to the baseline case with no harvesting. Here, I used probability of persistence rather than survival probability (as for the duiker-like) to differentiate between results of the validation experiment (where I was simulating harvesting of a more homogenous functional group consisting of herbivorous medium-sized endotherms and where expected survival threshold was based on empirical studies), and the outcomes of harvesting an ensemble of species for which the expected survival thresholds varied and were unknown.

A 90% and a 99% reduction in total population density constituted a high and a very high probability of extinction, respectively. Each simulation run was assigned a one or a zero depending on whether total population densities did (0) or did not (1) decline by 90%/99% at any point during the simulation run. The outcomes (n=30) were averaged to give an estimate of animal persistence at each harvest rate. I defined harvesting levels which could result in a high probability of extinction in at least 10% of the cases as the high risk harvesting, and harvesting which could result in very high probability of extinction in at least 10% of the cases as the very high risk harvesting.

Harvesting that maximised expected yields over 30 years was defined as *the maximum* harvesting strategy. Harvesting that maximised yield over 30 years, subject to the constraint of high risk of extinction (i.e. where harvest rates were constrained to ensure at least 10% of population survive on average in at least 90% of the cases), was defined as *the constrained high risk* strategy. Harvesting that maximised yield over 30 years, subject to the constraint of very high risk of extinction (i.e. where harvest rates were constrained to ensure on average at least 1% of population survive in at least 90% of the cases), was defined as *the constrained very high risk* strategy.

4.2.2.3 Ecosystem Response

The ecosystem-level information was recorded at each time step, such as, for each functional group, adult body masses, animal biomasses and abundances.

Overall, ecosystem-level response to harvesting was analysed as follows. First, each cohort was identified using a functional group identifier as belonging to herbivore, omnivore or carnivore functional group (f). Individuals were allocated into a body mass bin (b). The smallest body mass bin (b = -2) ranged from: 10^{-2} to 10^{-1} gram; and the largest bin (b = 6) ranged from: 10^{6} to 10^{7} gram. Because some of the bins were deemed too wide to be able to capture changes in cohort abundances due to harvesting, bins were further sub-divided into smaller sub-bins, where adult body masses were incremented in steps of 0.5 for 2 ≤ b ≤ 6 (Figure 4-4a and Figure 4-7b), and in even smaller increments of 0.25 for 3 ≤ b ≤ 5 (Figure 4-4b). Total abundances were then calculated for each functional group in each body mass bin, logged (on $\log_{10}$ scale) and normalised to month 1 of the simulation for visualisation purposes.

To account for temporal autocorrelation in animal abundances through time, changes in abundance due to harvesting were calculated as follows: change $\Delta_{m,n,f,b} = Abundance_{m,n,f,b}^{Baseline} - Abundance_{m,n,f,b}^{Harvested}$, where abundances are measured in month m, for functional group f (herbivore/omnivore/carnivore) in body mass bin b in simulation n. For the purposes of this study, I compared total animal abundances without harvesting ('Baseline') to abundances where 20%, 50%, 70% and 90% of population was targeted ('Harvested'). All data processing, statistical analysis and visualisation were done in R version 3.5.1 (R Core Team 2018), with some minor post-processing in Adobe Photoshop CS6.

4.3 Results

4.3.1 Harvesting duiker-like

4.3.1.1 Validation

The probability of survival and the expected yields from harvesting duiker-like herbivores in the Madingley Model were qualitatively and quantitatively similar to duiker harvesting in the Beverton-Holt model, with a few notable differences.

Both models predicted a gradual decline in survival probability with harvesting (Figure 4-2a). Extinctions were noticeably more common without and at very low levels of pressure in the Madingley Model (survival probability of 0.86±0.13; 95% CI, n=30) than in the Beverton-Holt model (survival probability of 0.99±0.001; 95% CI, n=30). The Beverton-Holt model also had a higher and a more pronounced threshold (at φ ≥0.15) harvesting beyond which conveyed a higher extinction rate. The opposite was true at intermediate and high levels of harvesting, where survival rates were significantly higher in the Madingley than in the Beverton-Holt. Both models estimated harvesting over 20% of population per year could result in a very high risk of extinction.

In both models, expected yields were unimodal peaking at intermediate extraction rates (Figure 4-2b). Yields were maximised at an annual harvest rate of 20-25% of the standing population. The interquartile ranges for yields did not overlap: the Madingley's median yields were on average 11.67±1.49 (95% CI, n=30) times higher than the Beverton-Holt's, and 4.64±0.44 (95% CI, n=30) times higher if mean yields were compared (Beverton-Holt's yields were strongly right-skewed). In the Madingley Model, more than one species fell under my body-mass defined categorisation of duiker-like. For example, in addition to Peters' and bay duiker, water chevrotain *Hyemoschus aquaticus* with mean body mass of 15kg, Ogilby's duiker *Cephalophus ogilbyi,* 19.5kg, also fell into the duiker-like category. Speculatively, I added yields from harvesting bay duiker *C. dorsalis* to Peters' duiker yields in the Beverton-Holt model. The difference between yields from harvesting duiker-like in the Madingley, and from Peters' and bay duiker combined using the Beverton-Holt, fell by half: to 5.35±0.66 times for the median yields, and to 2.71±0.35 times for the mean yields.

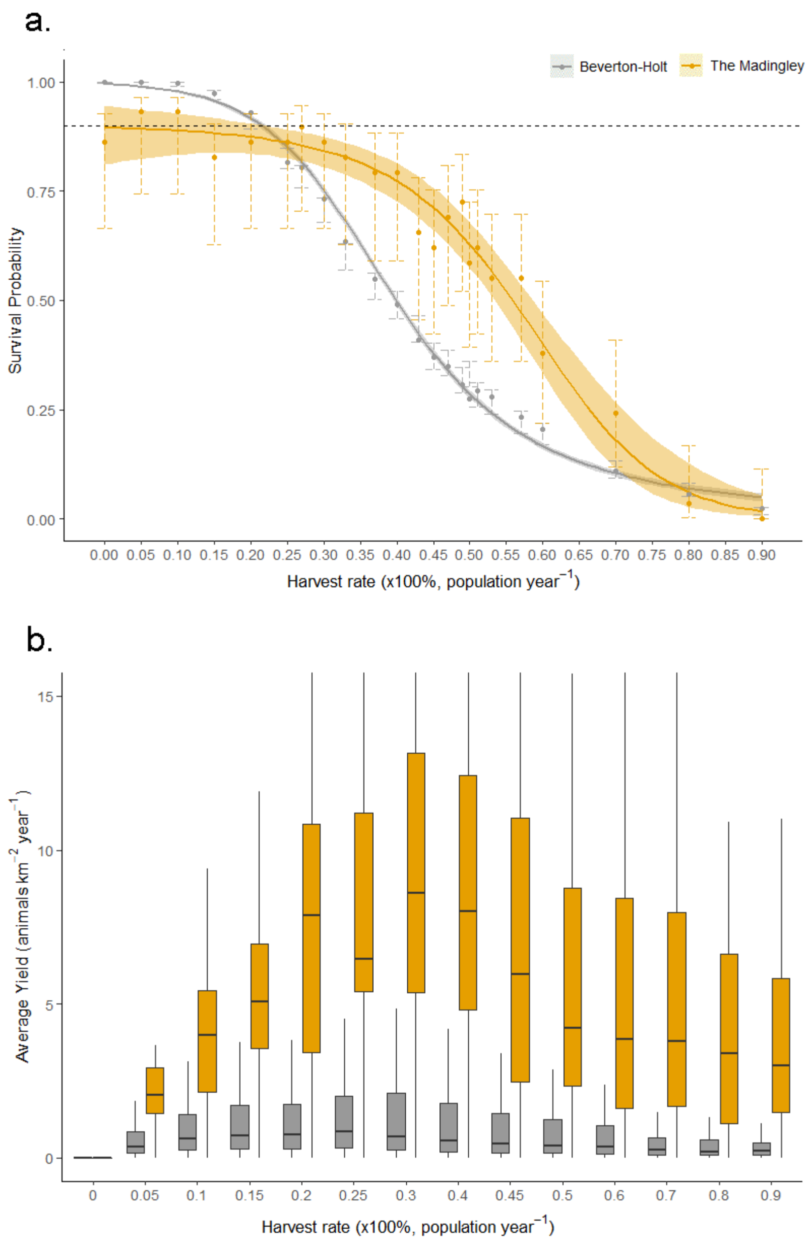


Figure 4-2 Survival probabilities (with 95% confidence intervals in grey/orange shading and 2 standard errors indicated by vertical error bars) in a. and estimated yields in b., from proportional harvesting of Peters' duiker using the Beverton-Holt model (in grey), and of duiker-like herbivores using the Madingley General Ecosystem Model (in orange). The horizontal dashed line in a. indicates the 90% survival target (i.e. extinction in less than 10% of the cases).

4.3.1.2 Impacts of harvesting duiker-like animals

4.3.1.2.1 Impacts on the target group

Here, the target group consisted of duiker-like herbivores. Harvesting above 20% (outputs not shown here) of duiker-like population resulted in significant declines in duiker-like abundances: on average, a 28% decline in duiker-like abundances was expected at φ=0.20, and a 59% decline in duiker-like abundances at φ=0.90 (the bold rectangle in Figure 4-3 and Figure 4-4).

The magnitude of the impact of harvesting on duiker-like abundances became clearer as I reduced the body mass bin ranges. When using the body mass range of 10-100kg, the duiker-like abundances declined by a factor of 2 (corresponding to differences in normalised abundances of 0.3) at φ=0.90 (the bold rectangle in Figure 4-3). When using the body mass range of 10-32.6kg, the duiker-like abundances declined by a factor of 2.5 (corresponding to differences in normalised abundances of 0.4) at φ=0.90 (the bold rectangle in Figure 4-4a). Finally, when using two even smaller body mass ranges of 10-17.8kg and 17.8-31.6kg, the duiker-like abundances declined by a factor of 3.2 (corresponding to differences in normalised abundances of 0.5) at φ=0.90 (the bold rectangle in Figure 4-4b). Interestingly, abundances of duiker-like herbivores with body masses of 17.8-31.6kg returned to pre-harvest levels in the last 10 years of harvesting (the bold rectangle in Figure 4-4b).

4.3.1.2.2 Impacts on the non-target groups

Harvesting duiker-like animals resulted in a number of changes in ecosystem structure. In particular, small-bodied (0.1-0.3kg) herbivores increased in abundance (by up to 206%) at low and medium-high levels of duiker harvesting (up to 70% of population year^{-1}; outputs not shown here), and remained unchanged at very high harvest rates (φ=0.90) (Figure 4-3 and Figure 4-4). Medium-sized (10-32.6kg) carnivores increased in abundance at high harvest rates ($\varphi \geq$0.70). While large-bodied carnivores and omnivores (316-1000kg) were negatively affected by duiker-like harvesting, decreasing in abundance by between 39-54% and 18-31% on average, respectively.

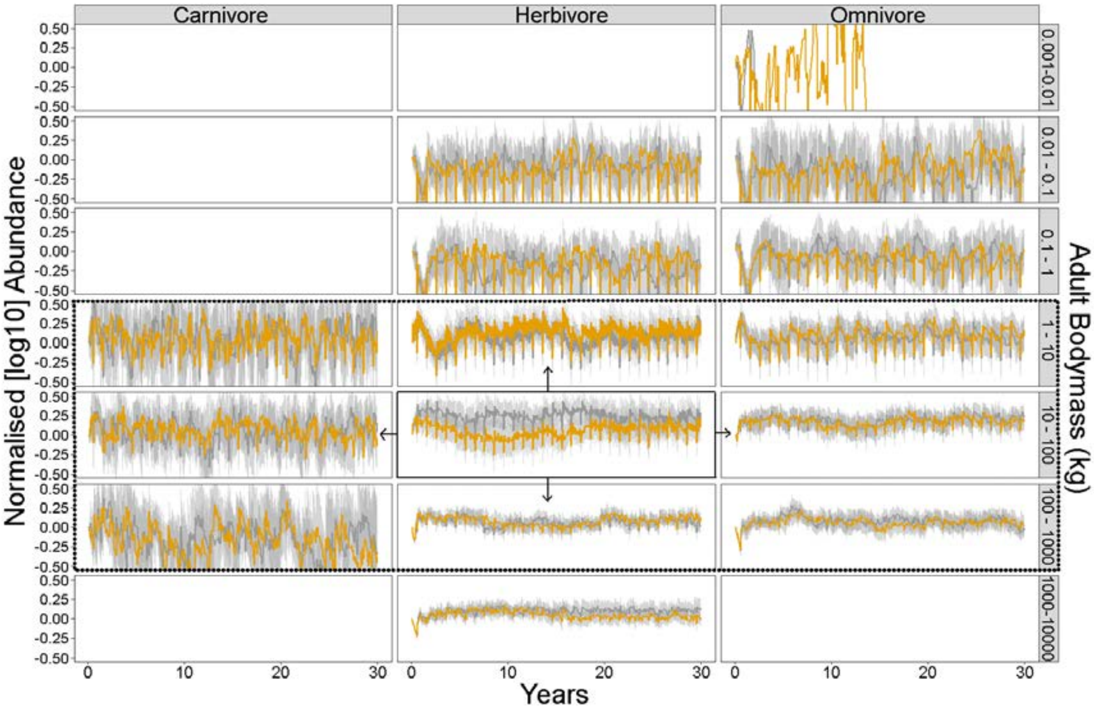


Figure 4-3 Total abundances of carnivores, herbivores and omnivores (on log-scale, normalised to month 0; with 95% confidence intervals) over 30 years, without (grey) and with (orange) harvesting of 90% of duiker-like herbivores. Animals were grouped into body mass bins. The impact of harvesting is explored under increasingly high resolution, by reducing the sizes of the body mass bins from Fig. 4-3 to Fig. 4-4a., to Fig. 4-4b. The target group (duiker-like herbivores) is emphasized by the bold rectangle; arrows and dotted rectangle indicate animal groups which were inspected in more detail in Figure 4-4a and b.

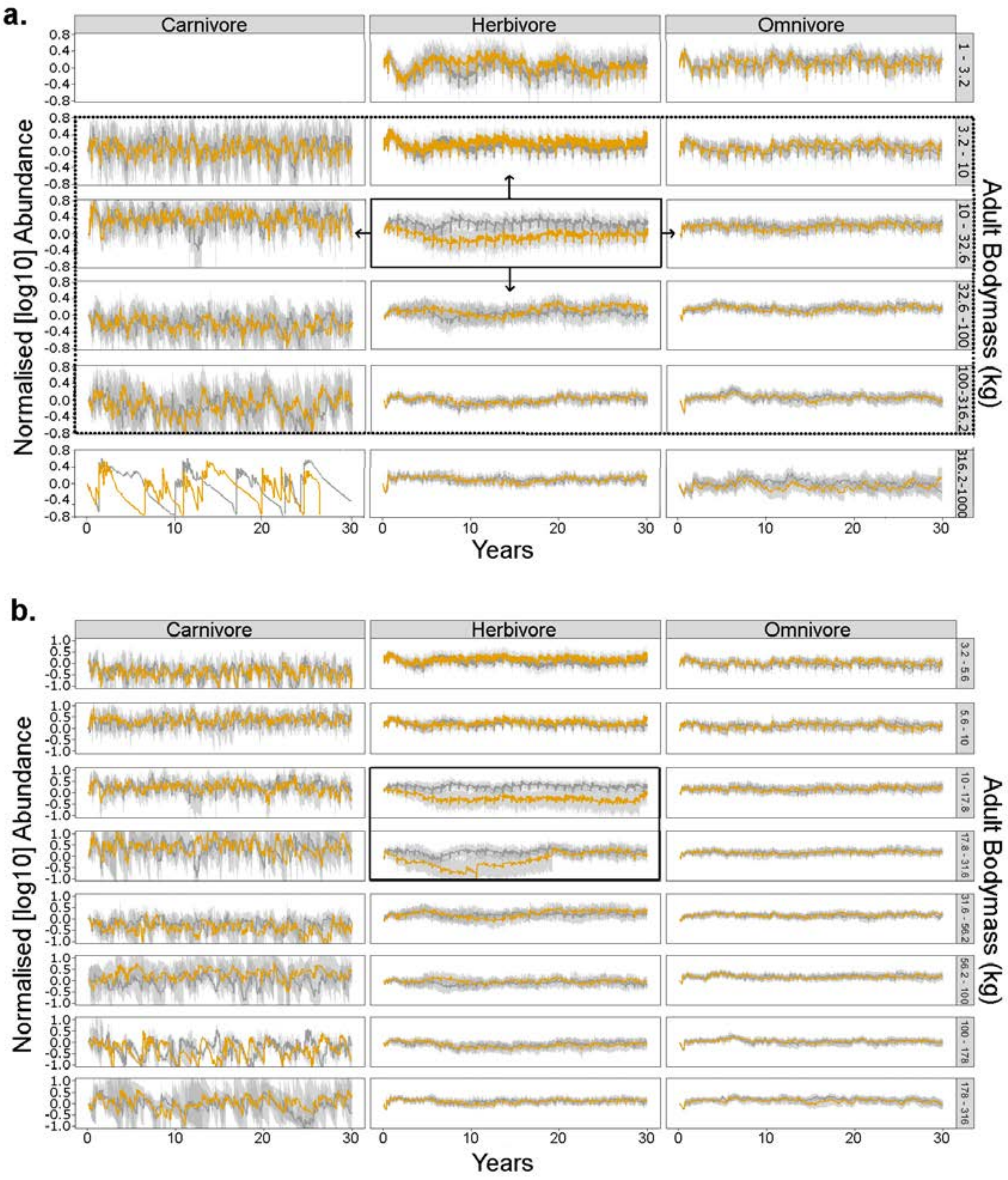


Figure 4-4 Total abundances of carnivores, herbivores and omnivores (on log-scale, normalised to month 0; with 95% confidence intervals) over 30 years, without (grey) and with (orange) harvesting of 90% of duiker-like herbivores. Animals were grouped into body mass bins. The impact of harvesting is explored under increasingly high resolution, by reducing the sizes of the body mass bins from a. to b. The targeted group (duiker-like herbivores) is emphasized by the bold rectangle. Arrows and the dotted rectangle in a. indicate animal groups that were inspected in more detail in b.

4.3.2 Harvesting an ensemble of species

4.3.2.1 Yields and probability of persistence

Here, I applied constant proportional harvesting to an ensemble of small and medium-sized herbivores, omnivores and carnivores (1-23kg) for 30 years. Yields and survival followed familiar trajectories: a unimodal increase in average yields up to the maximum harvest rate (65-70% of population per year), and a decline in probability of persistence with harvesting intensity (Figure 4-5). Baseline variability in survival outcomes was relatively low (Figure 4-5a).

Under the constrained high risk strategy (harvest rates are constrained to ensure at least 10% of population survive on average in at least 90% of the cases; orange line in Figure 4-5), the survival rates declined more or less linearly with an early inflection point (at φ=0.20). Under the constrained very high risk strategy (harvest rates are constrained to ensure at least 1% of population survive on average in at least 90% of the cases; green line in Figure 4-5), the inflection point was near the maximum harvest rate (harvest rate that maximises yield: 0.6-0.7 in Figure 4-5b), and was followed by a sharp increase in the proportion of populations under very high risk of extinction.

Unlike duiker-like harvesting, ensemble harvesting was more high-yielding at rates above the maximum than below the maximum: whereas for duiker-like harvesting, average yields declined sharply beyond the maximum harvest rate of 25%-30% population per year (Figure 4-2b), harvesting a wider ensemble of animals at rates above the maximum of 60%-70% population per year resulted in high average yields (and wide yield ranges – see Figure 4-5b), suggesting that ensemble harvesting was less constrained by animal density than duiker-like harvesting. At the maximum rate, yields of 4636 kg^{-1} km^{-2} $year^{-1}$ (95%CI: 4349.03-4923.02) resulted.

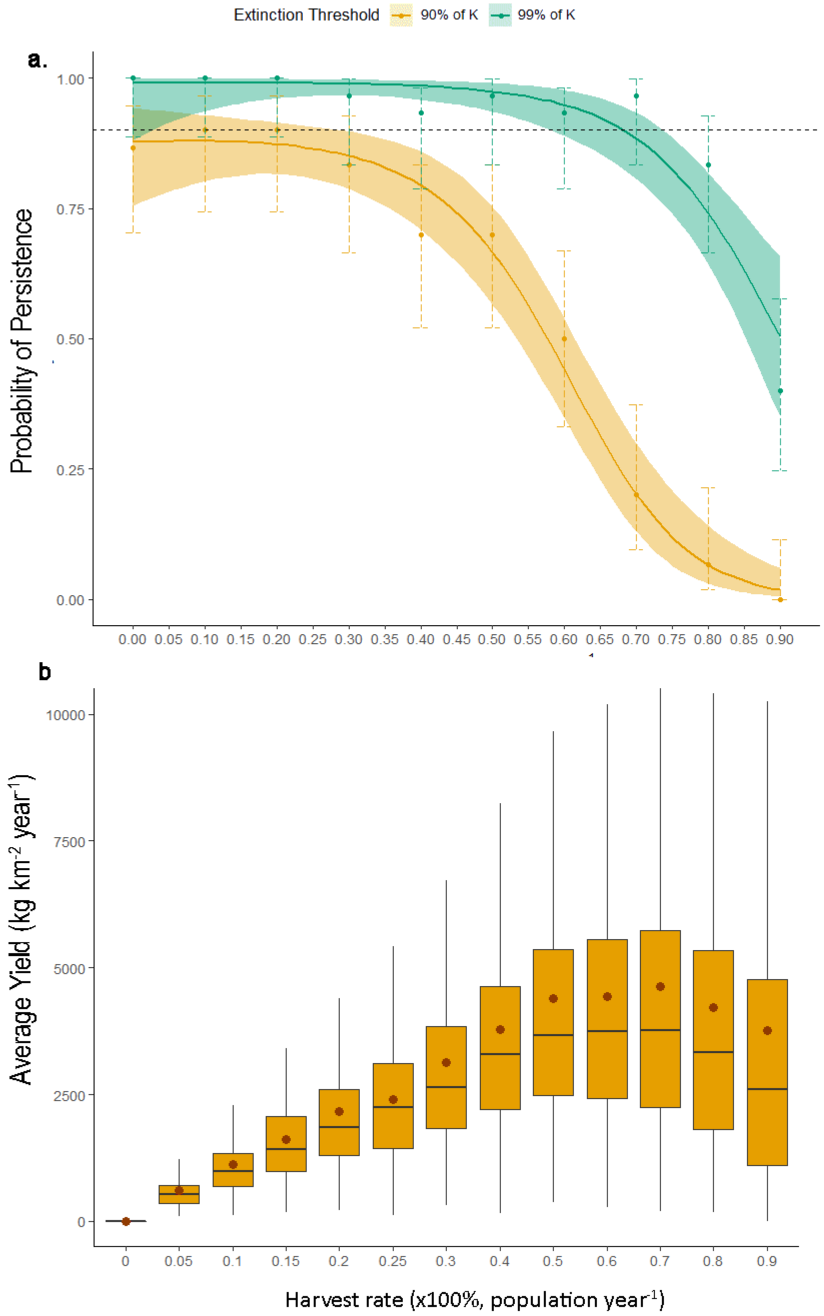


Figure 4-5 Probability of persistence (with 95% confidence intervals in orange/green shading and 2 standard errors indicated by vertical error bars) in a. and estimated yields in b. (boxes show the 25th and the 75th percentiles of the data, whiskers show values within 1.5 times interquartile range, red dots indicate mean average yield), from harvesting small-to-medium sized endotherms (ensemble harvesting) using the Madingley Model. Population persistence was estimated assuming a 90% (in orange) and a 99% (in green) reduction in density constituted extinction.

The accepted level of extinction risk had a bearing on predicted persistence and therefore, recommended harvest rates and yields. For instance if the constrained high risk strategy was followed, harvesting would be curtailed at the annual harvest rate of ≤ 20% of population. Compared to the maximum under the constrained very high risk, this could reduce yields by 53-87%. Near the maximum rate, total animal densities fell to 1% of their carrying capacity (less than 100 animals km^{-2}) in less than 10% of the cases: although densities were depressed (some, severely), quasi-extinctions were relatively rare and average yields were high. However, some species were lost and any increase in external pressure (human-made or natural) could trigger a windfall of extinctions (green line beyond harvest rates of 0.6-0.7 in Figure 4-5a).

4.3.2.2 Impacts of ensemble harvesting

4.3.2.2.1 Impacts on the target group

Harvesting resulted in reduced animal abundances in all targeted groups (Figure 4-6 and Figure 4-7). The magnitude of the decline depended on harvesting intensity and animal sizes.

Within the targeted ensemble (highlighted in yellow in Figure 4-6, and using the bold rectangle in Figure 4-7), medium and large-bodied herbivores and omnivores (>3.2kg and <32.6kg) were particularly sensitive to harvesting (declines of 17-100% predicted). Smaller animals (1-3.2kg) were generally more resilient to harvesting than medium and large-bodied animals. Depending on harvesting intensity, densities of the targeted small-bodied herbivores (1-3.2kg) increased (by up to 45%) at intermediate levels of harvesting, and declined on average by 24-38% at low and high harvest rates. The carnivores were relatively resilient, with declines of 4-39% and 11-54% in the 3.2-10kg and 10-32.6kg groups (in the 10-32.6kg group, only a share of the group, with body mass of 10-23kg, was targeted), respectively. A 61% increase in density was predicted for carnivores in the 10-32.6kg group at 70% harvest rate (n=11) (Figure 4-6c), likely in response to significant increases in small-bodied prey.

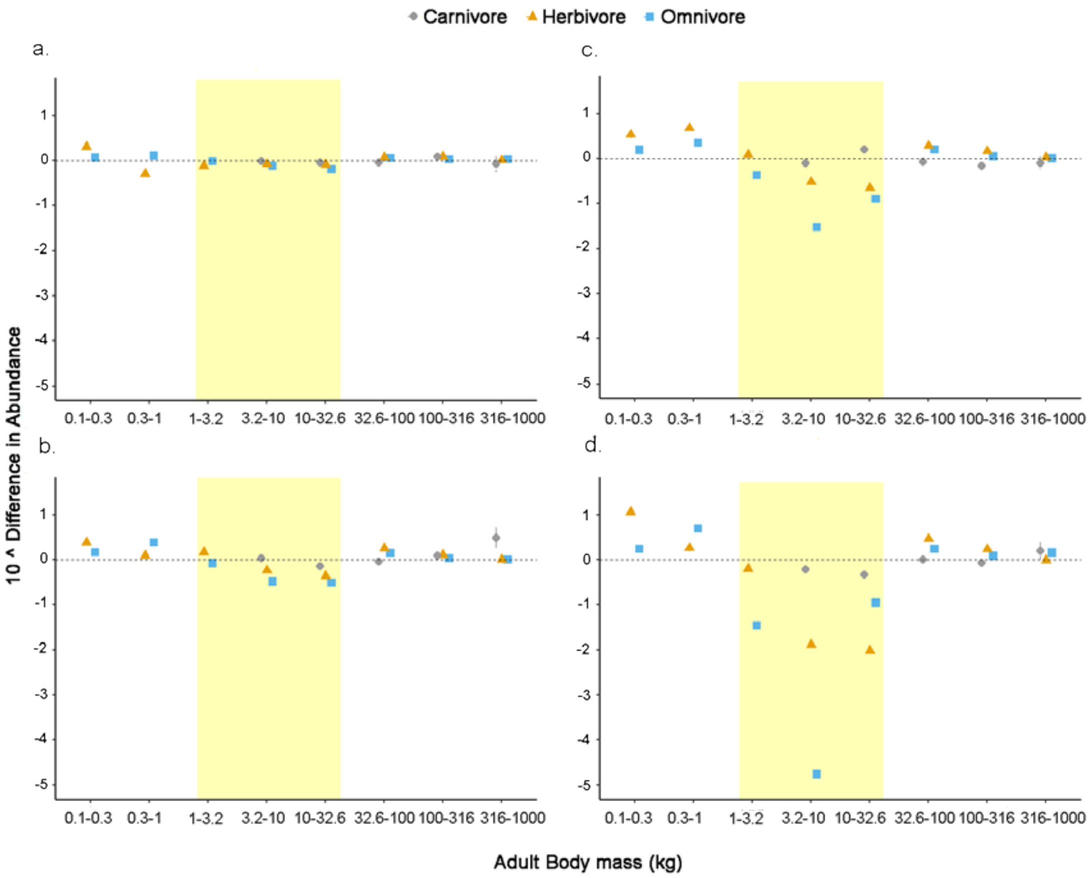


Figure 4-6 Changes in total animal abundances (with 95% confidence intervals) by functional group (carnivore, omnivore, herbivore) and body size (in kg) due to ensemble harvesting at different intensities: 20% (a.), 50% (b.), 70% (c.) and 90% (d.) population year^{-1}. Animals directly targeted by harvesting are highlighted in yellow. Values above the horizontal dashed line indicate increase in abundance, values at or close to the line suggest no change, and values below the line suggest a decrease in abundance with harvesting.

At 90% harvest rate (Figure 4-6d and Figure 4-7), herbivore and omnivore densities fell significantly compared to their pre-harvesting levels (by between 38-100% depending on body size). Density declines were severe at 70% maximum harvest rate (Figure 4-6c): by around 87-97% for medium-to-large omnivores and around 70-78% for same-sized herbivores. Reducing the harvesting rate by 20% (to 50% population year^{-1}; Figure 4-6b) resulted in a 10-times increase in omnivore densities and a 2-times increase in herbivore densities compared to the 70% maximum harvest rate (to about 30-32% and 43-58% of their pre-harvesting levels, respectively). At 20% harvest rate (Figure 4-6a), around 70% of omnivore abundances and around 80% of herbivore abundances remained.

Omnivores and herbivores in 10-32.6kg group showed signs of recovery after 10 years of harvesting (Figure 4-7), which, on closer inspection (results not shown here), was only true for animals 18-32.6kg in size which were largely untargeted by harvesting.

4.3.2.2.2 Impacts on the non-target groups

There was a significant increase in small-bodied (<1kg) omnivores and herbivores with removal of larger-bodied animals. The magnitude of this increase was generally positively correlated with harvesting intensity. Small herbivores (0.1-0.3kg) benefited the most from the harvesting of larger-bodied species, increasing in density by between 103% (at 0.20 harvest rate) and 1024% (at 0.90 harvest rate) (Figure 4-6). Slightly more moderate increases in density resulted for the omnivores: between 15% (at 0.20 harvest rate) and 72% (at 0.90 harvest rate) in the 0.1-0.3kg group, and between 3% and 382% in the 0.3-1kg group (Figure 4-6). It appeared that small-bodied animals were very sensitive to even moderate reductions in larger-bodied predators and competitors.

Non-target large-bodied (32-316kg) herbivores also benefited from harvesting the smaller body-sized animals: average densities increased by 18-182% in the 32-100kg and by 23-69% in the 100-316kg group (Figure 4-6).

Large-bodied omnivore densities also increased in the 32-100kg and 100-316kg groups (by 14-69% and 7-20%, respectively). The effects were particularly pronounced at high harvest rates (Figure 4-6c. and d.). The impact of harvesting on the non-targeted carnivores was mixed, with densities expected to increase (by around 20%) at lower rates of harvesting (Figure 4-6a. and b.) and to decline (by up to 31%) if over 70% of smaller-bodied prey was removed (Figure 4-6c. and d.).

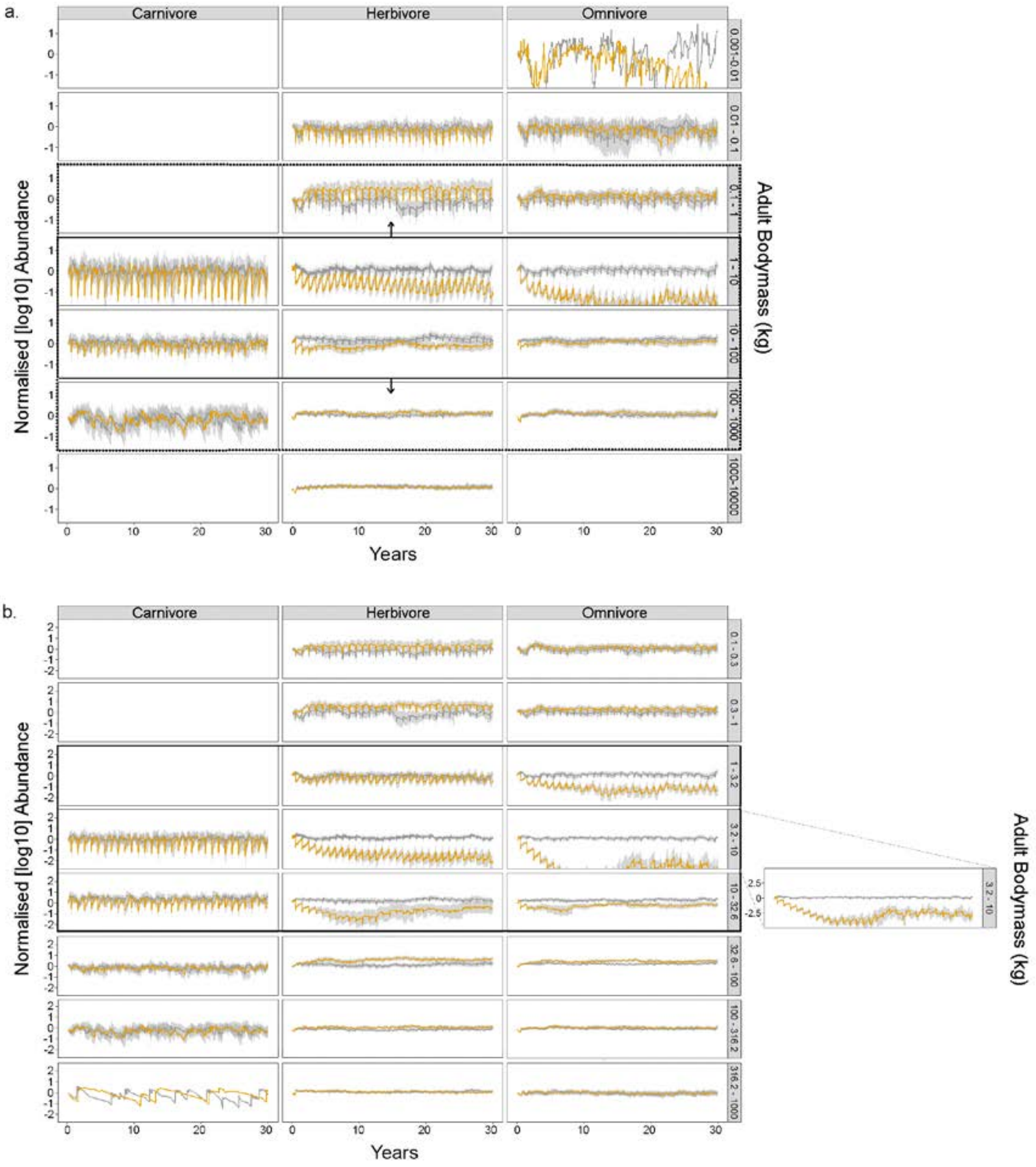


Figure 4-7 Total abundances of carnivores, herbivores and omnivores (on log-scale, normalised to month 0; with 95% confidence intervals) over 30 years, without (grey) and with (orange) harvesting of 90% small and medium-sized heterotrophs (‘ensemble harvesting’). Animals were grouped into body mass bins. The impact of harvesting is explored under increasingly high resolution, by reducing the sizes of the body mass bins from a. to b. The target is emphasized by the bold rectangle. Arrows and the dotted rectangle in a. indicate animal groups that were inspected in more detail in b. The rectangle on the right shows a ‘zoom-in’ into omnivore abundances in the 3.2-10kg group (note the larger scale on the y-axis).

4.4 Discussion

Verifying and validating estimates of duiker harvesting from the multi-trophic Madingley Model against a conventional Beverton-Holt model has shown high levels of quantitative and qualitative correspondence between these two independent models; survival probability, estimated yields and maximum harvest rates were all comparable, despite their non-equivalence. Both models estimated the maximum harvest rate at 20-25% of duiker population per year. Estimated yields from harvesting duikers in the Madingley Model were within an order of magnitude of estimates for Peters' duiker in the Beverton-Holt model. Harvesting an ensemble of small-to-medium-sized animals (1-23kg, i.e. broader than the duiker body mass range) in the Madingley gave the maximum harvest rate of 65-70% of population year^{-1}. Expected yields of 2248-5737 kg km^{-2} year^{-1} were within an order of magnitude of 645 kg km^{-2} year^{-1} bushmeat offtakes reported by Wilkie and Carpenter (1999) for the Congo Basin, and overlapped with the Congo Basin estimates by Fa, Ryan and Bell (2005) of 2645 kg km^{-2} year^{-1}.

The results from the Madingley Model for yields from harvesting duiker-like herbivores were above the Beverton-Holt's estimates for single species harvesting. As the Madingley operates on functional group rather than species-level, more than one species of duikers (as well as some non-duiker species, e.g. greater cane rat *Thryonomys swinderianus*; Fa and Purvis, 1997) would have fallen under my definition of duiker-like in the model, so increasing the total yields. Therefore, this difference between expected yields from duiker-like harvesting in the Madingley vs duikers in the Beverton-Holt was not surprising. The difference fell by half (from an order of magnitude to five times) once I added yields from another medium-sized duiker (Bay duiker *Cephalophus monticola*) to the yields from Peters' duiker. The fact that the same maximum rate of harvesting was suggested by the Madingley Model for herbivores that were duiker-like in size as by the Beverton-Holt model for Peters' and bay duiker is intriguing, particularly as it is the growth rate rather than carrying capacity that largely determines the sustainable rate of harvesting. As the Beverton-Holt model was parameterised using real-life estimates of growth rate for Peters' duiker, the same rate of maximum harvesting from these two independent models suggests that the Madingley Model may be used for estimating sustainable rates of harvesting, and perhaps even population growth rates, for species within the same functional group and where empirical estimates are lacking.

The 10% extinction rate without harvesting in the Madingley (Figure 4-2a), which was not represented in the Beverton-Holt model, is arguably more realistic in reflecting the effects of environmental and demographic stochasticity that are absent in the Beverton-Holt (Lande *et al*., 1995; Lande *et al*., 1997; Bousquet *et al*., 2008). Although stochasticity could be easily added to a single-species model (as demonstrated in Chapters 2 and 3), it emerges in the Madingley as a result of interactions between and within trophic groups, and with their environment. Similarly, higher population persistence rates in the Madingley than in the Beverton-Holt at moderate and high rates of harvesting were arguably more representative of real-life ecosystems, as: a) smaller animals would be more likely to avoid capture and reproduce (Wilkie and Finn, 1990), and b) predators would switch between similar-sized prey species as they became more rare (Allen, 1988). The population persistence dynamics revealed that harvesting near the maximum rate (i.e. harvest rate that maximised yield) brought populations very close to a level that could result in extinction (Lande *et al*., 1995; Bousquet *et al*., 2008); at 70% harvest rate, density declined by 70-97% for herbivores and omnivores. The Madingley Model could also roughly quantify the yield trade-off between these two risk attitudes for multiple species (ensemble) harvesting; a 50% yield reduction when switching from the harvest rate that maximised yield under the constrained very high risk to the corresponding maximum harvest rate under the constrained high risk strategy. Interestingly, keeping the risk of extinction below 10% on average implied harvesting not more than 20% of population year^{-1} for both duiker-like and ensemble harvesting - a rather low harvest rate, implying a trade-off that decision-makers may need to consider.

Here, the Madingley was used to predict the effect of over-harvesting on the ecosystem structure. Removing duiker-like herbivores had relatively low impacts on other functional groups, with the exception of small-bodied herbivores (which would likely compete with duikers for resources) and large-bodied predators. However, duiker-like herbivores contributed only between 2% and 4% of total abundance of similar-sized animals in the Madingley, which could also explain this relatively low impact.

Removing multiple functional groups, which were chosen to represent the focus for bushmeat hunting in reality, led to significant changes in ecosystem structure (Abernethy *et al.*, 2013). In particular, the model predicted significant increases in small-bodied (<1kg) herbivores and omnivores, particularly so at high harvesting intensity, and in large-bodied (32.6-100kg) herbivore and omnivore densities. The targeted carnivores were generally less sensitive to harvesting at moderate levels.

Studies of biological consequences of over-hunting on species in African tropical forest generally focus only on the target species; declines in density were recorded in duikers and other mammals (e.g. Fitzgibbon, Mogaka and Fanshawe, 1995; Noss, 1998a; Gates, 1996). In terms of effects of removal of target species on non-target animal groups; in the Amazon, faster increases in abundances of large rodents and artiodactyls were reported in areas with higher levels of harvesting of arboreal monkeys, compared to moderately-hunted areas (Bodmer *et al.*, 1997). Very high abundances of common opossums *Didelphis marsupialis* and spiny rats *Proechimys* spp. were reported in heavily fragmented forests of Brazil and central Panama, explained by the absence of their predators and/or competitors (Adler, 1996; da Fonseca and Robinson, 1990). Fa and Brown (2009) predicted that the abundance of non-target small and medium-sized species could remain unchanged or even increase depending on the availability of their prey and removal of competitors and other predators. According to Wright (2003), large-bodied species preferred by hunters would decline with harvesting pressure; the less desirable species would first increase due to lower competition for resources, and then decline; and small untargeted species would increase steadily. The trophic cascades theory predicts that higher abundances of mid-level consumers should result in lower abundance of basal producers (assuming ‘top-down’ control) (Pace *et al.*, 1999; Kennedy, 2012; Palmer *et al.*, 2015). However, changes in higher trophic levels do not always propagate to lower levels or have significant ecosystem impacts; higher resilience to perturbations is possible in systems with high trophic diversity and complex food webs (Wright, 2003; Pace *et al.,* 1999).

From a point of view of a bushmeat manager considering the wider ecosystem impacts of harvesting, the system, as indicated by the Madingley Model, was relatively robust to intensive harvesting. Many animals were heavily depleted but not extinct, smaller-bodied animals increased in abundance, and vacant ecological niches were being quickly filled-in by, presumably, more resilient quicker-reproducing animals (Adler, 1996; da Fonseca and Robinson, 1990). However, harvesting intensively also resulted in a very different ecosystem (Scheffer *et al.*, 2001), dominated by small-bodied short-lived animals. Considering the trade-off between high yields now, and lower yields, lower species diversity, and a different ecosystem structure and functioning later, should be a part of decision-making process in bushmeat management.

My harvesting protocol was relatively simple. Harvesting was applied to a single location approximately 100 x 100km; no inter-cell migration was allowed. Although duiker home ranges are relatively small, around 0.10km^{-2} (Payne, 1992), in reality local duiker populations would likely disperse (depending on strength of pressure on neighbouring ecosystems) and therefore replenish nearby areas, most likely then increasing species overall tolerance to pressure (Fa and Brown, 2009). I assumed constant non-adaptive harvesting which was not affected by the return per unit effort, the selectivity of hunters (Wright, 2003), or any other socioeconomic factors such as proximity to roads or access to salaried employment (Nielsen, 2006; Nielsen, Jacobsen and Thorsen, 2014). No provision was made in the model for the potential wastage due to animals captured and discarded as unsuitable for sale or consumption, or animals escaping after being injured (and likely dying later on), though it could add a quarter to recorded harvesting mortality (Noss, 1998a).

The Madingley's main strengths are its generality and ability to look at any species and locations including ones that have not yet been studied in any detail and thus are lacking in substantive data sets (Purves *et al.*, 2013; Bartlett *et al.*, 2016). The Madingley Model was able to produce reasonable estimates for duiker-like harvesting dynamics based solely on climate data. While the Beverton-Holt model was able to capture the salient features of single-species harvesting (Lande, Sæther and Engen, 1997; Fryxell *et al.*, 2010), in the absence of population parameter estimates the Madingley could offer adequate indication of harvesting outcomes. There is a lack of understanding of synergies and interactions within ecosystems (da Fonseca and Robinson, 1990; Wright, 2003) which we may not be able to address using traditional modelling for some time; predicting dynamics and potential impacts of multi-species harvesting is currently not feasible for many real-life populations (Hooper *et al.*, 2005). Using the Madingley Model allows approximations of such dynamics to be made (Newbold *et al.*, 2018). In the next Chapter I expand the model's remit by exploring how different African ecosystems may respond to harvesting.

Chapter 5 Modelling variation in bushmeat harvesting among seven African ecosystems using the Madingley Model: yield, survival and ecosystem impacts

Abstract

In principle, both the maximum sustainable yields of bushmeat, and the ecosystem impacts of extracting those yields, are likely to vary among ecosystems due to differences in the structure and function of ecosystems, but the data necessary to estimate this variation is lacking. Here, I compare seven different ecosystems on a North-South latitudinal gradient in Central Africa in terms of their trophic structure and capacity to support yields from bushmeat harvesting, using the Madingley General Ecosystem Model. The only factor that varies across these ecosystems is the climate which drives differences in vegetation structure and function, and this leads to differences in the structure of the ecological community that emerge from the model. In a series of experiments (n=30), I simulate constant proportional harvesting of small and medium-sized warm-bloodied heterotrophs (1-23kg) over 30 years, recording expected bushmeat yields, and impacts on ecosystem structure, including trophic structure. Predictions for animal densities and trophic structures in the pristine (no harvesting) case varied among the ecosystems, with implications for bushmeat harvesting. For example, wooded savannah ecosystems stood out as having the greatest pristine densities in the target groups (11000-12000 animals per kilometre squared), greatest yields (100% higher than the tropical forest and 1000% higher than the desert ecosystem), and were the most resilient to harvesting. By contrast, small and medium-sized endothermic heterotrophs contributed only a small proportion of heterotrophs in the desert ecosystem, and the potential for bushmeat harvesting here was low. In all ecosystems, harvesting at the rate that maximised yield (55-65% population per year, except for the southern desert ecosystem) had strong impacts, with forest and desert ecosystems particularly sensitive. Overall, the results suggest that, even for similar functional groups, bushmeat harvesting policies will need to vary substantially among ecosystems – and

imply that general ecosystem models could be a useful tool in helping to guide these policies.

5.1 Introduction

It has long been recognised that ecosystem structure and function, such as plant and animal biomasses, productivity, and turnover, are influenced by the environmental conditions, including climate, soil quality and availability of water (e.g. Walter, 1964; Levin, 1998; Hunter and Price, 1992; Parrott and Meyer, 2012) - and Africa is no exception. Vegetation types have been linked to mean annual precipitation for a variety of ecosystems (Butt *et al.*, 2008; Del Grosso *et al.*, 2008; Hirota *et al.*, 2011), with almost linear relationship between primary production and rainfall reported by Whittaker (1970) and Walter (1964) in a range of African vegetation types. Clear empirical relationships between large herbivore biomass and mean annual rainfall have been described by Coe *et al*. (1976) in the east-African plains and savannahs, by Barnes and Lahm (1997) in central African forests, and by Bell (1982) in the woodland and savannahs of Africa. Similarly, in the tropical forests of Amazon and Guyana, Peres (2000) reported a positive relationship between primate biomass and soil fertility, where soil fertility was strongly correlated with annual rainfall.

Environmental correlations also exist at the species- and functional group levels, but these are not yet well documented for most species in Africa (though see Coe *et al*., 1976; McNaughton, 1976). Understanding of variation in ecosystem processes, and variation in interactions among species, is even less well developed, albeit improving (Hunter and Price, 1992; Montoya, Pimm and Solé, 2006). For example, food web models have been used to examine the role of various links within communities in maintaining their stability in the face of species removal (Sol and Montoya, 2001; Thompson *et al.,* 2012; Borrett *et al*., 2014). Nonetheless, the relationships between ecosystem structures and their responses to broad disturbances are still not well-understood (Montoya, Pimm and Solé, 2006). In addition, even the more complex food web models often ignore the environmental variability (Hunter and Price, 1992).

The variation in ecosystem structure and function across Africa implies that optimal harvesting policies and yields, as well as ecosystem impacts of harvesting are all likely to vary among ecosystems (Christensen and Walters, 2004; Fulton *et al.*, 2011; Mokany *et al.*, 2016). This in turn implies that the consequences of the dearth of data for guiding bushmeat harvesting are even more severe. In effect, a lot of data would be required to reliably estimate a good 'one size fits all policy' (even if such policy existed) for all of Africa. A lot *more* data would be required to find a whole set of such policies, tailored to the many different ecosystems where bushmeat hunting occurs. In addition, even if spatially and temporally reliable data on harvested species and ecosystems became available, predictions based on the empirical models (e.g. about sustainable harvest rates) would be specific to conditions and ecosystem responses described by the data (Harfoot *et al.*, 2014; Newbold *et al.*, 2018), and would not account for the likely changes in biophysical conditions of the exploited systems, for example, due to climate change (Yates, Kittel and Cannon, 2000; Krinner *et al.*, 2005).

Previous chapters have studied how better data and information on both species life history and ecosystem structure could be used to improve decisions about hunting efforts required for sustainable yields of bushmeat. Species life history is certainly a key determinant; but I have shown that in the absence of species-specific information the use of an ecosystem model (the Madingley Model) can provide robust guidance, based solely on functional groups that are emergent from the ecosystem model. In this Chapter, I use the Madingley Model to explore how maximum sustainable yields, optimum harvesting policy, and ecosystem impacts, might vary among different ecosystems – a question that is currently almost impossible to address using anything other than a general ecosystem model.

The Madingley Model has been shown to give reliable predictions of trophic structure across a variety of terrestrial ecosystems (Harfoot *et al.*, 2014). The environmental inputs to the Madingley Model are spatially explicit, and include empirical data on air temperature, precipitation levels, number of frost days, seasonality of primary productivity and soil water availability (Purves *et al.*, 2013; Harfoot *et al.*, 2014). These inputs drive net primary production in the model. Plant and animal biomasses arise in the modelled ecosystems according to the locally specific climate and become components of ecosystem structure and function. Thus the distinctive feature of the model is that no species- or location-specific population parameters are input; they all emerge from the model structure and functions (Harfoot *et al.,* 2014). The Model has been used to explore independent and synergistic effects of habitat loss and fragmentation on ecosystem structure (Bartlett *et al.*, 2016), to predict non-linear regime shifts within ecological communities subjected to human removal of vegetation (Newbold *et al.*, 2018) and to examine the importance of arbuscular mycorrhiza symbioses for the trophic structure of the Serengeti ecosystem (Stevens *et al.*, 2018). Here, I use the model to simulate and compare dynamics of ecological communities that emerge in different ecosystems. I am modelling species populations for which no population parameters are available, but whose dynamics are determined entirely by the ecosystem model.

I use the Madingley Model to simulate the effect of constant proportional harvesting of small and medium-sized heterotrophs in seven ecosystems on a North-South latitudinal gradient through Central Africa. The objective is to compare how different harvesting levels drive ecosystem changes, ecological community structure and productivity. By only varying the model's environmental inputs while keeping all the other model inputs (such as the starting number of cohorts and stocks, and harvest rates) constant (Figure 5-1), any differences between ecosystems that result from harvesting are attributable to differences in ecosystem structure and functioning, as predicted by the model.

My expectation is to see marked differences in expected bushmeat yields and in sensitivity to harvesting between ecosystems. If successful, these experiments could contribute to the debate about the importance of environmental conditions in predicting ecosystems dynamics, and about the potential of large-scale models such as the Madingley Model, for supporting land-use and conservation policies.

5.2 Methods

5.2.1 Locations

Seven locations on a North-South latitudinal gradient in Africa were selected (Figure 5-2) to represent seven ecosystems in three broad vegetation types (Otte and Chilonda, 2002): savannah (grass and shrub, and wooded savannah in the North and South), forest (tropical forest, and woodland and shrub), and desert (North and South). Each ecosystem was modelled by a one-degree geographic grid cell (approximately 12307km^2), centred on the coordinates provided in Appendix 5-1. No inter-cell migration was included in the simulations.

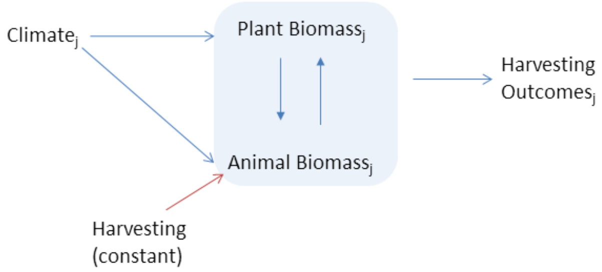


Figure 5-1 Summary of the experiment: climate for *j*-grid cells (n=7) is input into the Madingley Model; ecosystem structure emerges as a result of climate and of multi-trophic interactions; the same level of proportional harvesting is applied to all *j*-ecosystems; harvesting outcomes are output for each ecosystem *j*= 1 to 7.

Figure 5-2 The locations of sites used for harvesting simulations, representing seven ecosystems in three broad vegetation types: desert (orange), savannah (light green) and forest (dark green).

5.2.2 Harvesting simulations

In all sites the same harvesting strategy was applied targeting small and medium-sized endothermic carnivores, omnivores and herbivores with adult body masses of between 1kg and 23kg, and over 100 grams as juveniles (i.e. the same target group as my ensemble harvesting in Chapter 4), based on reported bushmeat species sizes (Fa, Ryan and Bell 2005).

In each ecosystem, constant proportional harvesting was applied to target animals for 30 years. All harvesting took place once a year in month 6. Harvesting was applied in a single month (i.e. once a year) to approximate discrete harvesting modelled in Chapters 2-4. The outcomes of continuous harvesting can be investigated in future work. The harvest rate (φ) was set to $0 \leq \varphi \leq 0.90$ in increments of 0.05 from $0.0 \leq \varphi \leq 0.70$, and in increments of 0.10 thereafter. I used smaller rate increments between 0 and 0.70 to get more detailed estimates of harvesting outcomes (yield, survival and ecosystem impacts) at moderate-to-high harvest rates which were more interesting from a practical point of view.

Each harvest rate was applied 30 times (n=*30*) in each ecosystem; i.e. 17 harvest rates per ecosystem were replicated 30 times resulting in 510 model runs for each location and 3570 model runs in total.

For each ecosystem simulation, a 1000-year burn-in (n=*30*) was run using the Madingley Model. Ecological communities were allowed to emerge in the model and to reach equilibrium states in terms of number of different cohort types (animal body mass, herbivore/omnivore/carnivore, and ectotherm/endotherm). These states were then used as the initial state for harvesting simulations in the given location.

The recorded ecosystem states without harvesting (simulations where φ=0) are the reference for the 'pristine state' of the ecosystem.

5.2.3 Outputs and processing

For target individuals only, total yields from harvesting and population densities were recorded during harvesting in years 0-30. For all individuals (target and non-target), I recorded ecosystem-level information such as: functional group identifiers, abundances, and adult and individual body masses, in years 0, 10, 20 and 30.

Using total population densities, I calculated the probability of persistence of the target animals, assuming that a 90% and a 99% reduction in total population density (compared to the pristine density in month 0, after the burn-in) at any point during the simulation run constituted a high risk and a very high risk of extinction, respectively. Each simulation run was assigned a one or a zero depending on whether total population densities did (0) or did not (1) decline by 90%/99% at any point during the simulation run. The outcomes were averaged across simulations to give an estimate of animal persistence for each harvest rate, by location. I define harvesting levels which could result in a high probability of extinction (declines of 90%) in at least 10% of the cases (i.e. 10% of simulations) as the high risk harvesting, and harvesting which could result in very high probability of extinction (declines of

99%) in at least 10% of the cases (i.e. 10% of simulations) as the very high risk harvesting.

I define three harvesting strategies:

Maximum harvesting strategy/maximum harvest rate – harvesting that maximises yield over 30 years.

Constrained high risk strategy – harvesting that maximises yield over 30 years, subject to the constraint of high risk of extinction (where harvest rates are constrained to ensure at least 10% of population survive on average in at least 90% of the cases).

Constrained very high risk strategy – harvesting that maximises yield over 30 years, subject to the constraint of very high risk of extinction (harvest rates are constrained to ensure at least 1% of population survive on average in at least 90% of the cases).

For each location, all heterotrophs were identified as ectotherms or endotherms belonging to one of the three functional groups (carnivores, omnivores or herbivores). Individuals in each functional group were also allocated into a body mass bin, ranging from the smallest (0.1-0.3kg) to the largest body size (316.2-1000kg) (i.e. the same bins as in Chapter 4).

To examine the trophic structure of pristine ecosystems, the total biomasses in each functional group and body mass bin in the final year of each simulation were summed, and then averaged across the 30 replicates.

To examine the potential effects of harvesting, I measured changes in abundances of animals in different body mass bins at different levels of harvesting pressure, focusing on the group directly impacted by harvesting: the endothermic heterotrophs.

5.2.3.1 Per Capita Yield Conversion

In order to compare bushmeat yield to that of farmed cattle in the same ecosystems, I collected estimates of human population density and beef offtakes by agro-ecological zones from Otte and Chilonda (2002); human population density estimates were used to convert bushmeat yields per kilometre squared to bushmeat yields per kilometre squared per capita.

All data processing, statistical analysis and visualisation were done in R version 3.5.1 (R Core Team 2018), with minor editing (image stitching and adding text to images) in Adobe Photoshop CC.

5.3 Results

5.3.1 Trophic structure of modelled ecosystems

The total heterotroph biomasses by functional group, and by functional group and body size in seven pristine ecosystems are presented in Figure 5-3 and Figure 5-4, respectively. The highest heterotroph biomasses were in the savannah (2.4-3.1 million tonnes) and forest ecosystems (2.3-2.6 million tonnes), followed by desert and desert shrub in the South (2.1 million tonnes) (Figure 5-3). Only around 1% (0.1 million tonne) of total heterotroph biomass was present in the northern desert (Figure 5-3).

The carnivores (Figure 5-3 and grey bars in Figure 5-4) were the dominant functional group in the forests (between 46%-52% of average total biomass in these ecosystems) and wooded savannah ecosystems (46%-47% of average total biomass in wooded savannah), but not in the grasslands (27%) or desert ecosystems (0%-2%). The herbivore (Figure 5-3 and orange bars in Figure 5-4) contribution to total biomasses was the highest in the desert ecosystems (62%-74% of average total biomasses) and the grasslands (64%), and the lowest in the forests (37%-38%). The omnivores (Figure 5-3 and blue bars in Figure 5-4) had the lowest total biomasses of all functional groups in all productive ecosystems (9%-17% of average total biomasses). In the deserts, the omnivores had the second-highest biomass densities after the herbivores (24%-38% of the total heterotroph biomasses).

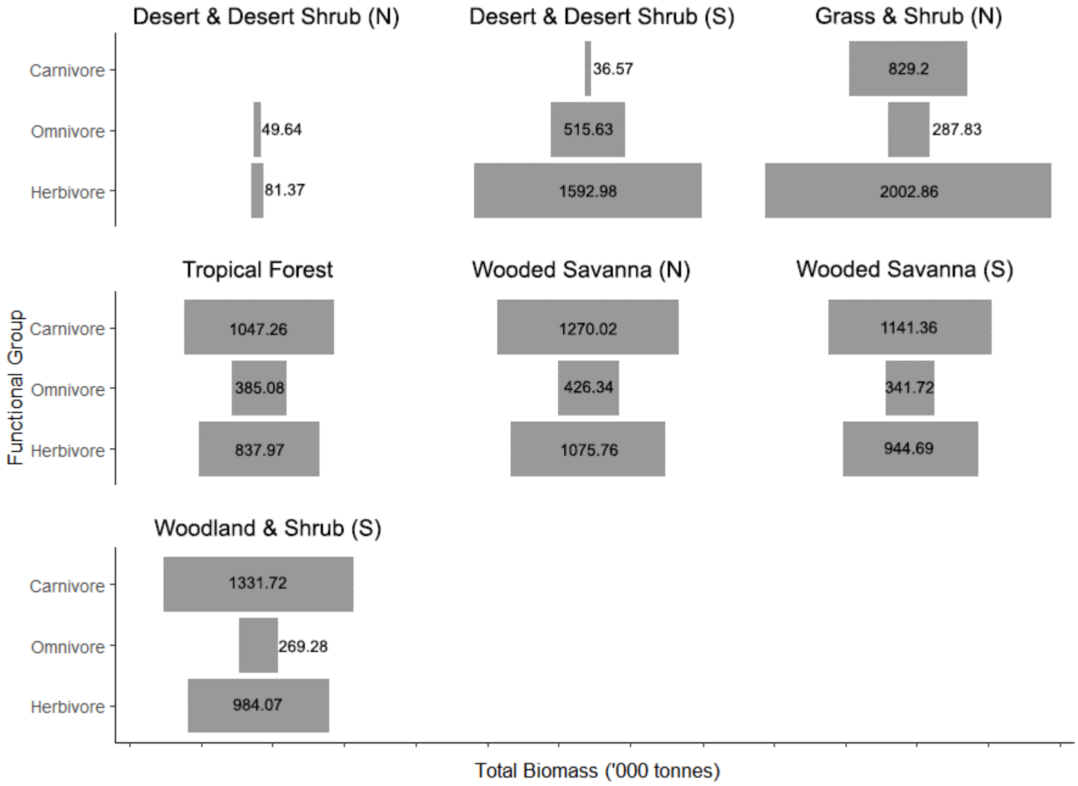


Figure 5-3 Trophic biomass pyramids in seven pristine ecosystems. Numbers inside or next to the bars represent total endotherm and ectotherm biomass ('000 tonnes).

In terms of body-size composition (Figure 5-4), all ecosystems had relatively high proportion of total ecosystem biomasses represented by top predators, i.e. large-bodied (>316.2kg) carnivores (around 40% of all carnivores in the forest and desert ecosystems, and 26%-30% in the wooded savannah ecosystems). The lowest biomass proportion of large carnivores was in the southern desert (approximately 1% of the total biomass), which coincided with the highest biomass proportion of large-bodied (100-316.2kg) herbivores. Interestingly, the model predicted the carnivores to be predominantly ectothermic (e.g. 99%-100% of the total carnivore biomasses in the savannah and the southern desert, on average), even in the larger body mass bins. The highest share of endothermic carnivores was in the tropical forest (around 11% of estimated total carnivore biomass in that ecosystem). The highest total biomasses of large-bodied (>100kg) endothermic herbivores were in the southern desert and in the grasslands ecosystem (Figure 5-4a): 13% and 7% of the total biomasses in these ecosystems, respectively, vs around 3% of the total biomass in the tropical forest ecosystem.

Targeted small and medium-sized endothermic herbivores (Figure 5-4a, highlighted by the yellow band) had the highest biomasses in the northern savannah ecosystems (21-103 thousand tonnes), followed by the southern wooded savannah and woodland and shrub (30% lower than the northern savannah, on average; 11-79 thousand tonnes), the tropical forest (on average, 55% lower than the northern savannah; 20-35 thousand tonnes), and the southern desert ecosystem (90% lower than the northern savannah; 3-10 thousand tonnes). Similarly, for small and medium-sized endothermic omnivores (Figure 5-4a, highlighted by the yellow band), the highest total biomasses (15-33 thousand tonnes) were returned in the northern savannah ecosystems, followed by the southern savannah (10-29 thousand tonnes) and forest ecosystems (12-19 million tonne; 30%-40% lower than the northern savannah), and the southern desert (circa 2 thousand tonnes; 90% lower than the northern savannah). Small and medium-sized (1-32.6kg) warm-bloodied carnivores were only present in the forests and in the wooded savannah in the South (22-50 thousand tonnes, and 20-39 thousand tonnes, respectively).

Endothermic heterotrophs were entirely absent from the northern desert ecosystem (Figure 5-4) (hence no bushmeat harvesting was modelled in the northern desert, see 5.3.2). The northern desert was expected to be dominated by small and medium-sized (3.2-32.6kg) ectothermic omnivores and herbivores.

Figure 5-4 Total biomass ('000 tonnes) of endothermic (a.) and ectothermic (b.) heterotrophs (carnivores, omnivores and herbivores) in different body mass bins in pristine ecosystems, by ecosystem. Targeted populations are indicated by yellow band in a. For clarity, very large (>1000kg) and very small (<0.1 kg) organisms had been removed.

5.3.2 Harvesting Outcomes

5.3.2.1 Population persistence

Qualitatively, targeted populations' responses to harvesting were similar between ecosystems (Figure 5-5). The proportion of persistent populations decreased with harvesting intensity, and, with the exception of the grassland and shrub, for each level of risk (high vs very high), there existed a threshold, beyond which persistence over 30 years declined rapidly. At harvesting rates below the threshold, persistence was high, and showed no relationship with harvest rate, or only a slight relationship. At harvest rates above the threshold, persistence declined rapidly with increasing harvesting. The exception was in the grassland ecosystem, for the high risk case. Here, persistence with no harvesting over 30 years was significantly lower than in the other ecosystems (47%±18%; 95%CI, n=30, compared to 83-100% in all other ecosystems), and the relationship between persistence was closer to linear, such that persistence declined steadily with increasing harvesting over the full range of harvesting rates. For the remaining cases, despite the general qualitative agreement, the location of the thresholds (i.e. the harvesting rates that caused persistence probabilities to begin to rapidly decline) differed between locations and according to the level of risk. The thresholds were closer for the two wooded savannah ecosystems (circa 0.45 vs circa 0.60), and for the two forest ecosystems (circa 0.25 vs circa 0.20). For all ecosystems, there were marked differences between the risk cases (the high vs the very high risk case; the orange and the green line in Figure 5-5), with the highest discrepancy between trajectories in the forests, and the grassland and shrub.

For setting real-life harvesting policies, the thresholds could, in principle, be used to set the maximum allowable harvesting rate that still returned a probability of persistence above 90% (analogous to the duiker survival constraint used in Chapters 2 and 3). Of all ecosystems, wooded savannah was the most resilient to harvesting according to this metric, with a potential to accommodate harvest rates of up to 40%-60% population year^{-1} under the constrained high risk strategy (at least 10% of initial population survived on average in at least 90% of the cases, corresponding the portion of the orange trend lines above the horizontal dashed line in Figure 5-5). These ecosystems also supported the highest densities of small and medium-sized heterotrophs in the pristine state (approximately 11000-12000 animals km^{-2}, Appendix 5-2). Here, the target population density declined by 4%-6% for each 5% increase in effort up to the annual harvest rate of 70% of population, with 26%-28% drop in density per 10% increase in effort thereafter (Appendix 5-3).

In the tropical forest, the thresholds were much lower than in the wooded savanna, allowing harvesting up to around 20-30% population year^{-1} under the constrained high risk strategy. Pristine population density of small and medium-sized heterotrophs was lower compared to the wooded savannah (around 9000 animals km^{-2}; Appendix 5-2); and the average densities declined by 6% for each 5% increase in effort up to 70% population per year (Appendix 5-3). In the southern desert, the maximum allowable harvest rate was 20%-25% population year^{-1} under the constrained high risk strategy, with the estimated target population densities of approximately 2700 animals km^{-2} (Appendix 5-2), declining by 16% for each 5% increase in effort up to 70% population per year, and by 37%, thereafter (Appendix 5-3).

In the woodland and shrub and the grassland ecosystems, the background extinction rates were above 10% of population on average. It was therefore impossible to find any harvest rates that returned a population persistence above 90%. Therefore, harvesting was only feasible under the constrained very high risk strategy, i.e. accepting that up to 99% of population could be lost due to a combination of harvesting and natural mortality (the green trend line in Figure 5-5). The percentage declines in average density of target populations with harvesting were lower in the grasslands than in other ecosystems: by 4% for each 5% increase in effort up to the annual harvest rate of 70% population per year, and by 12%, thereafter (Appendix 5-3).

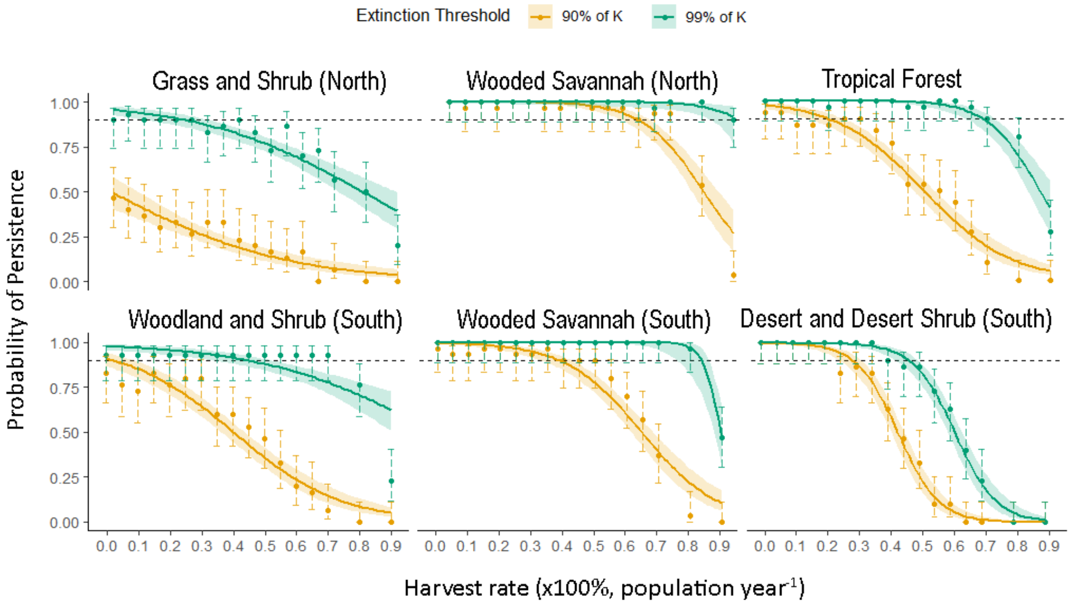


Figure 5-5 Probability of target species persistence (with 95% confidence interval in shaded orange/green, and 2 standard errors shown with error bars) with harvesting intensity over 30 years. On y-axis, values close to 1 indicate population density declining by 90% (in orange) or 99% (in green) during the 30-year harvesting period in only few replicate simulations; values below the horizontal dashed line indicate populations decline by 90% and 99%, respectively, in over 10% of the cases (high and very high risk of extinction, respectively) over 30 years.

5.3.2.2 Yields

The yields returned by the maximum, vs the constrained high risk, harvesting of small and medium-sized heterotrophs varied substantially among the ecosystems (Table 5-1). The average yield varied widely across ecosystems. In the wooded savannah, the maximum yield was almost twice that of forest ecosystems, over 200% higher than in the grassland and shrub, and almost 1000% higher than yields in the desert ecosystem (Figure 5-6). Yields in the grasslands and the tropical forest were comparable; however, the probability of low yields was significantly higher in the grassland and shrub ecosystem (note strong right skew in Figure 5-6).

Table 5-1 Bushmeat yields under the maximum and the constrained high risk strategies (in kg km^{-2} year^{-1} and in kg capita^{-1} year^{-1}, with 1 standard error, s.e.) by ecosystem, compared to the empirical beef offtakes (in kg capita^{-1} year^{-1}).

Ecosystem	Bushmeat				Beef Offtake, kg capita^{-1} year^{-1}
	Yields, kg km^{-2} year^{-1} (mean±s.e.)		Yields, kg capita^{-1} year^{-1} (mean±s.e.)		
	Maximum	High risk	Maximum	High risk	
Grass and Shrub	2221.73 (±83.43)	-	67.53 (±2.54)	-	11.1
Wooded Savannah (North)	6722.15 (±142.45)	6722.15 (±142.45)	652.64 (±13.83)	652.64 (±13.83)	7
Tropical Forest	3407.44 (±68.00)	2246.98 (±36.89)	224.17 (±4.47)	147.83 (±2.43)	1.9
Woodland and Shrub	3675.97 (±94.16)	-	356.89 (±9.14)	-	7
Wooded Savannah (South)	6319.67 (±126.45)	5635.69 (±105.54)	613.56 (±12.28)	547.15 (±10.25)	7
Desert and desert shrub (South)	616.97 (±11.49)	497.88 (±6.62)	-	-	-

The harvest rate that maximised yield (the maximum rate) was 55%-65% population year^{-1} in all ecosystems (Table 5-2), except for the desert and desert shrub (around 30-35%). In all ecosystems, harvesting at the maximum rate reduced target population densities by at least 90%, compared to their pre-harvest densities (i.e.

high or very high risk of extinction). In wooded savanna ecosystems and southern desert, the maximum rates and the constrained high risk rates were similar within ecosystems (Table 5-2). In all ecosystems bar one (the grass and shrub ecosystem), the maximum harvest rates were below the harvest rates under the constrained very high risk strategy (Table 5-2). The corresponding yields were the opposite: the maximum yields were above the yields under the very high risk harvesting (Figure 5-6). This suggests that using the 1% survival threshold to set harvest rates (the very high risk strategy) was sub-optimal compared to the maximum harvesting in terms of species survival (Table 5-2) and in terms of meat yields (Figure 5-6). In the grasslands and in both forest ecosystems, the maximum harvest rates were significantly higher than harvest rates under the constrained high risk (but not the very high risk strategy); for example, 60% vs 30% population year^{-1} in the tropical forest (Table 5-2). I.e. in the grasslands and forest ecosystems, maximising yield could result in extinction of 90-99% of animal population.

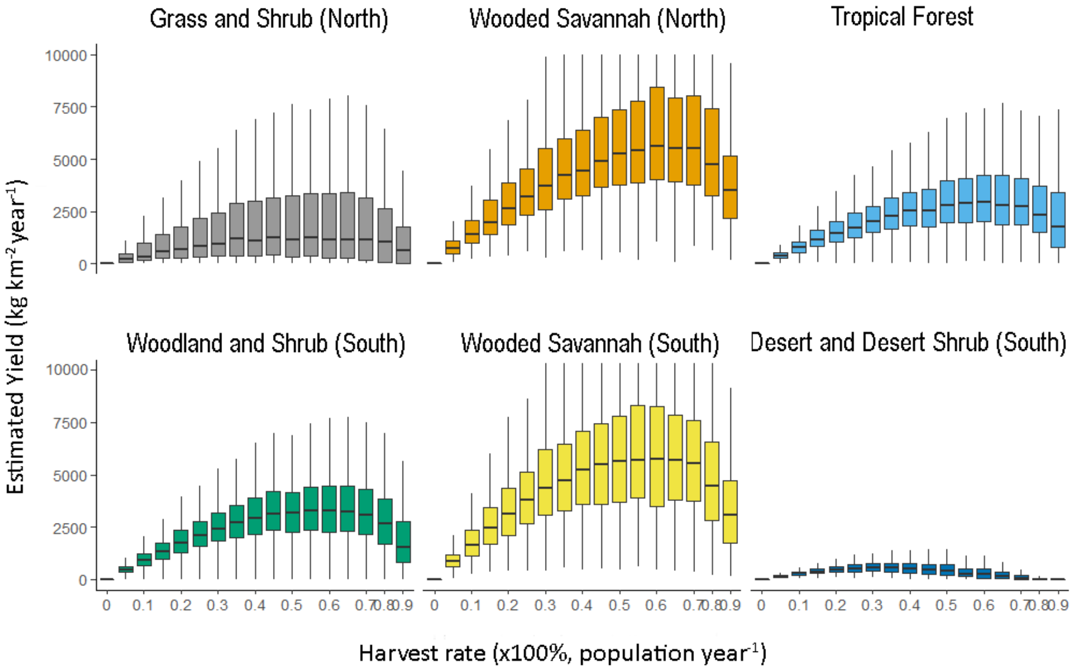


Figure 5-6 Average meat yields with harvesting intensity (not constrained by probability of persistence), by ecosystem.

Average bushmeat yields per capita per year under the maximum harvesting strategy were 6-117 times higher than the beef offtakes in sub-Saharan Africa, with the smallest difference (6 times) in the grasslands and the highest (117 times) in the tropical forest (Table 5-1); however, maximum harvesting was associated with high risk of extinction in all ecosystems except for wooded savannah in the North (Table 5-2). An estimate of human population density for the southern desert ecosystem was not available (possibly, very low); therefore, I couldn't calculate per capita bushmeat yields.

Table 5-2 Harvest rate, φ and associated probability of persistence, PP (calculated for the high risk harvesting, orange line in Figure 5-5; ±1 standard error, 95% CI, n=30) over 30 years, by harvesting strategy (constrained high and very high risk, and unconstrained maximum harvesting), by ecosystem.

Ecosystem	**Constrained High risk**		**Maximum**		**Constrained Very High Risk**	
	φ	**PP**	φ	**PP**	φ	**PP**
Grass and Shrub	0.00	0.47 (±0.09)	0.55	0.13 (±0.06)	0.25	0.27 (±0.08)
Wooded Savannah (North)	0.60	0.90 (±0.06)	0.60	0.90 (±0.06)	0.90	0.03 (±0.03)
Tropical Forest	0.30	0.90 (±0.06)	0.60	0.43 (±0.09)	0.70	0.10 (±0.06)
Woodland and Shrub	0.00	0.83 (±0.07)	0.65	0.17 (±0.07)	0.70	0.07 (±0.05)
Wooded Savannah (South)	0.50	0.90 (±0.06)	0.60	0.70 (±0.09)	0.70	0.37 (±0.09)
Desert and desert shrub (South)	0.20	1.00 (±0)	0.35	0.83 (±0.07)	0.40	0.63 (±0.09)

5.3.2.3 Impacts of harvesting

Across the ecosystems, and considering harvesting at three levels of intensity (20%, the maximum rate for each ecosystem, and 90%), there was evidence of a shared pattern of responses to harvesting, compared to the pristine baseline (Figure 5-7 and Figure 5-8). First, functional groups targeted for harvesting, i.e. mid-sized (1-23kg) herbivores, omnivores, and carnivores, tended to decline, as might be expected given that they were being removed. Second, within the target functional groups, omnivores tended to decline more than herbivores. Third, within the target functional groups, larger-bodied herbivores tended to decline more than smaller-bodied functional groups. Fourth, the declines in the targeted functional groups were coupled with increases in smaller-bodied non-targeted herbivores and omnivores, and less pronounced increases in larger-bodied non-targeted herbivores and omnivores. There were exceptions to this general pattern, and the individual changes were often not statistically significant. Nonetheless, comparing all responses together, the overall pattern was relatively clear (Figure 5-7 and Figure 5-8). However, there were marked differences in responses to harvesting between ecosystems, and between the functional groups within ecosystems.

Harvesting 20% of population per year had no statistically significant impact on target cohorts in any of the ecosystems (Figure 5-7a), except for the southern desert. Here, densities of omnivores and medium-sized (3.2-32.6kg) herbivores declined by 58%-66% and by 27%-39% on average, respectively. Non-target small-bodied (<1kg) herbivores and omnivores became more abundant in all ecosystems; however, at this level of harvesting, the effect of harvesting on small-bodied heterotrophs was statistically significant for one ecosystem (northern wooded savannah).

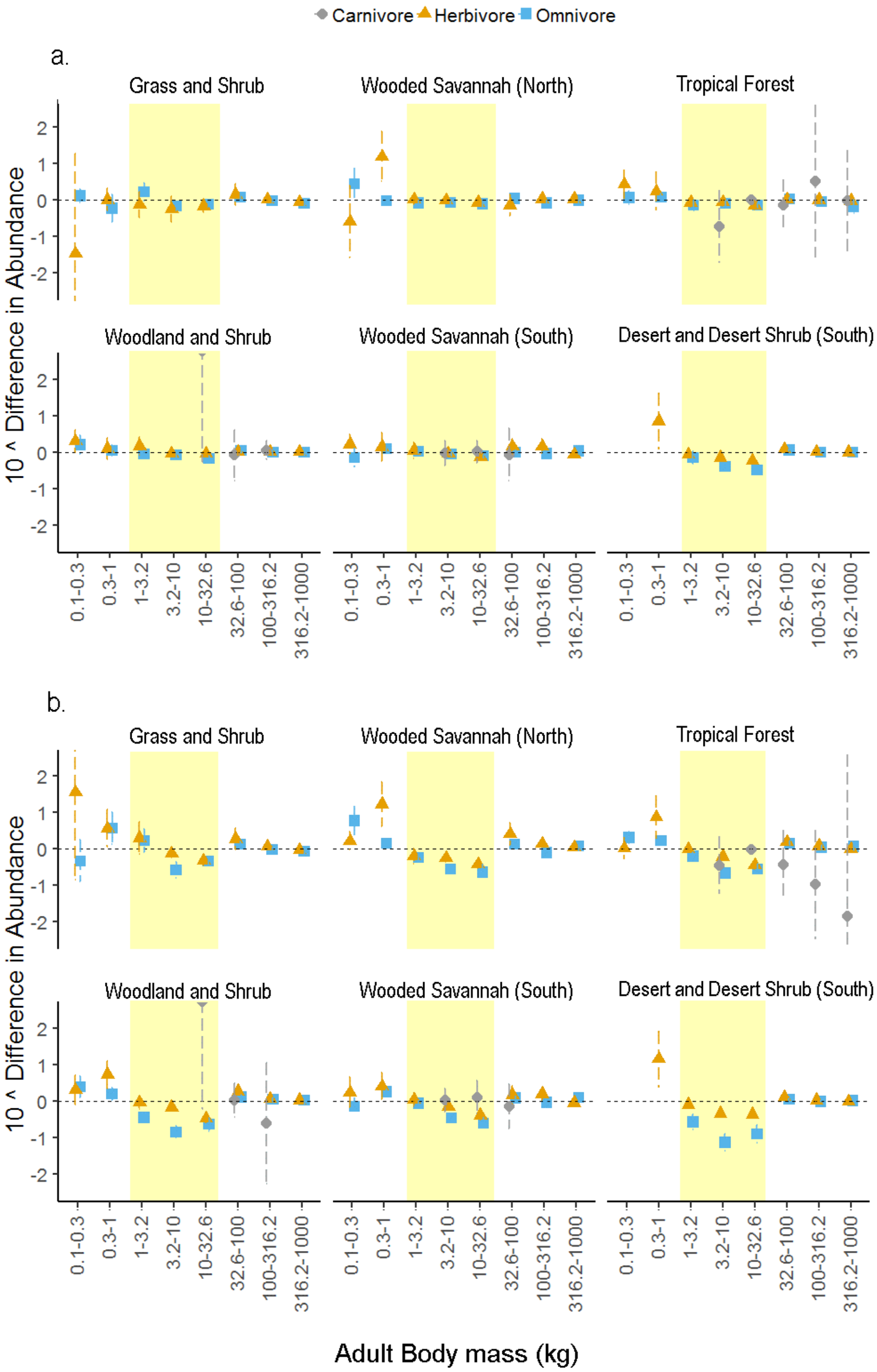


Figure 5-7 Changes in abundances of endothermic heterotrophs (with 95% confidence intervals) as a result of harvesting small-to-medium sized heterotrophs (highlighted in yellow) at the rate of 20% of population year^{-1} (in a.), and at the maximum rate of harvesting (in b.), by ecosystem and adult body mass. The horizontal dashed line indicates no significant impact of harvesting on abundances.

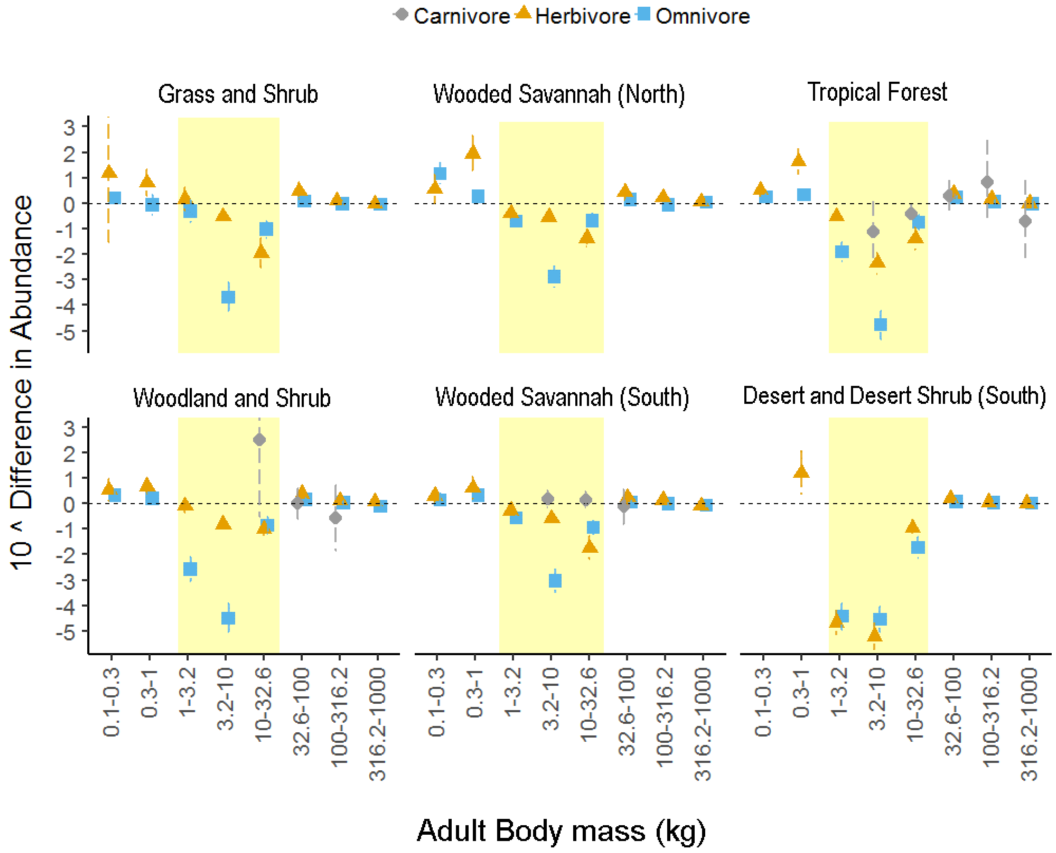


Figure 5-8 Changes in abundances (with 95% confidence intervals) of endothermic heterotrophs (with 95% confidence intervals) as a result of harvesting small-to-medium sized heterotrophs (highlighted in yellow) at the rate of 90% of population year^{-1}, by ecosystem and adult body mass. The horizontal dashed line indicates no significant impact of harvesting on abundances.

By contrast, at the maximum rate of harvesting (Figure 5-7b), significant changes in target cohort densities were seen in all ecosystems. Targeted omnivores declined by 84% in the desert ecosystem, 63%-75% in forest ecosystems, 50-64% in the wooded savannah, and around 20% in the grassland ecosystem. Densities of medium-large herbivores (3.2-32.6kg) declined, on average, by 53%-55% in the desert, 48%-52% in forest ecosystems, 43-53% in wooded savannah, and 40% in the grassland and shrub ecosystem. Despite being targeted for harvesting, small-bodied (1-3.2kg) herbivores were largely unaffected or even increased in abundance (in the grassland and shrub ecosystem). Targeted carnivores were largely unaffected (with the exception of the woodland and shrub ecosystem) though sample sizes were relatively small and outcomes had significant variation. Densities of non-target small-bodied (0.3-1kg) herbivores increased significantly in all ecosystems: by 161% in the wooded savannah in the South; 262% in the grasslands; 448%-648% in the forest ecosystems; and by over 1000% in the desert and the wooded savannah in the North. Small-bodied omnivore densities were also expected to increase: by between 39%-84% in the wooded savannah and forest ecosystems and by 268% on average in the grassland ecosystem.

Annual harvest of 90% of small and medium-sized heterotrophs (Figure 5-8) resulted in catastrophic declines in the target group densities in all ecosystems, losing 96% of herbivores and 99% of omnivores in the desert ecosystem; 88% of herbivores and 94% of omnivores in the tropical forest; 65% of herbivores and 95% of omnivores in the woodland and shrub; 74% of herbivores and 87% of omnivores in the wooded savannah ecosystems; and 41% of herbivores and 81% of omnivores in the grassland and shrub. Within the target group, smaller-bodied (1-3.2kg) herbivores were more resilient to harvesting than medium and large-bodied herbivores and omnivores. Densities of small-bodied non-target herbivores (0.3-1kg) increased by approximately 300% in the wooded savannah in the South, by over 4000% in the tropical forest, and by almost 9000% in the northern wooded savannah.

5.4 Discussion

The purpose of employing the Madingley Model in this chapter was to explore how potential bushmeat yields, maximum harvesting rates, and the impact of harvesting, might vary across African ecosystems. The model predicted that potential bushmeat yields varied by a factor of ten (or factor of three if we ignore desert). The harvesting rates required to achieve these yields did not vary significantly (55% to 65% per year, except for desert at 35%). The impact on ecosystem structure of harvesting at the maximum rates (harvest rates that maximised yield) varied quantitatively, but the qualitative pattern was relatively consistent (Figure 5-7 and Figure 5-8). Results such as these, produced by general ecosystem models, which are in their infancy, should be treated with caution (Purves *et al.*, 2013; Harfoot *et al.*, 2014). However, this class of models is at least able to begin to explore questions for which direct data are currently almost entirely lacking (Travers *et al.*, 2007; Link, Fulton and Gamble, 2010; Bartlett *et al.*, 2016; Newbold *et al.*, 2018).

A thorough mathematical analysis, beyond the scope of this thesis, would be needed to understand exactly why the Madingley Model made the predictions it did for potential yields from bushmeat hunting in Africa. No other variability has been introduced to the model's inputs, except for the variation in the ecosystems' structure and function which emerge in the model by varying the location of harvesting simulations, and it is possible that important variation in ecosystem parameters has been missed. Nonetheless there is sufficient evidence to make two tentative conclusions. First, it is notable that animal biomasses (and therefore the potential bushmeat yields) are not predicted simply by Net Primary Productivity (NPP) (Lieth, 1975; Coe *et al.*, 1976; Levin, 1998). NPP, which measures the total annual production of plant material (Roxburgh *et al.*, 2005) and is the ultimate source of productivity for all other ecosystem components including the animals targeted in bushmeat hunting (Del Grosso *et al.*, 2008; Petz *et al.*, 2014), is greatest in the tropical forest (Kicklighter *et al.*, 1999), whereas the greatest potential bushmeat yields appear in savannahs and woodlands. This simple result suggests that the potential bushmeat yields reflect the overall structure and function of the ecosystem, which emerges from a complex interaction between climate, plants, and animals, in a way which is at least partly, and approximately, captured by the Madingley Model.

Second, the potential yields were greatest where the ecosystem in the pristine state had higher total biomass represented in functional groups targeted by the bushmeat hunting. Higher biomasses of endothermic small and medium-sized (1-23kg) heterotrophs were returned in the wooded savannah ecosystems than in the forests, grasslands and shrub, and the southern desert, with the latter two ecosystems dominated by large-bodied herbivores outside my harvesting target range (Figure 5-4). Although empirical estimates of bushmeat yields were not available for the majority of the modelled ecosystems (though see below regarding yield estimates in the tropical forests of the Congo Basin), the ecosystems biomass pyramids (Figure

5-4) corresponded relatively well with the current literature (Bell, 1982; Bennett and Robinson, 2000). For example, high biomasses of large-bodied herbivores in arid and semi-arid ecosystems (southern desert, grasslands and wooded savannah), and low herbivore biomasses in the forest ecosystems, corresponded with Bennett and Robinson's (2000) estimates of high mammalian biomasses in the open grasslands and woodlands (5-7 times higher than the evergreen forest) and low abundances of ungulates in tropical forests (attributed to the scarcity of grasses and browse) (Table 5-3). Similarly, high total biomasses of small and medium-sized herbivores in the grasslands and the northern wooded savannah agreed with Bell's (1982) estimates of high densities of small herbivores in open short- and medium-length grasslands of East-African savannahs. The number of inverted trophic pyramids in my results (Figure 5-3) was surprising (Elton, 1927): Trebilco *et al*. 2013 showed that top-heavy pyramids could indicate an overestimation of predator abundance or energy available to carnivores. Furthermore, the model predicted the carnivores to be predomonantly ectothermic (Figure 5-4). The ectothermic top carnivores were believed to be 5 times heavier than endothermic top carnivores (Burness *et al*., 2002), which, combined with overestimed abundances, could explain very high biomass estimates for ectothermic carnivores predicted here. High biomass estimates for large-bodied carnivores in the more productive forest and savannah ecosystems were also reported by Harfoot *et al.* (2014).

Further work could examine the potential impacts of shifting the harvesting in response to the local biomass pyramid. For example, it would make sense to harvest larger animals in the savannahs, compared to size classes harvested here, which were based on bushmeat hunting data mainly from forest ecosystems (Fa, Ryan and Bell, 2005).

The Madingley Model predicted bushmeat yields that were substantial on a per capita basis (Table 5-1). However, the model also predicted that bushmeat harvesting at these rates would have profound effects on ecosystem structure, with substantial reductions in target functional groups (reductions of 80% or more were typical; Table 5-2) coupled with substantial increases in non-target groups (increases of 200% or more were typical; Figure 5-7). These effects were not restricted to just one, sensitive ecosystem, but seen across all of the ecosystems. Such large ecosystem impacts call for a careful consideration of what it means for a harvest policy to be deemed sustainable (see below).

Table 5-3 Comparison of the Madingley Model's estimates of animal biomasses (adult body mass≥1kg; with no harvesting), vs observed animal biomasses of mammals (body weight≥1kg) in sub-Saharan Africa (Bennett and Robinson, 2000).

Ecosystem	**Total animal biomass (kg/km^2)**	
	Model Outputs	**Observed for mammals**
Evergreen forests	150000	>3000
Open forests/grasslands	170000-200000	circa 15000
Open grasslands	240000	circa 20000

The quantitative ecosystem impacts of harvesting differed among the ecosystems, something that may not be obvious at first when viewing the summary figures (Figure 5-7 and Figure 5-8). For example, overall, the northern and southern savannahs showed similar impacts from harvesting (Figure 5-7); however, the northern savannah showed a large (circa 20 times) increase in small-bodied herbivorous endotherms not seen in the southern savannah (circa 2 times increase only). The grassland and woodland ecosystems had the highest extinction rates without harvesting (Figure 5-5). The exact reasons for high background extinction rates in the woodland and shrub and the grasslands ecosystems (Figure 5-5) are unclear and could be addressed in future work. One possible explanation could be a higher share of smaller-bodied animals with shorter life spans and higher rates of turnover compared to other ecosystems (although based on Figure 5-4, this does not appear to be the case). Opposite to expectation (Woodroffe, 2000; Azhar *et al.*, 2014; Newbold *et al.*, 2018), the omnivores were more sensitive to harvesting than the carnivores and herbivores. The omnivores had the lowest total biomass in all simulated ecosystems except for the deserts (Figure 5-3) with a higher share of medium-sized animals compared to the other functional groups (Figure 5-4). The non-linear responses to exploitation are a manifestation of complex trophic interactions and dynamic predator-prey responses in the Madingley Model (Newbold *et al.*, 2018). The omnivores' higher sensitivity to harvesting could be explained by a combination of harvesting, increased competition for limited resources and an increase in predation (Figure 5-7 and Figure 5-8). The 90% removal of all animals simulated here (Figure 5-8) is not likely in real-life systems; nevertheless, the model results show that such intensive harvesting would have profound effects on ecosystem structure. Empirical evidence of ecosystem responses to perturbations is still limited (Newbold *et al.*, 2018) with studies focusing on particular ecosystems and on incomplete subsets of the species in these ecosystems (though see Frank *et al.*, 2005; Carpenter *et al.*, 2011). These results underscore the need for ecosystem-specific studies to inform harvesting policies. Overall, grasslands and wooded savannah were the least affected by harvesting, and tropical forest and deserts the most affected. A global analysis of variances in vegetation productivity over the past 14 years identified tropical forests and desert regions of Africa as more sensitive to climate variability compared to savannah regions, which suggested that these areas were also more sensitive to anthropogenic pressures (Seddon *et al.*, 2016), such as bushmeat harvesting.

The low impact of harvesting on carnivore abundances was explained by a very low percentage of endothermic target carnivores in the pristine state in all ecosystems (below 1% of total biomass, with the exception of the tropical forest). The variation on predicted impacts of harvesting on carnivore abundances was high (Figure 5-7 and Figure 5-8), and any potential impacts of harvesting on carnivore abundances may have been offset (fully or partially) by large increases in abundance of their small-bodied prey. Nevertheless, for this region, the Madingley Model appears to have a structural problem with this aspect of its predictions – although good data is lacking, it is impossible to believe that over 90% of mid- and large-sized carnivores in these ecosystems are ectothermic (or would be, in the pristine state that is being simulated). This problem does not necessarily have a large overall impact on the Madingley Model used for general questions, but it is of central importance here because the harvesting policy distinguishes between these two groups. Complete absence of carnivores in some of the simulated ecosystems (e.g. in desert ecosystem, also reported by Newbold *et al.*, 2018) is also unrealistic. Further work could seek to improve the model, and in the meantime, examine the predicted yields if the ectotherms were effectively treated as endotherms for the purposes of hunting removals.

The model's predictions for potential bushmeat yields were large enough to have implications for human nutrition. When taking human population density into account, the annual yield per capita was 67 kg for northern grass and shrub; over 200 kg for northern and southern wooded savannah, and tropical forest (desert was an exception, given the lack of human population data). To put these figures into context, the annual meat consumption per capita in the United States is estimated to be 62 kg (FAO, 2013), although a fairer comparison is with US meat production, at 124 kg (losses between production and consumption are around 50%).

Are these predictions realistic? Data are scarce, but the model's estimate of yields under the high risk strategy for the tropical forest ecosystem of 2246.98 kg km^{-2} year^{-1} ($\pm$36.89) compared surprisingly well with estimated meat offtake in the Congo basin of around 2645 kg km^{-2} year^{-1} by Fa, Ryan and Bell (2005). Taken at face value, then, the Madingley Model predicts that this rate of hunting is sustainable, at least within this ecosystem, and suggests further that even higher sustainable yields are possible in savannahs. However, there are several important caveats here. First, as mentioned above, according to the model, harvesting at these rates has drastic effects on ecosystem structure, and so is sustainable in the narrow sense only. Second, again according to the model, to achieve the maximum yield in the tropical rainforest requires the removal of 30% of all animals in the target group (i.e. all carnivores, herbivores and omnivores of body mass 1-23 kg) every year. This may not be feasible in practice (e.g., it will be met with strong opposition from national conservation organisations), and even if it was, underscores why such harvesting would be likely to have profound effects on the ecosystem. The final caveat is a reminder that general ecosystem models, such as the Madingley, are still in their infancy, and as such their predictions should be treated with caution. Nonetheless, the results do suggest that substantial sustainable bushmeat yields may be possible in African ecosystems – and that general ecosystem models can begin to estimate these yields, and/or raise important questions for further study. The Madingley's estimates for duiker-like harvesting agreed fairly well with the results for duiker harvesting using the parameterised Beverton-Holt model (validation experiment in Chapter 4).

The differences between bushmeat yields and beef offtakes (Otte and Chilonda, 2002) were particularly high in the tropical forest and wooded savannah ecosystems, and relatively low in the grasslands, where bushmeat yields were at the their lowest and beef offtakes were maximised (Table 5-1). Cattle, goats, sheep, poultry and pigs all contribute to protein intake in Africa; however, the livestock distribution across Africa is uneven, with more than half of all ruminant livestock in sub-Saharan Africa concentrated in the arid and semi-arid areas (Otte and Chilonda, 2002). Intensive land management including animal husbandry has been shown to significantly impact biodiversity, particularly in pristine ecosystems (Newbold *et al.*, 2015). If achieved, sustainable well-regulated bushmeat harvesting could help alleviate some of the negative impacts of livestock husbandry by providing an alternative source of protein in the tropical forests of Africa, at least in the near future.

Because the model was set to target small and medium-sized animals, it did not necessarily capture the highest possible yields in each ecosystem. The decision to keep the body size of the target group constant was based on: a) the sizes of animals caught by snare, bow and arrow, or rifle, by a single hunter (Fa, Peres and Meeuwig, 2002); b) the complexities of identifying animal sizes that maximised yields in each ecosystem: these 'optimal' animal sizes may or may not be reasonable in reality, and c) the ease of comparison between ecosystems. One could also argue that the preference for small and medium-sized animals was more conservative, due to lower reproductive rates and densities of larger-bodied animals. The question of optimal body sizes for harvesting in different ecosystems can be explored in future work.

By harvesting once a year (rather than continuously) and assuming constant, non-adaptive harvesting I might have disadvantaged ecosystems with higher seasonality (such as grasslands). More sophisticated harvesting strategies could be implemented, though one could argue that more sophisticated harvesting regimes would make the modelled processes more obscure and could confound interpretation of the results.

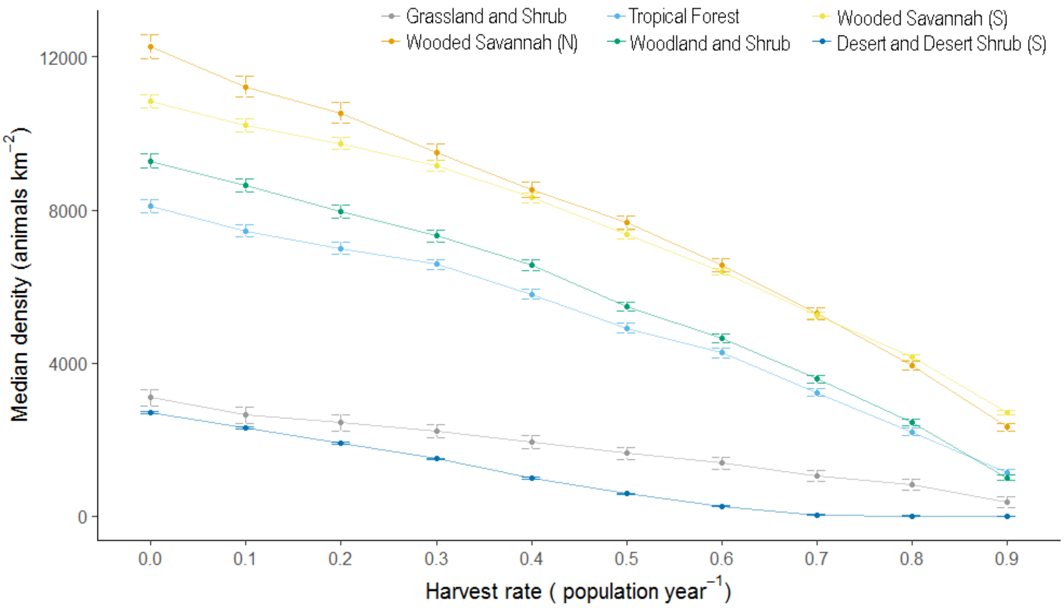
Here, I examined how the ecosystems differed in their capacity to support bushmeat harvesting and in responses to harvesting, as predicted by the Madingley Model. Although it wasn’t possible to identify the exact ecological interactions and processes that determined ecosystems capacity for supporting sustainable bushmeat yields, some ecosystems were much more productive and resilient to harvesting than the others suggesting that the ecosystem structure and functioning were important predictors of productivity and resilience. Because the Madingley Model does not require specific parameter inputs (Harfoot *et al.*, 2014), I was able to compare the dynamics of ecosystem communities consisting of species that we may not have population parameter estimates for, and therefore, may not be able to model otherwise. In addition, the modelled ecosystem communities not only incorporated the effects of multi-trophic interactions but also the effects of the environmental conditions on plant and animal biomasses. As climate plays a crucial role in determining ecosystem features (e.g. Coe *et al*., 1976; Levin, 1998), it follows that the ecosystems capacity for wild meat production, as well as livestock husbandry, will change in the future. These results are experimental, but they demonstrate the potential of a general ecosystem model such as the Madingley Model, as an additional tool for informing decisions in conservation and land management.

Appendices

Appendix 5-1 Geographic coordinates of the Madingley harvesting simulations.

Location	Vegetation Type	Coordinates
Desert and desert shrub – North	Desert	19^{0}N 22^{0}W
Grass and Shrub – North	Savannah	10^{0}N 22^{0}W
Wooded Savanna – North	Savannah	7^{0}N 22^{0}W
Tropical Forest	Forest	0^{0}N 22^{0}W
Woodland and Shrub – South	Forest	9^{0}S 22^{0}W
Wooded Savanna – South	Savannah	16^{0}S 22^{0}W
Desert and Desert Shrub – South	Desert	30^{0}S 22^{0}W

Appendix 5-2 Median densities of target species (with 95% confidence intervals) with annual harvest rate, by ecosystem.



Appendix 5-3 Average declines in target animal densities per 0.05 population year^{-1} increase in harvest rate, φ up to $\varphi \leq 0.70$, and per 0.10 population year^{-1} increase in harvest rate, φ, thereafter, by ecosystem.

Ecosystem	Harvest rate φ	
	≤0.70	**0.70-0.90**
Grass and Shrub – North	0.04	0.12
Wooded Savanna – North	0.06	0.28
Tropical Forest	0.06	0.31
Woodland and Shrub – South	0.06	0.32
Wooded Savanna – South	0.05	0.26
Desert and Desert Shrub – South	0.16	0.37

Chapter 6 Final Discussion

Species data and modelling limitations have been identified as limiting factors for effective assessment of sustainability of bushmeat harvesting in sub-Saharan Africa. To explore how more advanced modelling might address these limitations, I put to the test three different modelling approaches: two approaches built around a single-species model (Beverton and Holt, 1957), parameterised for duiker antelope *Cephalophus* spp. (*C. callipygus, C.dorsalis and C.monticola*); and an alternative approach utilising a General Ecosystem Model called the Madingley Model (Harfoot *et al.*, 2014), which bypassed the need for location- and species-specific data, and could explore several questions for which information would be almost completely lacking otherwise (Purves *et al.*, 2013; Bartlett *et al.*, 2016; Newbold *et al.*, 2018), including the effects of harvesting multiple species; the ecosystem-level impacts of harvesting; and the variation among ecosystems in both of these.

The aim of the thesis was to advance more efficient ways to improve bushmeat harvesting on the ground, through the use of newer statistical, analytical and computational tools and techniques. According to the results from my single-species models, I showed that proportional harvesting outperformed quota-based harvesting in terms of both yield and species survival, under both constant (Chapter 2) and adaptive (Chapter 3) harvesting approaches. From a theoretical perspective then, proportional harvesting was clearly advantageous (Lande *et al*., 1997; Bousquet *et al*., 2008). However, proportional harvesting is often considered impractical (Mockrin and Redford, 2011). The results of Chapter 3 suggested that combining considerations of uncertainty, with adaptive harvesting (Holling, 1978; Walters, 1986), and parameter updating via field data, could improve yields, and improve survival, and thus begin to close the gap between quota-based and proportional harvesting. However, gathering more field data is very difficult in sub-Saharan Africa because of operational constraints (Coad *et al.*, 2013; Milner-Gulland and Shea, 2017).

I then explored the Madingley Model (Purves *et al.*, 2013; Harfoot *et al.*, 2014) as an alternative to extensive monitoring. The results of the model's verification against a conventional single-species model (Chapter 4); its reasonable dynamics under harvesting, such as relationships between ecosystem structure, and ecosystem productivity and resilience to harvesting (Chapter 5); and the general correspondence of its trends to the current literature (Bell, 1982; Bennett and Robinson, 2000; Fa, Ryan and Bell, 2005), tentatively suggest that the Madingley Model is ready to contribute to bushmeat management. Moreover, the Madingley Model results suggest that, in principle at least, sustainable bushmeat yields could be substantial enough to have implications for human nutrition (FAO, 2013), albeit with substantial impacts on ecosystem structure (Chapter 4 and Chapter 5). By providing results such as these, in the absence of detailed species- or location-specific knowledge, the Madingley Model could potentially be used to begin to complement advances in more conventional approaches.

Actually improving our understanding of bushmeat harvesting in Africa, or in other regions, requires a multifaceted approach that considers ecology, socioeconomics, land use, and other factors (Milner-Gulland and Bennett, 2003; Robinson and Bennett, 2004; Bennett *et al.*, 2007; Nasi *et al.*, 2008), and consults with many stakeholders (Elmberg *et al.*, 2006; Nichols *et al.*, 2007). However, any such approach would benefit from a greater quantitative understanding of potential yields (van Vliet and Nasi, 2008), species survival (Elmberg *et al.*, 2006), and ecosystem impacts (Abernethy *et al.*, 2013), and how these might vary among contrasting regions with contrasting ecosystems, such as explored here.

In Chapter 2, I built a Bayesian-type model of constant (quota-based and proportional) harvesting around a conventional single-species Beverton-Holt model (Beverton and Holt, 1957), parameterised for three duiker antelope *Cephalophus* species. Unlike most previous estimates of sustainable bushmeat harvest in the tropics (e.g. Payne, 1992; Feer, 1993; Noss, 1998; Noss, 2000), my method explicitly modelled parameter uncertainty for the three duikers (based on a comprehensive literature review). The first key result was that incorporating uncertainty revealed a trade-off between yield, survival, and attitude to risk, which was not evident when uncertainty was ignored (May, 1973; Lande, Engen and Saether, 1995). When ignoring uncertainty, there appeared to be a clear optimum harvest rate, at which yield was maximised, and at which survival probability was close to 1. By contrast, when incorporating uncertainty, it became evident that the maximum harvest rate depended on attitude to risk (Canessa *et al.*, 2016); i.e. the rate that maximized the median yield differed from the rates that maximized the upper or lower quartiles, and moreover, such harvest rates may be accompanied by a substantial reduction in survival (Mace and Lande, 1991). Thus, when uncertainty was considered, the choice of harvest rate, even for this simple single-species model, was not nearly so simple.

The second key result was that constant proportional harvesting clearly outperformed quota-based harvesting, in multiple ways. Proportional harvesting not only returned greater yields and greater survival, but also the choice of harvest rate was not so dependent on risk attitude, or on whether the harvest was constrained using considerations of survival probability. Compared to proportional harvesting, quota-based harvesting carried a higher risk to species survival, especially under high parameter uncertainty and environmental variability (Lande, Engen and Saether, 1995; Engen, Lande and Sæther, 1997).

However, quota-based harvesting, rather than proportional harvesting, is being used on the ground (Mockrin and Redford, 2011), and is always going to be easier to implement and will therefore be preferred by managers. My method nonetheless established clear potential benefits of incorporating parameter uncertainty under constant quota-based policy, in terms of weighing up the risks and expected rewards of harvesting decisions. In other words, for simple assessments of sustainability of harvesting on the ground, including uncertainty was useful for increasing transparency of decision-making (Keith *et al.*, 2011; Nuno, Bunnefeld and Milner-Gulland, 2014; Milner-Gulland and Shea, 2017), and was therefore preferable to ignoring uncertainty altogether.

Hunting management practices vary around the world. In developed countries, hunting rights belong to either landowner (e.g. the UK, much of Europe) or the state (North America, Hungary, Poland and Estonia) (Mustin *et al.,* 2011). In the UK, the right to hunt belong to the landowner, who is also responsible for setting the hunting limits and, usually, for monitoring of game population (Newey and Smith, 2010). State regulation only determines the species which may be hunted, the hunting season, and permitted hunting methods (Mustin *et al.,* 2011). In Nordic countries (Finland, Norway, Sweden, Denmark and Iceland), the hunting rights belong to the landowner and may be leased; harvest levels are set by the state which is also responsible for monitoring of game populations (Mustin *et al.,* 2011). In their review of schemes used to monitor migratory European ducks, Elmberg *et al*. (2006) highlighted an urgent need for a pan-European monitoring scheme to allow managers to produce effective predictive tools which could form a basis for management decisions for species harvesting and conservation. Successful collaborations in harvest management are possible, as demonstrated by the US Fish and Wildlife Service responsible for managing the harvest of mid-continent Mallards *Anas platyrhynchos* across the United States of America and Canada (Williams, 1996a; Nichols *et al.*, 2007). Community-based schemes that involve local population in management of natural resources are being trialled in the tropics (e.g. Nielsen, 2006; Hurst, 2007). However, their effectiveness is limited by socio-economic factors such as poverty, lack of employment and low number of domestic animals in the sub-Saharan region (Nielsen, 2006; Milner-Gulland and Bennett, 2003), and by poor understanding of species ecology (van Vliet and Nasi, 2008).

Another way to deal with uncertainty in exploited systems is the adaptive management approach (Holling, 1978; Walters, 1986). Importantly for bushmeat, this approach does not require cessation or severe restriction of harvesting efforts (as is often the case under constant quota-based harvesting); instead, optimal strategies are determined given the best available knowledge of species, and harvesting is followed by collecting information about harvested species and their responses to harvesting (Chadès *et al.*, 2017; McCarthy and Possingham, 2007; Probert *et al.*, 2011).

In Chapter 3 I replaced Chapter 2's assumption of constant harvesting, with adaptive harvesting. In this model, harvest rates (proportion or quota) were adjusted yearly based on changes in population densities as a result of the previous year's harvesting. In addition, a gradual improvement in knowledge of the species (in this case, population growth rate and carrying capacity) was built into the decision-making process. To study the potential implications of this kind of model-based adaptive harvesting, I carried out a 'virtual ecology' study (Hilborn and Mangel, 1997), which separated models of the actual populations, from the models used by a decision maker to manage those populations.

The results showed that adaptive harvesting could be expected to be beneficial in terms of yield and species survival (Williams, 1996a; Parma, 1998; Elmberg *et al.*, 2006; McCarthy and Possingham, 2007; Nichols *et al.*, 2007; Butler *et al.*, 2015), under both quota-based and proportional harvesting. Documenting populations densities post-harvesting led to significant improvements in harvesting outcomes (Nichols *et al.*, 2007): this was true even for cases where uncertainty was being ignored, and parameters were not being updated. The implication is that all model-based adaptive harvesting, however simple, will tend to reduce harvest rates when populations decline, and increase them when populations increase – even when population parameter are not known perfectly (Rout *et al.*, 2018; van Vliet and Nasi, 2008), and, therefore, the decision model differs substantially from the true population dynamics. This view is reinforced by the fact that adaptive harvesting was less beneficial under proportional harvesting, which naturally scales the harvest rate in proportion to the (estimated) population density. By contrast, the benefits of adaptive harvesting were greater for quota-based strategies, which without some form of adaptive harvesting do not vary systematically from year to year.

As before, adaptive proportional harvesting outperformed quota-based harvesting in general. However, with parameter updating, adaptive quota-based harvesting could closely approximate the benefits of proportional harvesting. Because quotas are widely used for setting harvest targets in bushmeat (Nichols *et al.*, 2007; Mockrin and Redford, 2011), these results are potentially useful in terms of emphasising data collection and annual model-based planning as a potentially high-value-adding activity within practical bushmeat management (McCarthy and Possingham, 2007; Moore and McCarthy, 2010).

The modelling methods explored in Chapters 2 and 3 were designed to address issues around lack of data. Nonetheless, the methods required at least some knowledge of harvested species population parameters, and this knowledge was expected to increase through monitoring over time under adaptive harvesting. Presently, there are very few examples, even in the developed countries (Elmberg *et al.*, 2006; Nichols *et al.*, 2007), where monitoring programmes are in place to support harvest management, primarily because such programmes entail big investments in terms of time, money, know-how and leadership (McCarthy and Possingham, 2007; Butler *et al.*, 2015). Recent advances in data collection (Dolman, Panter and Mossman, 2012; Koh and Wich, 2012; Turner *et al.*, 2015; Vatresia *et al.*, 2016) and analysis (van Strien, van Swaay and Termaat, 2013; Isaac *et al.*, 2014) have the capacity to change this trend.

In practice, multiple species are harvested together in sub-Saharan Africa (Fa and Peres, 2001), and for the majority of these species population-level data and parameters are not available (Fa and Brown, 2009). In addition, single-species models ignore potentially important trophic interactions and environmental conditions, which are likely to alter species responses to harvesting (Bhattacharya and Begum, 1996; Song and Chen, 2001). Moreover, single-species models cannot be used to address the wider ecosystem impacts of harvesting (Abernethy *et al.*, 2013). Therefore, in Chapters 4 and 5, I addressed some of these data and modelling limitations, using the Madingley General Ecosystem Model (Purves *et al.*, 2013; Harfoot *et al.*, 2014).

In Chapter 4, I used the Madingley Model to simulate harvesting of duiker-sized herbivores in a tropical forest ecosystem, and then compared the model's estimated yields and survival probability for the duiker-like herbivores against my single-species model's estimates for Peters' duiker (Chapter 2). Although the Madingley Model does not distinguish between organisms on a species level (Harfoot *et al.*, 2014), the assumption that all animals within a certain body size are targeted by hunters is more realistic than assuming only certain species are extracted (Fa and Brown, 2009). Without any tuning, the Madingley General Ecosystem Model produced estimates of yield, maximum sustainable harvest rate and survival probability for the duiker-like herbivores that were comparable with estimates for Peters' duiker harvesting using the Beverton-Holt model (Figure 4-2). The absolute yield estimates from the Madingley were 5-10 times higher than yield estimates from the single-species Beverton-Holt model; however, this was expected as more than one duiker-like species were targeted in the Madingley Model, increasing the total yield. The ecosystem was surprisingly robust to single-species harvesting, with animals in several neighbouring size classes increasing in abundance to compensate for the removals of the duiker-like animals (Figure 4-3 and Figure 4-4) (da Fonseca and Robinson, 1990; Adler, 1996; Bodmer *et al.*, 1997; Fa and Brown, 2009). Otherwise, ecosystem impacts were negligible.

The fact that the single-species model, and the Madingley Model, produced comparable results for this harvesting scenario is a key result from the thesis. As illustrated in Figure 4-1, the models are entirely independent, using different input data sources and model formulations to provide their estimates. Therefore, the model agreement acted to increase confidence in both types of model, and to increase confidence in using the Madingley Model for a wider range of simulations, which could not be compared directly to single-species models. It indicated that the model could have wider utility for evaluating sustainable hunting strategies that were directed at broad groups of animals (e.g. all animals in the small and medium-sized body mass range, which was a more realistic focus for hunters in the forest; Fa, Ryan and Bell, 2005).

Reassured by these results, I then went on to use the model to simulate harvesting an ensemble of small and medium-sized endothermic heterotrophs (an experiment which would not have been possible without the Madingley Model), based on body size ranges reported for hunters in the Congo Basin, which rarely or never hunt single species (Fa, Ryan and Bell, 2005). For this scenario, the predicted maximum harvest rates were much greater (around 65%, compared to 20% for duiker-like animals), and the yields were greater. Importantly, the predicted yields (around 4500 kg km^{-2} $year^{-1}$, see Figure 4-5) were comparable to bushmeat offtakes reported from field surveys (around 2700 kg km^{-2} $year^{-1}$ in the Congo Basin; Fa, Peres and Meeuwig, 2002).

The ecosystem-level impacts of harvesting multiple groups were more pronounced than for duiker-like harvesting alone. Some predicted ecosystem impacts were in agreement with the current literature; for example, untargeted small-bodied (<1kg) herbivores increased in density significantly at high levels of removal of larger-bodied animals (Figure 4-6) (da Fonseca and Robinson, 1990; Adler, 1996; Bodmer *et al.*, 1997; Wright, 2003; Fa and Brown, 2009). Other predictions, such as omnivores being more sensitive to harvesting than herbivores or carnivores, should be treated cautiously (Woodroffe, 2000; Azhar *et al.*, 2014), as new hypotheses that could be further examined given sufficient data. Overall, the results presented in Chapter 4 suggest the Madingley Model is mature enough to begin to explore bushmeat hunting, and its wider impacts, in this region.

Therefore, in Chapter 5, I went on to use the model to examine the potential variation in yields, maximum harvest rates and ecosystem impacts across different locations with contrasting ecosystems. To date, it has not been possible to separate out ecosystem effects from the species dynamics (though see Coe *et al.*, 1976; McNaughton, 1976). But the interactions may become more important in future as ecosystems alter with climate change (Walther *et al.*, 2002; Abernethy *et al.*, 2013; Seddon *et al.*, 2016) and other global changes (Brashares, 2003; Fa, Currie and Meeuwig, 2003; Rudel, 2013). Can an ecosystem model still provide information on meat yield in the absence of any information on the animal populations? I simulated harvesting of small and medium-sized heterotrophs in a range of African ecosystems (forest, savannah and desert) in the Madingley Model, and compared the emergent ecosystems structure, as well as ecosystems productivity (expressed as yields from harvesting small and medium-sized heterotrophs), probability of persistence under harvesting, and ecosystem-level impacts of harvesting.

The yields from harvesting small and medium-sized heterotrophs in the Madingley Model differed significantly between the seven ecosystems. This suggested that the ecosystems' relative productivity was not simply the function of Net Primary Productivity (NPP), which determined the total production of plant material and animal productivity (Roxburgh *et al.*, 2005; Del Grosso *et al.*, 2008; Petz *et al.*, 2014), including productivity of the animals targeted by bushmeat hunting. The relative yield and probability of animal persistence were also impacted by the complex interactions within and between functional groups and stocks (Wright, 2003).

In the model, the ecosystem structure and functioning were important predictors of ecological communities' relative capacity to support bushmeat harvesting (Bennett and Robinson, 2000). The ecosystems with higher total biomass in functional groups targeted by hunting returned higher yields. For example, tropical savannahs were significantly more productive than the tropical forest ecosystem, grasslands and desert ecosystems (Figure 5-6). The model's high biomasses of large-bodied herbivores in semi-arid grasslands and wooded savannah, and low herbivore biomasses in the forest ecosystems, corresponded relatively well with trends reported in empirical studies of African ecosystems (Bennett and Robinson, 2000; Bell, 1982). Apart from the southern desert, the harvest rate that maximised the yield did not vary significantly between ecosystems (Table 5-2). The ecosystem-level impacts of harvesting were quantitatively different, with desert and forest ecosystems showing higher sensitivity to harvesting, compared to wooded savannah ecosystems. However, qualitatively, ecosystem-level impacts did not differ, with all ecosystems returning substantial reductions in abundances of target animal groups (Fitzgibbon, Mogaka and Fanshawe, 1995; Gates, 1996; Noss, 1998a), and substantial increases in abundances of non-target small-bodied animals (Figure 5-7 and Figure 5-8).

I found that the Madingley Model provided interesting insights into ecosystem-level behaviour, such as systems' general robustness to harvesting (with ecosystem shifts predicted under intensive harvesting regimes but not an ecosystem collapse (Newbold *et al.,* 2018). At the very least, the model could be useful for developing and exploring hypothesis about current and future scenarios of human-made perturbations. The model's undeniable strength is in helping address two important knowledge gaps: limited species knowledge and poor understanding of ecosystems complexity (Purves *et al.*, 2013). Its mechanistic nature also means that it is well-suited for exploring ecosystem changes under different levels of human-made perturbations (Bartlett *et al.*, 2016; Newbold *et al.*, 2018) and climate change scenarios (Willis *et al.*, 2013).

The final key result from Chapter 5 was that the Madingley Model predicts that substantial bushmeat yields are possible in all ecosystems, although the estimated maximum sustainable yields varied substantially among the ecosystems (Table 5-1). When taking human population density into account, the annual yield per capita was 67 kg for northern grass and shrub; then over 200 kg for northern and southern wooded savannah, and tropical forest (desert was an exception, given the lack of human population data). To put these figures into context, the annual meat consumption per capita in the United States is estimated to be 62 kg (FAO, 2013), which corresponds to a meat production of 124 kg (because losses between production and consumption are around 50%). Moreover, this level of meat consumption is considered excessive according to many sources of nutritional advice (e.g. WCRF, 2007).

Thus, at face value, the results presented in Chapters 4 and 5 imply that the potential maximum sustainable yields are greatly in excess of dietary requirements in tropical forests and savannahs; and somewhat in excess of requirements in northern grass and shrub. It is crucial that these results be viewed with caution, because the Madingley Model parameters have not yet been rigorously constrained against data (see below). However, for the tropical forest and savannahs, the Madingley's predicted yields are very high (approximately fivefold greater than US levels of meat production), and are within an order of magnitude of published estimates of current offtakes (Wilkie and Carpenter, 1999; Fa, Peres and Meeuwig, 2002). Therefore, the results raise the possibility that current harvesting rates are sustainable, at least in the narrow sense, i.e. that it might be possible to sustain the yields themselves.

However, a second major prediction from Chapters 4 and 5 was that harvesting at the maximum levels would have drastic impacts on ecosystem structure, which in turn implies that these yields may not be viewed as sustainable, if the definition of sustainability includes wider ecosystem impacts (Abernethy *et al.,* 2013). Whether some compromise exists, where bushmeat hunting can sustainably provide economically and nutritionally important yields, with acceptable levels of impact on population survival and wider ecosystem impacts, remains to be seen.

Conclusions and Further Developments

Simple models have obvious merits, such as ease of interpretation and solid grounding in empirical research (Beddington and May, 1977; Fryxell *et al.*, 2010). In the world of perfect data for all targeted species and in all ecosystems, these simple models could be all that is needed. In practice, however, collecting data is prohibitively expensive and time-consuming, particularly in the tropics (Coad *et al.,*, 2013). New methods of collecting population-level data, such as camera-trapping (Rowcliffe *et al.*, 2008; Hooker *et al.*, 2015) and drone technology (Koh and Wich, 2012), combined with technological advances in artificial intelligence and feature recognition (Karczmarski and Cockcroft, 1998), are already helping to save time and reduce the labour costs of monitoring, as well as making monitoring possible where it has not been previously (Rowcliffe *et al.*, 2008). Citizen science has a potential to become a major source of habitat and species-level information in Africa, as demonstrated by monitoring schemes in the UK (Isaac *et al.*, 2014; Barlow *et al.*, 2015) and the Netherlands (e.g. van Strien *et al.*, 2016). In the longer term, such methods could lead to orders of magnitude more data (Turner *et al.,* 2015; Koh and Wich, 2012).

The fairly complex methods presented in this thesis will need to be made accessible to bushmeat practitioners who may not have the skills or the time needed to replicate them. Mobile online applications are used to measure the performance of the conservation activity in Indonesia (Vatresia *et al.*, 2016) and to identify and tackle wildlife crime in China, Vietnam and the US (Kretser *et al.*, 2015). In Chapter 2, I built a prototype interactive online application (available at http://tinyurl.com/duikerantelope, see Appendix 2-7) that could, with some more work, be used by decision-makers on the ground.

Balancing the benefits of collecting new data against the value of making the best management decision given what is already known about the system is not a straight-forward exercise (McCarthy and Possingham, 2007). At the moment, monitoring efforts are rarely guided by a preliminary investigation of alternative monitoring outcomes (though see Field, Tyre and Possingham, 2005), but rather by economic and observational constraints. In conservation, optimal survey design could help maximise positive outcomes (or minimise adverse outcomes), given management constraints and the system under study (Field, Tyre and Possingham 2005). The results of my single-species adaptive model of harvesting suggest that continual incremental improvements in parameter estimates could eventually provide large improvements in outcomes, which suggests further that well-designed field surveys, aiming to estimate these parameters, could potentially justify the expense of the surveys.

At first glance, the Madingley Model may seem like a completely alternative route to addressing the bushmeat harvest, since, in its current form, the model does not require any additional input from the user (though harvesting scenarios need to be specified). However, the ultimate value of complex models like the Madingley Model is in the accuracy of their predictions, and this accuracy depends on how carefully the model has been parameterised and validated against data. The vegetation part of the Madingley Model has been carefully parameterised and validated against data (Smith *et al.*, 2013) but the animal part is more speculative, with some functional forms taken from empirical studies, and other parameters with little empirical support. Therefore, the upcoming increase in ecological data that can be expected to help with population-based modelling of harvesting, should also help with complex models such as the Madingley Model. The Madingley Model differs in this regard however, because it makes use of high-level environmental data, such as changes in temperature or vegetation types. At the moment, the value of such environmental data for simple bushmeat harvesting models is low. However, environmental data is of high value to a global model such as the Madingley Model, where it could help improve accuracy and resolution; therefore, making predictions more reliable. On the other hand, the Madingley Model predictions will need to be treated with a large degree of caution for some time to come. Ultimately, the best understanding of bushmeat is likely to come from combining multiple modelling approaches, with multiple sources of data, and will need to bring in multiple stakeholders to consider every aspect of the problem.

The vast majority of current modelling efforts in bushmeat harvesting, including the ones in this manuscript, are supply-driven, i.e. estimates of the maximum that nature can sustainably supply (e.g. Barnes, 2002; Fa *et al.*, 2006; van Vliet, Nebesse and Nasi, 2015). Despite its arguably higher practical value, the question of present and future demand for bushmeat as a driver of harvesting targets, and what it could mean for sustainability and ecosystem impacts of bushmeat harvesting, has not yet been addressed (Wilkie and Godoy, 2001).

Of course, modelling is only a small part of the problem. In the developing African countries issues of social injustice and economic inequality are infinitely more pressing. However, sustainable development cannot be put on hold until these issues are resolved. Between 2000 and 2012, the growth in African GDP was only second to Asia. Provided investments in infrastructure, African economies are forecast to grow (Randers, 2012). The question is at what cost to the environment; whether some mistakes made in the developed world can be prevented; and whether African and other developing countries could alter their current environmental trajectories towards a more sustainable path to economic and social prosperity.

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