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Managing social-ecological systems under uncertainty: implications for conservation

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Declaration of Originality

This dissertation is the result of my own work and includes nothing which is the outcome of work done by or in collaboration with others, except where specifically indicated in the text.

Ana Nuno, September 2013

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Abstract

Natural resource managers and conservationists are often confronted with the challenges of uncertainty. Limits to knowledge and predictability challenge conservation success and socio-economic, institutional and political context affect implementation of conservation interventions. Using a management strategy evaluation (MSE) conceptual framework, I use a multidisciplinary approach to gain a better understanding of the role and implications of different sources and types of uncertainty for the management of social-ecological systems, giving special attention to the issues of observation and implementation uncertainty. The conservation of harvested ungulate species in the Serengeti, Tanzania, is used as a case study.

I investigated which factors should be prioritized in order to increase survey accuracy and precision, and explored the potential effects of budgetary scenarios on the robustness of the population estimates obtained for different savannah ungulate species. The relative importance of each process affecting precision and accuracy varied according to the survey technique and biological characteristics of the species. I applied specialized questioning techniques developed for studying non-compliant and sensitive behaviour, using the unmatched-count technique (UCT) to assess prevalence of illegal hunting in the Serengeti. I found that poaching remains widespread in the Serengeti and current alternative sources of income may not be sufficiently attractive to compete with the opportunities provided by hunting. I explored trade-offs between different types of error when monitoring changes in population abundance and how these are affected by budgetary, observational and ecological conditions. Higher observation error and conducting surveys less frequently increased the likelihood of not detecting trends and misclassifying the shape of the trend but the differences between multiple levels of observation error decreased for higher monitoring length and frequency. Using key informant interviews with the main actors in the monitoring and management system, I provided recommendations for the development and implementation of interventions within long-term integrated and adaptive frameworks.

The research presented in this thesis highlights the need to consider the role of people as influential components within social-ecological systems in order to promote effective conservation interventions. Monitoring and implementation must be understood as dynamic features of the system, instead of merely acting upon it, and the multiple sources of uncertainty must be fully considered in conservation planning, requiring the development and application of tools to aid management decision-making under uncertainty.

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"There are known knowns; there are things we know that we know.
There are known unknowns; that is to say, there are things that we now know we don't know.
But there are also unknown unknowns – there are things we do not know we don't know."

Donald Rumsfeld

and

"Minus saepe pecces, si scias quod nescias"

(You would err less often, if you knew what you do not know)

Publilius Syrus

Abbreviations & acronyms

AIC	Akaike's Information Criterion
AM	Adaptive Management
BLUPs	Best Linear Unbiased Predictors
CCSs	Community Conservation Services
COCOBA	Community Conservation Bank
CV	Coefficient of Variation
df	degrees of freedom
FZS	Frankfurt Zoological Society
GCA	Game Controlled Area
GGR	Grumeti Game Reserve
GLM	Generalized Linear Model
GR	Game Reserve
IGR	Ikorongo Game Reserve
IWMA	Ikona Wildlife Management Area
LGCA	Loliondo Game Controlled Area
MGR	Maswa Game Reserve
MNRT	Ministry of Natural Resources and Tourism
MSE	Management Strategy Evaluation
MWMA	Makao Wildlife Management Area
NBD	Negative Binomial Distribution
NCA	Ngorongoro Conservation Area
NCAA	Ngorongoro Conservation Area Authority
NGO	Non-Governmental Organisation
RRT	Randomized Response Technique
SD	Standard Deviation

SE	Standard Error
SENAPA	Serengeti National Park
SES	Social-Ecological System
TANAPA	Tanzania National Parks
TAWIRI	Tanzania Wildlife Research Institute
UCT	Unmatched-Count Technique
WD	Wildlife Division
WMA	Wildlife Management Area

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1. Introduction

1.1. Problem statement

Natural resource managers and conservationists are often confronted with the challenges of uncertainty (Ludwig, Hilborn, & Walters 1993; Harwood & Stokes 2003; McBride *et al.* 2007; Kujala, Burgman, & Moilanen 2013). The outcomes of management interventions are frequently constrained by factors that may be difficult to account for, potentially explaining many of the failures in conservation and natural resource management (Regan *et al.* 2005; Punt & Donovan 2007; Holland & Herrera 2009). Managed systems are subject to natural variation, the data collected might be biased, the managers often have incomplete knowledge about the systems, and shifts in social, political and economic institutions affect how people use natural resources over time (Nicholson & Possingham 2007; Rammel, Stagl, & Wilfing 2007; Gavin, Solomon, & Blank 2010; Fulton *et al.* 2011). Acknowledging that conservation is both uncertain and dynamic is thus essential for planning and implementing effective interventions (Meir, Andelman, & Possingham 2004; Williams & Johnson 2013). The role and implications of multiple types of uncertainty when managing social-ecological systems (SESs) have, however, been given limited attention in conservation.

In times of increasing demand for transparent and accountable criteria and processes in conservation (Knight, Cowling, & Campbell 2006; Bottrill *et al.* 2008; McDonald-Madden *et al.* 2010; Armitage, de Loë, & Plummer 2012), conservation scientists are required to provide robust advice to aid decision-making and support management decisions (Punt, Knight, & Pullin 2003; Williams & Johnson 2013). Addressing the research-implementation gap (i.e. the weak linkages that are common between science and management decisions) (Sutherland *et al.* 2004; Pullin *et al.* 2004; Knight *et al.* 2008), will require the intrinsic uncertainty found throughout the relevant sciences to be accounted for, minimized and well communicated (Smith & Stern 2011; Cook *et al.* 2013). Uncertainty affects the ability to provide robust support for decision-making, decreasing trust and buy-in by stakeholders, and jeopardizes intervention effectiveness (Murphy & Noon 1991; Harwood & Stokes 2003; Smith *et al.* 2009; Williams & Johnson 2013). To minimize the risks and consequences of making bad management decisions, research which aims to inform conservation decisions should explicitly incorporate uncertainty (Regan, Colyvan, & Burgman 2002), clearly state the risks involved in each alternative scenario, and clarify the trade-offs between different options (McAllister *et al.* 1999). Failure to communicate uncertainties prevents decision-makers and the public from evaluating alternative options and their risks (Pidgeon & Fischhoff 2011). Ultimately, understanding and planning for uncertainty will provide greater resilience to perturbations and unexpected occurrences (Wilen *et al.* 2002; Peterson, Cumming, & Carpenter 2003; Adger *et al.* 2005; Polasky *et al.* 2011).

Uncertainty is termed and treated differently across disciplines and sciences (Regan, Colyvan, & Burgman 2002; Walker *et al.* 2003; Ascough II *et al.* 2008). For example, in the scientific literature about climate change, epistemic uncertainty (i.e. associated with knowledge of the state of a system) is more commonly treated than linguistic or human decision uncertainty, but linguistic and human decision uncertainties are better treated in the literature on socio-politics or economics than in natural sciences (Kujala, Burgman, & Moilanen 2013). Although most studies in conservation consider some level of uncertainty (Barry & Elith 2006; Nicholson & Possingham 2007; Drechsler *et al.* 2007; Schmolke *et al.* 2010), many focus only on parameter and process uncertainties (i.e. due to variation in the system itself) and few attempt to deal with it. However, conservation deals with complex adaptive systems composed of social and ecological components and processes (Ostrom 2009; Ban *et al.* 2013). This means that many of the sources and types of uncertainty affecting decisions about SESs are of social nature (Fulton *et al.* 2011). For example, unforeseen behavioural responses of resource users or their noncompliance with rules often affect the implementation of conservation interventions (Keane *et al.* 2008).

Simulation modelling within a decision-theoretic framework has been often described as a useful tool to deal with uncertainty because it allows exploration of multiple scenarios and objective investigation of their trade-offs (Shea 1998; Drechsler 2000; Milner-Gulland *et al.* 2001; Milner-Gulland 2011). Models are, however, still not used in many conservation decision-making contexts and the incorporation and exploration of multiple types and sources of uncertainty within such decision-theoretic approaches have been given particularly little attention in the conservation literature (Nicholson & Possingham 2007; Schlüter *et al.* 2012; Addison *et al.* 2013). In addition, modelling applications in traditional approaches to natural resource management and conservation are often concerned with single objectives related to maximizing yield and the sustainability of the wildlife populations (Nicholson & Possingham

2006; Hilborn 2007), but other, often conflicting, socio-economic, cultural and ecosystem objectives set by multiple stakeholders have been increasingly recognized as important (Mapstone *et al.* 2008; Milner-Gulland 2011; Plagányi *et al.* 2013).

Challenges to predictability and uncertainties in implementation require tools and findings from socio-economic and political sciences to be incorporated into conservation planning (St. John, Edwards-Jones, & Jones 2010; Milner-Gulland 2012; Raymond & Knight 2013). Human decision-making and behaviour are important causes of implementation error (Wilen *et al.* 2002; Fulton *et al.* 2011); for example, these may be responsible for imperfect policy implementation as a result of changing market forces, incentives for non-compliance, and institutional inertia (Milner-Gulland & Rowcliffe 2007; Bunnefeld, Hoshino, & Milner-Gulland 2011). However, operationalizing the integration of findings from multiple disciplines into unified modelling and implementation frameworks remains challenging (Knight, Cowling, & Campbell 2006; Ohl *et al.* 2010; Collins *et al.* 2011). Implementation operational models often fail to adequately address social, economic, and institutional issues (Knight, Cowling, & Campbell 2006), while social-ecological modelling is often complex and lacks a common analytical framework (Schlüter *et al.* 2012).

Different forms of uncertainty may interact, making it challenging to study each in isolation (Regan, Colyvan, & Burgman 2002). Limits to knowledge and predictability challenge conservation success (Rammel, Stagl, & Wilfing 2007; Ostrom 2009), and socio-economic, institutional and political context affect implementation of conservation interventions (Keane *et al.* 2008; Waylen *et al.* 2010). Jointly considering the effects of multiple types and sources of uncertainty on the management of SESs, will allow conservation scientists and practitioners to address the following overarching questions: i) what role does uncertainty play in our understanding of SESs? and ii) how can management advice for effective conservation interventions be given under uncertainty?

1.2. Conceptual framework, aims and objectives

Managing for resilience of a SES is only possible if both social and ecological dynamics and feedbacks are understood (Holling & Meffe 1996; Folke 2006). A multidisciplinary approach is thus appropriate to investigate the roles and implications of multiple types of uncertainty. While the importance of multidisciplinary studies in conservation has often been highlighted

(Newing 2010; Sievanen, Campbell, & Leslie 2012), operationalizing this integration in unified frameworks remains challenging (Knight, Cowling, & Campbell 2006; Ohl *et al.* 2010; Collins *et al.* 2011). This study addresses this by combining insights and methods from ecology and social sciences under a conceptual framework adapted from fisheries management.

Management strategy evaluation (MSE) is a powerful conceptual and operational framework developed to facilitate management of natural resources under uncertainty (Punt & Donovan 2007; Kell *et al.* 2007; Bunnefeld, Hoshino, & Milner-Gulland 2011). MSE is used in this thesis to illustrate the composition and dynamics of SESs, making explicit the linkages between monitoring and management decisions and potential sources of multiple types of uncertainty. When used as a quantitative tool, MSE tests the robustness of decisions to a range of uncertainties by modelling the whole system (Butterworth and Punt 1999). MSE generally simulates the dynamics of the natural resources and their harvest ("operating model") and a “management procedure” which includes their monitoring, the assessment of resource status and the implementation of subsequent harvest control rules (Butterworth and Punt 1999). Further information about MSE is provided in Chapter 2.

MSE conceptual frameworks can be designed to emphasise the perspectives of different groups within the system (e.g. “resource users”, “managers” and “monitors”; Figure 1.1). Despite having been used primarily as a modelling approach within fisheries science, MSE has potential as a flexible and intuitive conceptual framework for analysing the interactions between stakeholders (Milner-Gulland 2011; Bunnefeld, Hoshino, & Milner-Gulland 2011). The conceptual framework used by this study builds on the standard MSE (Chapter 2) and adopts an integrated MSE approach (Figure 1.1) (Milner-Gulland 2011), in which a resource user component is added to explicitly incorporate harvester decision-making and behaviour, and consider how decision-making may affect the success of different interventions through resource use behaviour. Finally, in order to more realistically represent interventions that account for measures of human welfare, in this integrated MSE framework monitors observe both the biological populations and the local communities.

I aim to use this integrated MSE conceptual framework and a multidisciplinary approach to gain a better understanding of the role and implications of different sources and types of uncertainty for the management of SESs, using the conservation of harvested ungulate species in the Western Serengeti, Tanzania, as a case study. Based on a scoping study carried out within an international interdisciplinary project (HUNTing for Sustainability; http://fp7hunt.net/) to highlight the key areas of ignorance in current understanding of the SES, I focus on the observation and implementation uncertainties highlighted in the MSE framework. The research aim is addressed through the following objectives:

1) Investigate how estimates from wildlife monitoring surveys are affected by multiple types of uncertainty, with a focus on observation error;

2) Explore trade-offs between effectiveness and efficiency when monitoring changes in population abundance and how these are affected by budgetary, observational and ecological conditions;

3) Test the application of specialized indirect questioning techniques to obtain information on illegal hunting behaviour when assessing resource behaviour using social surveys;

4) Identify challenges and potential barriers to successful conservation implementation in the Serengeti;

5) Make recommendations for the development and implementation of conservation interventions within long-term integrated and adaptive frameworks.

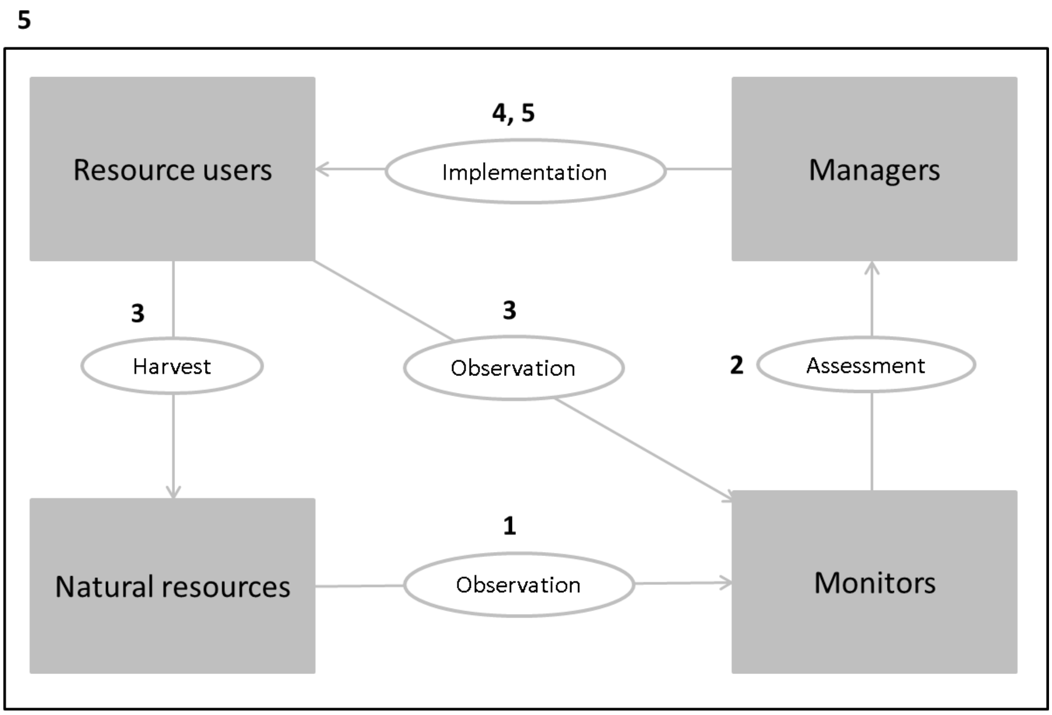

Figure 1.1. Schematic diagram illustrating the conceptual framework for the research based on an integrated MSE approach, illustrating simplified interactions between natural resources, monitors, managers and resource users in managed social-ecological systems. Numbers indicate where the research objectives fit within the framework.

1.3. Thesis outline

Subsequent to this introductory chapter, the thesis has the following structure:

Chapter 2: Research background and case-study

This chapter provides a review of the relevant literature and a description of the case study, including information about geography, climate, wildlife migration, local communities, natural resource management and bushmeat hunting in the Serengeti, Tanzania.

Chapter 3: Matching observations and reality: using simulation models to improve monitoring under uncertainty in the Serengeti

Using monitoring of two contrasting ungulate species in the Serengeti ecosystem as a case study, I employed simulation modelling to investigate how abundance estimates are affected by multiple types of uncertainty, with a focus on observation error. Specifically, I investigated which factors should be prioritized in order to increase survey accuracy and precision, and explored the potential effects of different budgetary scenarios on the robustness of the population estimates obtained for species of different ecological characteristics.

This chapter has been published as:

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Chapter 4: A novel approach to assessing the prevalence and drivers of illegal bushmeat hunting in the Serengeti

I investigated the potential of specialized questioning techniques developed in the social sciences for studying non-compliant and sensitive harvest behaviour. I used the unmatched-count technique (UCT) and identified socio-demographic characteristics of noncompliant households to assess prevalence of illegal hunting in the Serengeti. I considered the effectiveness of the technique at minimizing question sensitivity by analyzing respondents' perceived anonymity and discomfort.

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Chapter 5: Trade-offs in effectiveness and efficiency when monitoring abundance trends under uncertainty

Using monitoring of two contrasting ungulate species and multiple scenarios of population change in the Serengeti ecosystem as a case study, I used a 'virtual ecologist' approach to investigate monitoring effectiveness and efficiency under uncertainty. Specifically, I explored trade-offs between different types of error when monitoring changes in population abundance and explored how these interactions vary depending on budgetary, observational and ecological conditions.

Chapter 6: Management under uncertainty: implementation in the real world

Using the bushmeat hunting system in the Serengeti as a case study, I used a management strategy evaluation framework as a conceptual model to investigate the challenges and potential barriers to successful conservation implementation. Using key informant interviews with the main actors in the monitoring and management system, I obtained insights into the constraints and opportunities for fulfilling stakeholder aspirations for the social-ecological system. I developed social network models to describe the interactions between different actor types, and described the main challenges to implementation of effective conservation action. I provided recommendations for the development and implementation of conservation interventions within long-term integrated and adaptive frameworks.

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Nuno A., Bunnefeld N., Milner-Gulland, EJ. Management under uncertainty: implementation in the real world.

Chapter 7: Discussion

This chapter provides a synthesis of the findings of the research, key implications for conservation and management of social-ecological systems and directions for future research.

2. Research background and case study

2.1. Social-ecological systems

Resource use, management and conservation occur within social-ecological systems (SESs; Ostrom 2009). SESs are complex adaptive systems composed of social and biophysical agents organized in multiple subsystems that interact at several spatial and temporal scales (Levin 1998; Ostrom 2009). Embedded into broader social, economic and political settings and related ecosystems, these subsystems cannot be fully understood in isolation as this provides a partial and incomplete understanding (Matthews 2007); their reciprocal effects and feedbacks loops are fundamental to maintaining system structure and function in the face of disturbance (Folke 2006; Liu *et al.* 2007; Ostrom 2007). An integrated social-ecological perspective thus provides a better understanding of systems involving people and natural resources than focusing only on the effect of people on the environment or the effect of interventions on people (Miller, Caplow, & Leslie 2012; Ban *et al.* 2013).

Contrary to traditional approaches to natural resource management, in which it is often assumed that people (e.g. “managers”, “monitors” and “resource users”) are external to the system (Walker *et al.* 2002; Waltner-Toews *et al.* 2003), using SES frameworks makes it explicit that humans are integral parts of these systems, observing and affecting them, but also being influenced (Anderies, Janssen, & Ostrom 2004). Adopting social-ecological approaches to conservation stresses the importance of social considerations into the planning and implementation stages, highlights trade-offs between alternative decisions, identifies constraints and opportunities that shape conservation and, ultimately, results in more effective initiatives (Knight et al. 2006a, 2006b, Hirsch et al. 2011, Ban et al. 2013). In addition, it emphasises the adaptive and flexible nature of the systems in which conservation takes place; these are systems often characterized by non-linear dynamics leading to multiple possible outcomes and adaptation of rules, behaviour and structures both to external drivers (e.g. climate effects) and internal “emergences” (i.e. patterns arising from interactions within the system, such as change of management policy) (Rammel, Stagl, & Wilfing 2007; Koch *et al.* 2009).

2.2. Uncertainty in natural resource management and conservation

Uncertainty is a feature of natural resource management and conservation (Ludwig, Hilborn, & Walters 1993; Harwood & Stokes 2003; Polasky *et al.* 2011). The outcomes of management interventions are constrained by, for example, stochastic environmental variation, limited abilities to observe wildlife and resource users, a lack of understanding about the processes driving system dynamics and limited predictability of SESs (Nicholson & Possingham 2007; Rammel, Stagl, & Wilfing 2007; Fulton *et al.* 2011). These affect the ability to provide robust support for decision-making, decreasing trust and buy-in by stakeholders, and jeopardize intervention effectiveness (Murphy & Noon 1991; Harwood & Stokes 2003; Smith *et al.* 2009; Williams & Johnson 2013). Additionally, failure to communicate these uncertainties prevents decision-makers and the public considering alternative options and their risks (Pidgeon & Fischhoff 2011).

In scientific terms, uncertainty is present when outcomes occur with a probability that cannot be estimated (Knight 1921). Other related terms include risk (the odds and range of outcomes are known), ignorance (lack of knowledge of relevant outcomes), indeterminacy (causal chains and networks are open, meaning that there is no unique way of defining the system) and error (variation in the estimates or flaws and mistakes related to the estimation process) (Knight 1921; Wynne 1992; Walker *et al.* 2003). The definition of uncertainty is, however, not straightforward; these terms can be interpreted differently depending on the discipline and context and are often used loosely and interchangeably (Barry & Elith 2006; Refsgaard *et al.* 2007). For example, Harwood and Stokes (2003) defined uncertainty as "incomplete information about a particular subject" and Walker et al. (2003) as "any deviation from the unachievable ideal of completely deterministic knowledge of the relevant system" while in civil matters uncertain is defined as "not able to be relied on; not known or definite" (Oxford English Dictionary 2010).

In the fisheries, ecology and environmental literature, several different typologies of uncertainty have been presented. Hilborn (1987) categorized statistical uncertainty, model uncertainty and fundamental uncertainty (novel situations for which existing models do not apply), while Regan et al. (2002) distinguish between epistemic (associated with knowledge of the state of a system) and linguistic uncertainties, and Harwood and Stokes (2003) consider process stochasticity, observation error, model error and implementation error as sources of epistemic uncertainty. Multiple types of uncertainty may interact and these categories are often interdependent; Regan et al. (2002), Walker et al. (2003), Ascough II et al. (2008) and Kujala et al. (2013) provide detailed discussions and typologies of uncertainty. In this thesis, I use the categorization and definitions described by Milner-Gulland and Rowcliffe (2007), who consider process uncertainty, measurement uncertainty (thereafter called observation uncertainty), structural uncertainty and implementation uncertainty as the main types (Table 2.1).

Table 2.1. Main sources of uncertainty

(based on Milner-Gulland and Rowcliffe 2007, Bunnefeld et al. 2011)

Designation	Definition	Example
Process uncertainty	Due to variation in the system itself	Population fluctuations due to climate variations from year to year
Observation uncertainty	Due to the process of measurement	Sensitive nature of the activity leads to harvest underestimation when interviewing users about offtake
Structural uncertainty	Due to lack of understanding of the true dynamics of the system	Functional form of density dependence
Implementation uncertainty	Related to translation of policy into practice	Institutional inertia and non-compliance with management rules

Tools for dealing with uncertainty vary greatly in their complexity and goals, and have been applied in multiple fields, including climate change, fisheries and conservation (Walters & Hilborn 1978; Katz 2002; Peterson, Cumming, & Carpenter 2003). For example, when predicting species distributions these approaches include providing confidence intervals, model averaging, using fuzzy sets and running Monte Carlo simulations (Elith, Burgman, & Regan 2002). Bayesian probabilistic methods may be used by expressing the uncertainty related to a phenomenon as a probability distribution and then updating it in the light of new data (Newton 2010). Info-gap theory was developed as a non-probabilistic methodology for supporting model-based decisions under severe uncertainty (Ben-Haim 2006); it seeks robust outcomes that are most immune to failure due to uncertainty by investigating how wrong an estimate can be and still provide an acceptable outcome (Hayes *et al.* 2013).

Modelling and decision support tools have been increasingly used for comparative analysis and uncertainty assessment (Ascough II *et al.* 2008). Decision theory encourages decision-makers to be explicit about the relevant criteria and use the information critically, and can help in the decision process if combined with simulation models which synthesise all the accessible information (Wilson, Carwardine, & Possingham 2009; Williams & Johnson 2013). These can integrate a number of different techniques for handling uncertainty; Refsgaard et al. (2007) reviewed multiple methods commonly used in uncertainty assessment and characterisation in the environmental modelling process, such as: expert elicitation, scenario analysis, sensitivity analysis and stakeholder involvement. Simulation modelling within a decision-theoretic framework has been often described as a useful tool because it allows exploration of multiple scenarios and objective investigation of their trade-offs (Shea 1998; Drechsler 2000; Milner-Gulland *et al.* 2001; Milner-Gulland 2011). Models are, however, still not used in many conservation decision-making contexts and the incorporation and exploration of multiple types and sources of uncertainty within such decision-theoretic approaches have been given particularly little attention in the conservation literature (Nicholson & Possingham 2007; Schlüter *et al.* 2012; Addison *et al.* 2013).

2.3. Monitoring

The importance of monitoring in natural resource management and conservation has been widely recognized (Sinclair *et al.* 2007; Magurran *et al.* 2010; Jones 2011); monitoring is essential to trigger interventions, inform decisions, measure success against stated objectives, detect unexpected change, and learn about the system (Yoccoz, Nichols, & Boulinier 2001; Lindenmayer *et al.* 2012; Jones *et al.* 2013). Monitoring aims to draw inferences about changes in the observed system over time (Yoccoz, Nichols, & Boulinier 2001) and, in order to be useful, must be effective (i.e. able to detect true trends over time) while considering trade-offs between effectiveness and efficiency (Kinahan & Bunnefeld 2012). Given the general scarcity of funding available for monitoring and the need to guarantee its sustainability over time and feasibility even in challenging conditions (Danielsen *et al.* 2003; Brashares & Sam 2005), the costs of the monitoring programmes and of the subsequent management implications must be fully considered (Field *et al.* 2004).

The actual value for conservation of many monitoring programmes has, however, often been questioned (Yoccoz, Nichols, & Boulinier 2001; Legg & Nagy 2006; Lindenmayer & Likens 2009). Monitoring may be very costly (in terms of time and/or money) and its effectiveness may be affected by multiple sources of uncertainty (Caughlan & Oakley 2001; Wintle, Runge, & Bekessy 2010; Tulloch, Possingham, & Wilson 2011). For example, monitoring results may be affected by the spatial structure of the populations (Rhodes & Jonzén 2011), monitoring target (Katzner, Milner-Gulland, & Bragin 2007), environmental variability (Hauser, Pople, & Possingham 2006), sampling design (Jackson *et al.* 2008), survey technique (Ogutu *et al.* 2006) as well as the analytical methods (Thomas & Martin 1996). Poorly designed monitoring programmes may represent not only a waste of resources but also result in poor decision-making (Legg & Nagy 2006); under great time, budget and observational constraints, managers may be better off allocating resources to other interventions instead of monitoring (Field, Tyre, & Possingham 2005; Salzer & Salafsky 2006; McDonald-Madden *et al.* 2010).

Monitoring should allow identifying changes in the biological and social components of SESs, as well as about their evolving relationships (Redman, Grove, & Kuby 2004; Miller, Caplow, & Leslie 2012). For example, monitoring should occur for the state of the resource, the behaviour of the resource user and interactions between them. While considerable attention has been given to the importance and challenges of ecological monitoring, information about social monitoring in conservation is limited and social factors are often considered secondary when implementing monitoring programmes (Polasky 2008; Wilder & Walpole 2008; Gavin, Solomon, & Blank 2010). Social monitoring aims to collect data on the social processes and patterns connected to specific conservation issues, providing insights into the social, political, economic and cultural impacts and opportunities of conservation (Redman, Grove, & Kuby 2004; Stem *et al.* 2005). Lack of integration across ecological and social monitoring programmes makes it particularly difficult to investigate links between social conditions and ecological changes (Redman, Grove, & Kuby 2004). Additionally, due to difficulties in measuring human behaviour (Gavin, Solomon, & Blank 2010), most evaluations of social impacts of conservation interventions are based on attitudes and behavioural intentions although actual behavioural change is the ultimate goal of conservation interventions (Holmes 2003; St. John, Edwards-Jones, & Jones 2010).

2.4. Management of social-ecological systems

Managing for resilience requires understanding the composition and dynamics of SESs across multiple scales in space, time and social organization (Folke 2006). Heterogeneity in SESs is particularly important because human organizational units, each with different socio-demographic characteristics and motivations, are likely to differ in their choices and behaviours (Waltner-Toews *et al.* 2003). For example, the ability for resource users to self-organize within a SES depends on a number of factors, including predictability of the resource system, number of users, leadership, norms, knowledge, importance of resource to users and collective choice rules (Ostrom 2009). An effective system of governance is thus integral to successful management over the long term; these processes and institutions through which societies make decisions should operate at appropriate scales and be flexible to changes in time (Armitage, de Loë, & Plummer 2012). Static command-and-control management strategies are generally not suitable for SESs (Holling & Meffe 1996; Walker & Janssen 2002), while co-management involves shared responsibilities and rights, recognizing the plurality of institutions in governance structure (Plummer & Fitzgibbon 2004), and adaptive co-management provides the ability to link adaptive and collaborative mechanisms across social groups (Armitage *et al.* 2009). Moreover, given their complex composition, limited predictability and the absence of a global controller (Levin 1998; Liu *et al.* 2007; Ostrom 2007), management advice about SESs must be given under variable levels of uncertainty and requires transparent and robust operational frameworks (Anderies, Janssen, & Ostrom 2004; Folke 2006).

Dealing with uncertainty and complexity in SESs is dependent on the ability of managers and resource users to learn and adapt (Adger *et al.* 2005). Based on structured "learning by doing" (Walters & Holling 1990), adaptive management (AM) has been developed as an approach to dealing with uncertainty about the impacts of various policy decisions in natural resource management (Holling 1978; Walters & Hilborn 1978). AM implements two or more strategies in a comparative setting, monitors them and then uses information on system dynamics to improve management outcomes through experimentation in the real world (Keith *et al.* 2011). AM emphasizes learning through management because it assumes that surprises are inevitable, knowledge is incomplete and systems are dynamic and evolving (Allen *et al.* 2011). AM acknowledges that policies must be flexible for adaptation to multiple, potentially changing, objectives (Gunderson 2000); policies are tested by considering different management actions as treatments in an actual experimental setting and then evaluating outcomes and trade-offs between pre-defined criteria (Walters 2007; Probert *et al.* 2011). AM, thus, deals with uncertainty by supporting active learning in an integrated way, highlighting uncertainties and evaluating hypotheses around a set of desired outcomes (Williams 2011). AM also highlights the importance of monitoring to achieve objectives because failing to monitor constrains the learning process (Lindenmayer *et al.* 2011).

Given the widely advocated potential use of AM for managing SESs in natural resource management and conservation but its limited use in practice (Walters 2007), actual implementation is one of its main challenges to be addressed. Lack of stakeholder engagement, not using learning to modify policy and management and a focus on planning instead of action are critical to the failure of AM (Allen & Gunderson 2011) and institutional barriers are among the major impediments to its implementation (Keith *et al.* 2011). These are often related to a lack of leadership, unwillingness to embrace uncertainty, lack of a long-term vision and inadequate funding for monitoring programs (Walters 2007; Allen & Gunderson 2011). Additionally, the specific uncertainty conditions and controllability of the managed systems also affect the feasibility of applying AM; Allen et al. (2011) suggested that AM functions best when both uncertainty and controllability are high, which means the potential for learning is high, and the system can be manipulated. Guaranteeing long-term funding for AM activities, better communication of the benefits of doing AM (and risks of not doing it) and making sure AM projects are of management relevance must be achieved in order to circumvent the difficulties of implementing AM (Westgate, Likens, & Lindenmayer 2013).

2.5. Management strategy evaluation

Management strategy evaluation (MSE) is a powerful conceptual and operational framework developed in fisheries to facilitate management under uncertainty, and has great potential for use in conservation due to incorporating multiple sources of uncertainty, being explicit about the links between monitoring and management decisions, as well as allowing decision-makers to consider various, often conflicting, management objectives as defined by different stakeholders in SESs (Punt & Donovan 2007; Kell *et al.* 2007; Bunnefeld, Hoshino, & Milner-Gulland 2011). Pioneered by the International Whaling Commission Scientific Committee during the 1980s, MSE tests the robustness of decisions to a range of uncertainties by modelling the whole system (Figure 2.1). MSE generally simulates the dynamics of the natural resources and their harvest ("operating model") and a “management procedure” which includes their monitoring, the assessment of resource status and the implementation of subsequent harvest control rules (Butterworth and Punt 1999).

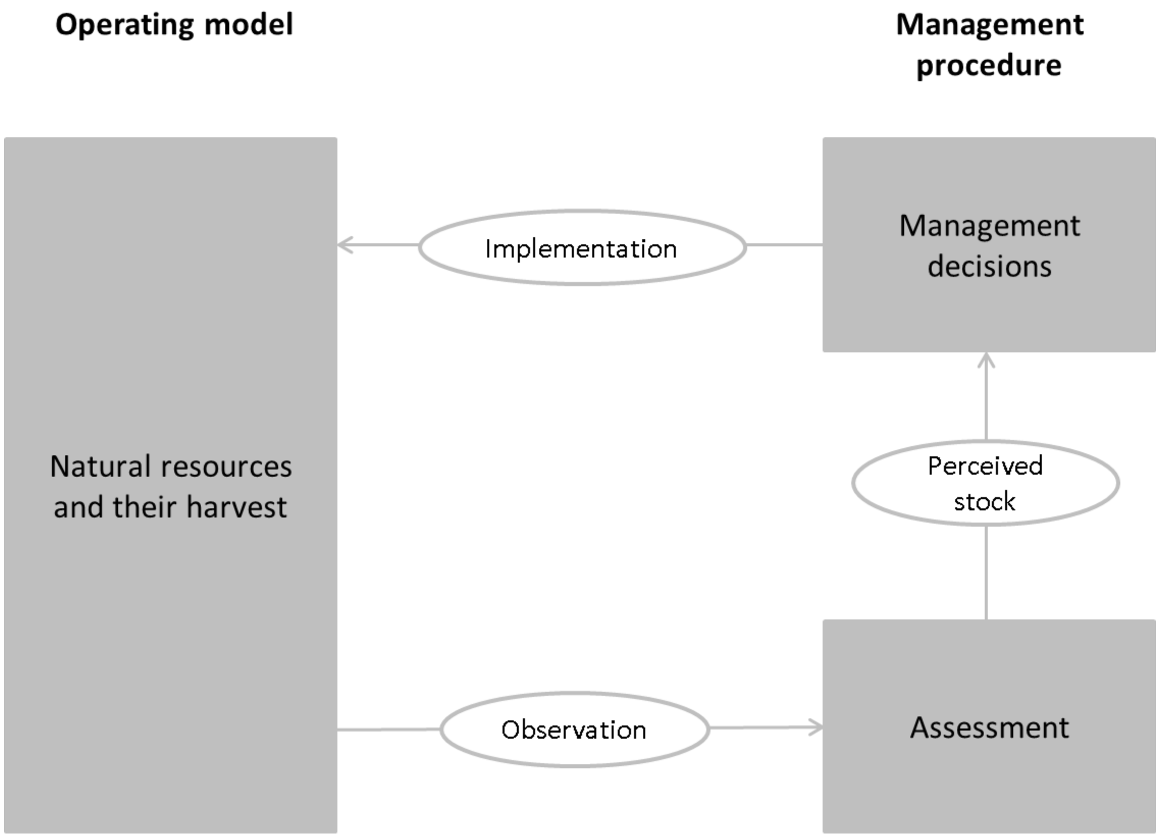

Figure 2.1. Conceptual framework of managed systems using a standard MSE approach.

MSE can be used to assess the relative performance of each alternative management strategy to achieve set criteria, given the uncertainty inherent in the system being managed, and thereby to improve the design of management strategies (McAllister *et al.* 1999; Sainsbury 2000). By including all relevant system components and actors in a single modelling framework, MSE requires explicit consideration and representation of the various types of uncertainty (Punt & Donovan 2007; Kell *et al.* 2007). This can be achieved by, for example, testing multiple scenarios, comparing many operating models and assessing results from different algorithms (Holland & Herrera 2009). Because MSE does not seek single-objective optimization, it allows stakeholders to recognize trade-offs and risks associated with different scenarios, incorporating assessment of uncertainty into the definition, development and selection phases of the MSE (Punt & Donovan 2007).

Another major advantage of this approach is the involvement of multiple stakeholders in the establishment of the criteria, definition of scenarios and final scenario choice; the results stimulate discussions between and within stakeholders and decision-makers (McAllister *et al.* 1999). In addition, by providing advice on strategies that are actually being considered by multiple stakeholders, it generates interest and buy-in because it gives them the information most relevant to their current decisions (Ives, Scandol, & Greenville 2013). Moreover, while logistics and ethical reasons may constrain the implementation of different strategies in the real world, testing them in a "virtual world" allows not only the comparison of the potential effectiveness of different management activities but also reductions in experimentation costs and minimisation of the consequences of real-world experimentation on wildlife and local communities (Bunnefeld, Hoshino, & Milner-Gulland 2011; Boyce, Baxter, & Possingham 2012).

MSE also provides a framework for interaction with stakeholders, synthesizing available information and prompting clearer thinking about long-term and short-term objectives, system dynamics and linkages (Butterworth 2007). While its quantitative abilities have often been demonstrated (e.g. Dichmont et al. 2006, Mapstone et al. 2008), its qualitative application for generating information for decision-making and planning has been given very little attention. An exception is the study by Smith et al. (2007) who undertook a "qualitative" MSE, where the operating model used to test alternative strategies was replaced by projections based on expert judgement; this work helped stakeholders confront a range of problems and issues in the fishery, and was used for restructuring the fishery to achieve the changes that were identified as needed.

Currently, more effort in MSE development is being directed towards including economics (Hoshino, Hillary, & Pearce 2010; Ives, Scandol, & Greenville 2013), taking an ecosystems approach (Dichmont *et al.* 2010; Szuwalski & Punt 2012) and development of technical tools (Kell *et al.* 2007; Hillary 2009). Implementation uncertainty, however, has been poorly considered in MSE studies and remains a challenge (Dichmont *et al.* 2006; Bunnefeld, Hoshino, & Milner-Gulland 2011). An understanding of resource use behaviour, potential non-compliance with management rules, and of the management decision-making processes is, however essential for the development of applied and functional MSE approaches in natural resource management and conservation (Milner-Gulland 2011).

2.6. Case study: the Serengeti social-ecological system

Well known for its charismatic wildebeest (*Connochaetes taurinus*) migration and for having some of the largest herbivore and carnivore populations in the world, the Serengeti is one of the most emblematic SESs and has attracted the attention of explorers, missionaries, hunters, researchers and tourists over the last 150 years (Sinclair 2012). After a period of excessive and indiscriminate sport hunting, the process for the establishment of protected areas within the system started in the 1920s. The Serengeti national park (SENAPA) was proclaimed in 1951. In 1959, the boundaries of the national park were realigned, including the area of what was assumed to be the migratory route of the wildebeest (Thirgood *et al.* 2004). Prompt by the need to define the limits of the wildebeest migration and protect the system, the book "Serengeti Shall Not Die" (Grzimek & Grzimek 1959) and subsequent movie were released around the same time; although often criticized for providing a romanticized representation of the Serengeti as "a piece of primordial wilderness", these were essential in illustrating the value of this system to an international audience and setting the global commitment for its conservation (Shetler 2007; Lekan 2011). In 1981, SENAPA was internationally recognized as part of a World Heritage Site and a Biosphere Reserve. SENAPA is nowadays one of the most visited protected areas in the world (UNDP 2012) and its importance for biodiversity conservation, development and cultural heritage is widely acknowledged (Shetler 2007; Sinclair *et al.* 2007). The Serengeti is one of the most intensively studied systems in Africa; monitoring and research have been conducted since the 1950s, producing several long-term biological datasets and hundreds of scientific publications and reports (Sinclair *et al.* 2007; Sinclair 2012).

2.6.1. Geography, climate and wildlife migration

The Serengeti-Mara ecosystem comprises an area of approximately 25,000 km^2 on the border of Tanzania and Kenya, East Africa (34º to 36º E, 1º to 3º30' S). The major climatic influence is rainfall (Norton-Griffiths, Herlocker, & Pennycuick 1975); this system is characterized by a strong rainfall gradient from southeast (450 mm/year) to northwest (>1000 mm/year) linked to increasing soil depth, sand to clay ratio, and declining soil fertility (Sinclair 1979). Rainfall and topography affect the distribution and structure of vegetation in the Serengeti, which are also affected by herbivory and fire (Dublin *et al.* 1990), and trophic cascades mediated by disease outbreaks (Holdo *et al.* 2010). The Serengeti can be broadly divided into areas of grassland in the southeastern plains and woodland in the rest of the system. Rain falls in a bimodal pattern, with short rains in November-December and long rains lasting from March to May, and the temperature is relatively constant year-round with a mean maximum of 27-28ºC in Seronera, although the daily maximum varies from 15ºC to 30ºC according to region (Sinclair *et al.* 2008).

Wildebeest, zebra (*Equus burchelli*), Thomson's gazelle (*Gazella thomsoni*) and eland

(*Taurotragus oryx*) migrate within the ecosystem, showing similar seasonal habitat shifts (Sinclair *et al.* 2008). The wildebeest use the Serengeti plains during the wet season (mid-October to end of April), moving west and north at the beginning of the dry season (May to mid-October) and giving birth synchronously in February (Thirgood *et al.* 2004). Many potential explanations have been given as to the cause or timing of the wildebeest migration (cf. Boone et al. 2006) and the most recent research suggests wildebeest movement based primarily on optimizing access to high quality food is dictated by new forage growth (Boone, Thirgood, & Hopcraft 2006), or opposing rainfall and plant nutritional gradients (Holdo, Holt, & Fryxell 2009). The importance of the wildebeest migration, currently encompassing around 1.3 million animals (Hilborn & Sinclair 2010), has often been demonstrated, both for its ecological significance as a keystone species and as a source of tourism revenue (Sinclair 2003; Norton-Griffiths 2007; Kaltenborn, Nyahongo, & Kideghesho 2011; Holdo *et al.* 2011).

2.6.2. Local communities

Fossil evidence showed modern humans were present in the Serengeti 17,000 years ago, suggesting interactions of humans with the Serengeti environment across many millennia (Olff & Hopcraft 2008). These were important in shaping the Serengeti, particularly through the deliberate and controlled use of fire, domestication of livestock and development of agriculture, potentially affecting the present day heterogeneity in the landscape (Shetler 2007). Marked by a complex history of migration, traders and colonization affecting their political, economic and socio-cultural systems (Shetler 2007; Kideghesho 2008; Sinclair 2012), the local communities currently living in the Serengeti are composed by a mix of ethnic groups. The agropastoralists Ikoma, Natta, Sukuma and Kurya came from other parts of northern Tanzania and Kenya and gradually spread over the last centuries into north-west, west and south-west areas of the Serengeti, where climate is more conducive to agriculture (Kideghesho 2008; Estes *et al.* 2012). In the last 200 years, the pastoral Maasai moved in from Kenya and occupied the grasslands, avoiding the Serengeti savannah due to the tsetse flies and their effects on livestock (Sinclair 2012). A small group of hunter-gatherers, the Hadzabe, live on the southern edge of the ecosystem, and occupied the Serengeti for some thousands of years (Lee & Daly 1999). When SENAPA was proclaimed a national park in 1951, and up to 1969 when some of the last evictions occurred, local communities residing within currently protected areas were evicted to adjacent land, leading to some events of conflict (Shetler 2007). Due to their nomadic pastoralist lifestyle, the Maasai were allowed to remain in the multiple-use areas in the east (Sinclair *et al.* 2008). Nowadays, the Kurya, Sukuma, Ikoma and Nata are the main ethnic groups in the north-western Serengeti, while the Sukuma predominate in the south-west and the east is mainly occupied by Maasai (Kideghesho 2008).

Currently, there are about 2.3 million people in the districts surrounding SENAPA with an annual population growth rate of approximately 3% (NBS Tanzania 2006). Livelihood strategies are predominantly based on a combination of occupations, including farming, livestock herding and hunting (Loibooki *et al.* 2002). Maasai in the east predominantly own livestock and practice small-scale farming of beans and maize (Fratkin & Mearns 2003). In the western Serengeti, livelihoods are based on subsistence agriculture (maize, millet, sorgum and cassava), livestock (cattle, goats, sheep and poultry) and cotton as a cash crop (Johannesen 2005; Schmitt 2010). Agriculture is the most common source of income for these rural households, followed by livestock, while the importance of bushmeat hunting for the local economy has been suggested to be considerable but has been difficult to quantify (Barnett 2000; Knapp 2007, 2012). In the last 30 years, agricultural conversion and population growth were greatest closer to the national park (up to 20km away), likely due to movement away from areas with high population densities and land scarcity (Estes *et al.* 2012).

2.6.3. Natural resource management

All natural resource use within SENAPA has been prohibited since the park's establishment. The Tanzanian side of the system, the focus of the work in this thesis, also includes protected multiple-use areas and village areas with agricultural and livestock systems, and with a range of different restrictions on hunting and settlement (Figure 2.2): the Ngorongoro Conservation Area (NCA) was established as a multiple land-use area without hunting while accommodating the existing Maasai pastoralists; the Loliondo Game Controlled Area (GCA) allows human settlement and licensed hunting; the Ikorongo, Grumeti and Maswa Game Reserves (GRs) allow licensed hunting but not human settlement; and the Ikona and Makao Wildlife Management Areas (WMAs) are recently created and still incipient community-managed areas where wildlife use is encouraged in order to generate income for the villages (MNRT 1998; Polasky *et al.* 2008).

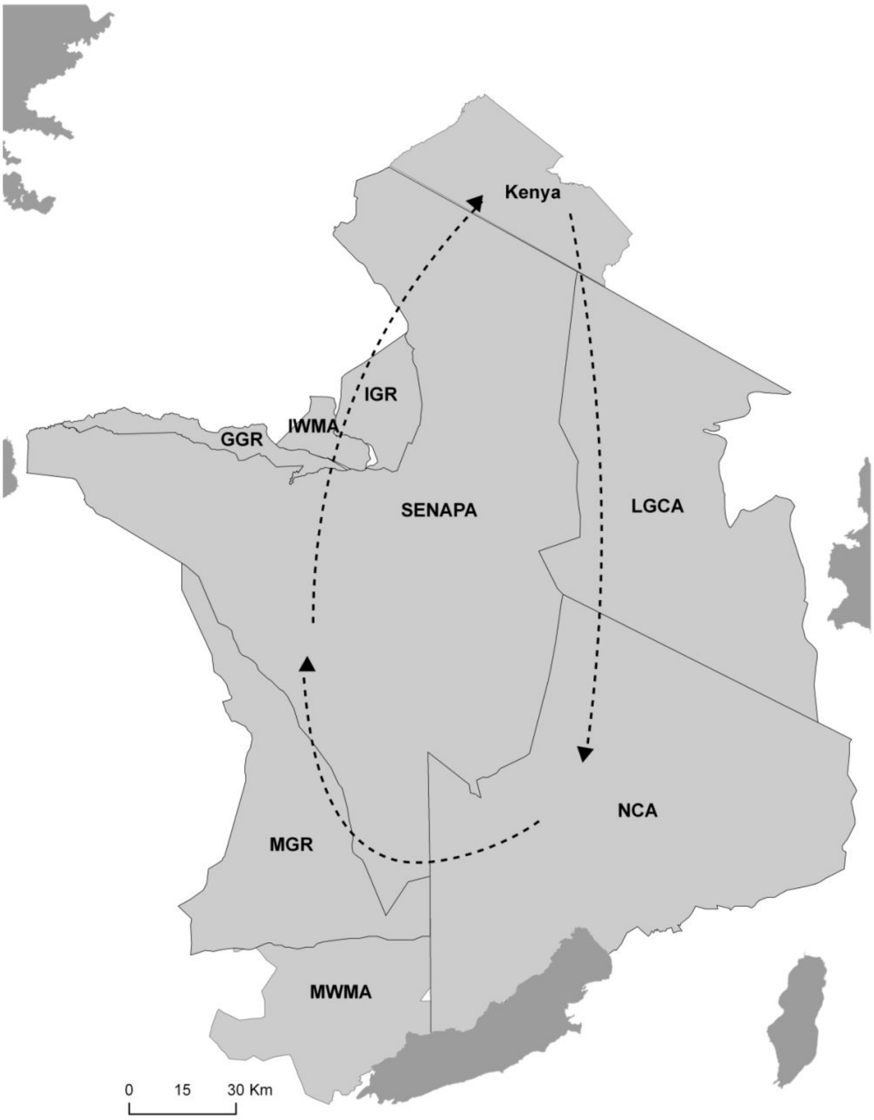

Figure 2.2. Protected areas and lakes (darkest grey) within and surrounding the Serengeti ecosystem. SENAPA = Serengeti National Park, LGCA = Loliondo Game Controlled Area, NCA = Ngorongoro Conservation Area, MGR = Maswa GR, GGR = Grumeti Game Reserve, IWMA= Ikona Wildlife Management Area, MWMA= Makao Wildlife Management Area, and IGR = Ikorongo Game Reserve. Dashed arrows indicate broad wildebeest migration patterns.

The protected areas are managed by a range of governmental, non-governmental and private sector organizations. Tanzania National Parks (TANAPA) is a parastatal organization responsible for managing and regulating national parks while the Ngorongoro Conservation

Area Authority (NCAA) oversees wildlife conservation in the NCA. The Wildlife Division (WD) of the Ministry of Natural Resources and Tourism (MNRT) has oversight of GRs, GCAs and WMAs. The Tanzania Wildlife Research Institute (TAWIRI) is a parastatal organization under the MNRT responsible for conducting and coordinating wildlife research and advising the government and wildlife management authorities. Private tourism and hunting companies, such as Singita Grumeti Reserves, manage the GRs and enter into contracts with communities within other multiple-use areas. Frankfurt Zoological Society (FZS) is one of the most prominent international non-governmental organizations operating in the Serengeti, active in the system since the 1950s.

2.6.4. Bushmeat hunting

Bushmeat is, in theory, a state-controlled natural resource in Tanzania and hunters must obtain a licence for hunting according to quotas set annually by the WD. However, illegal bushmeat hunting and consumption is widespread throughout the Serengeti (Loibooki *et al.* 2002). Bushmeat hunting in the Serengeti is mainly non-selective and conducted through wire snaring, although use of weapons, hunting dogs and night hunting with flashlights are also common (Holmern *et al.* 2002). The wildlife migration passes close to villages during the dry season and the seasonally available migratory ungulates, such as wildebeest, represent the bulk of harvested wildlife, but poaching affects a wide range of resident ungulates, such as impala (*Aepyceros melampus*) and topi (*Damaliscus lunatus*), and non-target species, such as spotted hyena (*Crocuta crocuta*) (Hofer *et al.* 1996; Loibooki *et al.* 2002; Holmern, Muya, & Røskaft 2007).The local hunting of bushmeat is responsible for an estimated 40,000–141,000 annual wildebeest offtake (Rentsch & Packer in press; Mduma, Hilborn, & Sinclair 1998).

Bushmeat hunting has been perceived as a threat to wildlife in the Serengeti for several decades (Watson 1965; Arcese, Hando, & Campbell 1995; Hilborn *et al.* 2006). Law enforcement has been one of the main interventions aimed at deterring poaching since the establishment of the protected areas (Arcese, Hando, & Campbell 1995). Game cropping schemes have also been used in the past, without success, in an attempt to reduce bushmeat hunting (Holmern *et al.* 2002). The main ongoing initiatives aimed at controlling illegal hunting, which vary in temporal and spatial scale, include: Law enforcement carried out by TANAPA rangers and personnel of the GRs; Community Conservation Banks (COCOBAs;

facilitated by FZS and based on a lending model that provides access to micro-credit for environmentally-friendly enterprises); WMAs; Community Conservation Services (CCSs; program conducted by TANAPA to share benefits with communities surrounding SENAPA); and several outreach and environmental education programs (e.g. one conducted by Grumeti Fund, a local NGO associated to Singita Grumeti Reserves). The effectiveness of these interventions has been difficult to ascertain and potentially limited to localized areas (but see Hilborn et al. (2006) on the positive effects of anti-poaching activities on wildlife abundance in the national park). Due to the illegal and sensitive nature of bushmeat hunting, it is hard to quantify compliance with the laws, catch composition and hunting effort, and offtake uncertainty is an essential consideration for the management of protected wildlife resources in the area (Loibooki *et al.* 2002; Knapp *et al.* 2010).

3. Matching observations and reality: using simulation models to improve monitoring under uncertainty in the Serengeti

3.1. Introduction

The importance of ecological monitoring for conservation has often been acknowledged (Stem *et al.* 2005; Nichols & Williams 2006). Among its main objectives are to inform management decisions, measure success against stated objectives, and learn about the system (Yoccoz, Nichols & Boulinier 2001). Monitoring is, however, often inadequate. Insufficient statistical power, lack of goal and hypothesis formulation, faulty survey design and data quality are common problems affecting monitoring schemes worldwide (Legg & Nagy 2006). The implications of these problematic issues are multiple; they not only affect monitoring effectiveness but also reduce resource availability for other potentially useful conservation interventions (McDonald-Madden *et al.* 2010). Resources for conservation are generally scarce (Bottrill *et al.* 2008), especially in developing countries (Danielsen *et al.* 2003). Planning for conservation success thus requires identifying effective and efficient monitoring strategies (Reynolds, Thompson & Russell 2011).

Monitoring is affected by multiple uncertainties (Harwood & Stokes 2003). Process uncertainty due to variation in the system itself (e.g. wildlife spatial distribution) interacts with observation uncertainty, which is a consequence of sampling effort and survey design as well as the process of observation. Observation uncertainty has multiple drivers and consequences. For example, estimates obtained from aerial surveys may be affected by a number of factors, such as: animal detectability, observer performance, variation in aircraft height and deviations from the transect (Norton-Griffiths 1978; Jachmann 2002). Having imperfect knowledge of the true status of natural resources plays a central role in management decisions. For instance, Sethi *et al.* (2005) incorporated multiple types of uncertainty into a bioeconomic model of fisheries and found that observation uncertainty has the largest impact on policy, profits and extinction risk. The direction and magnitude of the effects of these processes on final abundance estimates have to be considered in order to establish error minimization priorities and maximize monitoring efficiency.

Optimization of sampling effort to achieve monitoring goals is demonstrably an essential consideration (Field, Tyre & Possingham 2005; Sims *et al.* 2006), but considerably less attention has been given to the effects and, particularly, the drivers of observation error. The effects of undercounting or the misidentification of the sex or age of an individual have received limited attention (Elphick 2008), most likely because multiple processes may occur simultaneously and discerning their impacts from monitoring data may be difficult. Knowing which types of errors are most important and should be tackled first is particularly challenging. Experimentation is often difficult, due to terrain, lack of capacity and the financial and time costs involved. For convenience and model simplicity, observation uncertainty is often considered as an overarching composite process when using simulations, modelled through lognormally distributed errors (e.g. Hilborn & Mangel 1997; Shea & Mangel 2001).

Modelling is a particularly useful tool because it allows experimentation through simulation. Previous studies have used modelling, for example, to investigate how to improve survey effort and design but without taking specific errors in the observation process into consideration (Sims *et al.* 2006; Blanchard, Maxwell & Jennings 2008), correct observation bias based on herd size detectability (McConville *et al.* 2009), assess the effects of data quality on harvest strategies and income (Milner-Gulland, Coulson & Clutton-Brock 2004), and estimate the risk of failing to detect a trend and wasting resources (Katzner, Milner-Gulland & Bragin 2007). By using a modelling approach it is possible to explicitly simulate “true” scenarios of wildlife abundance and distribution. Each step of the observation procedure can then be replicated in order to investigate how the quality of the data collected ("observed state") may be improved, and particularly how researchers' actions and assumptions affect precision (uncertainty or variability in the estimates which is used to produce confidence intervals around them) and accuracy (difference between the set of estimates and the truth they represent).

The Serengeti ecosystem is one of the most intensively studied systems in Africa. Long-term research in the Serengeti includes monitoring of a range of species, with wildlife censuses having been conducted since the 1950s (Sinclair *et al.* 2007). Monitoring resources are, however, very limited, especially given that this ecosystem covers more than 25 000 km^2. Monitoring must therefore be adjusted according to available budgets, while still being able to provide accurate and precise abundance estimates. Using monitoring of two contrasting ungulate species in the Serengeti ecosystem as a case-study, we employed simulation modelling to investigate how abundance estimates are affected by multiple types of uncertainty, with a focus on observation error. Specifically, we investigated which factors should be prioritized in order to increase survey accuracy and precision, and explored the potential effects of different budgetary scenarios on the robustness of the population estimates obtained for species of different ecological characteristics. This enables us to provide insights into the likely effect of different types of observation and process error on population estimates for savannah ungulates, and more generally to present a framework for evaluating monitoring programmes in a virtual environment.

3.2. Methods

3.2.1. Study area and species

We chose two species to investigate the contrasting issues involved in monitoring ungulate species in savannah ecosystems. The migratory wildebeest population (*Connochaetes taurinus*) is monitored throughout the Serengeti ecosystem using aerial surveys to take photographs within sampling blocks (Figure A1, Appendix A). By contrast, a resident population of impala (*Aepyceros melampus*) is monitored using systematic flights along transects in a Game Reserve adjoining the Serengeti National Park (Grumeti-Ikorongo GR). Surveys are conducted approximately every 3-5 years in February/March to assess populations of resident and migratory ungulates (Campbell & Borner 1995; TAWIRI 2010).

The wildebeest population is highly gregarious and composed of bachelor herds and large nursery herds, with territorial males at certain times of year (Estes 1992). Wildebeest use the Serengeti plains in large herds during the wet season (mid-October through April), when the monitoring is conducted, moving west and north at the beginning of the dry season (May to mid-October). They give birth synchronously in February (Thirgood *et al.* 2004). Impala occur in the Serengeti woodlands and their populations are composed of large groups of females with a single dominant male (Jarman & Jarman 1973). These sedentary ungulates move up to 3 km in the dry season and 0.95 km in the wet season (Estes 1992). Currently, there are around 1.3 million wildebeest in the Serengeti and 10 000 impala in the Grumeti-Ikorongo Game Reserve (Grumeti Fund 2010; Hilborn & Sinclair 2010).

3.2.2. Methodological framework

We simulated the monitoring process for the two ungulate populations to investigate monitoring precision and accuracy. The methodological framework was divided into four main components (Figure 3.1): (a) a spatial distribution model which provided the “true scenario” against which simulated monitoring data were compared; (b) an “observation model” which simulated monitoring of these populations; (c) a data analysis component which estimated wildlife abundance from simulated monitoring data, the "assessment model"; and (d) an assessment of survey accuracy and precision, in which discrepancies between “true” and “observed” population sizes and their drivers were investigated.

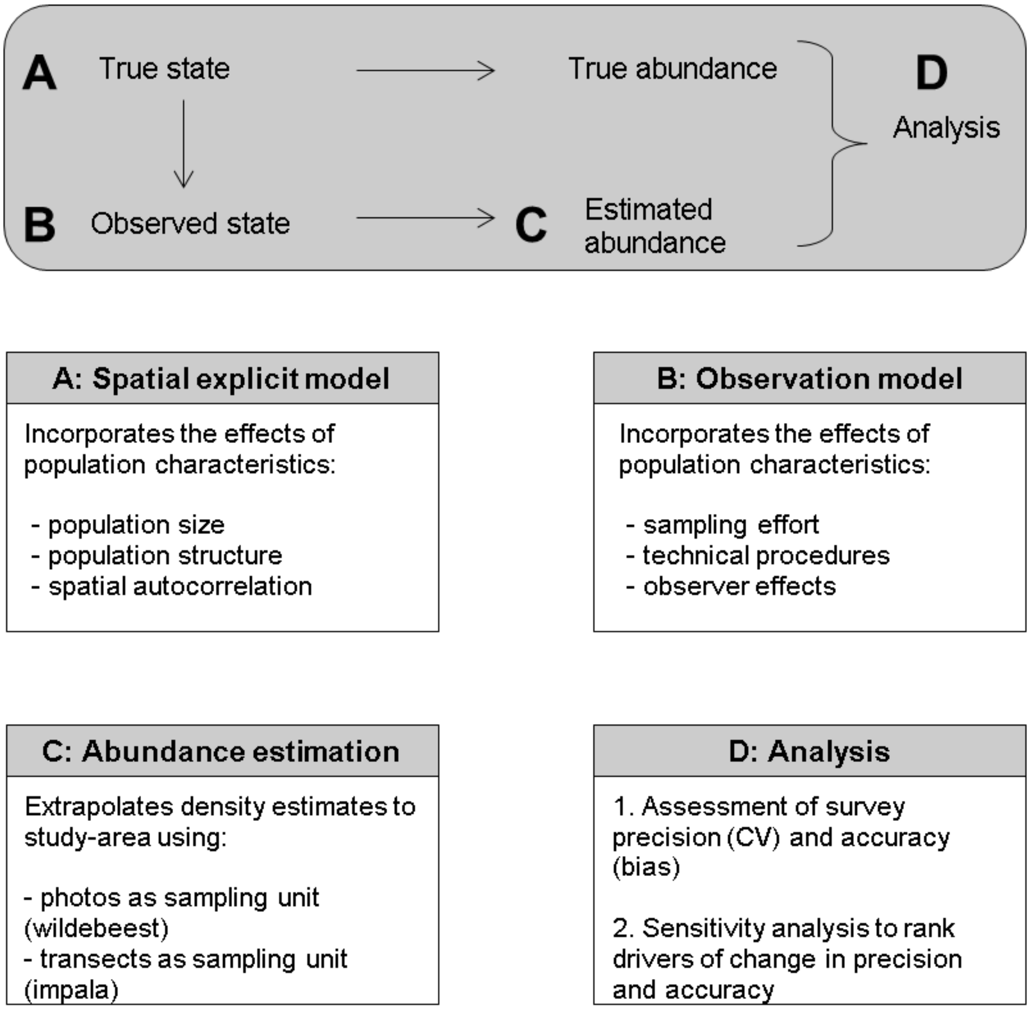

Figure 3.1. Conceptual description of the study’s methodological approach.

3.2.3. Modelling the distribution of wildlife

a) Wildebeest

A virtual wildebeest population was distributed in a 90x35 km grid with a total area of 3150 km^2 (2887 km^2 was surveyed in 2009; Hilborn & Sinclair 2010). Grid units were sized to be equivalent to a "potential photograph" capturing around 0.05km^2. Numbers of wildebeest per grid unit were simulated using a negative binomial distribution (NBD) with two defining parameters: the mean (μ) and the aggregation (k), with lower values of k representing more aggregated populations. Pieters *et al.* (1977) compare the efficiencies of several methods of estimation of the parameter k; the method of moments estimate relates it to the empirical mean μ and variance σ^2 by:

$$k = \frac{\mu^2}{\sigma^2 - \mu} \qquad \text{eqn 1.}$$

A NBD allows us to account for, and investigate the effects of, differing degrees of animal aggregation on survey counts (Matthiopoulos 2011). To check its suitability to describe wildebeest counts, the goodness of fit was assessed through comparison of fitted and actual counts from the 2006 census (χ^2=338, df=887, P>0.99; J.G.C. Hopcraft, unpublished data).

The number of wildebeest in each cell is likely to be affected by abundance in neighbouring cells, so we adopted a geostatistical approach to incorporate spatial autocorrelation using the R package *geoR* (Ribeiro Jr & Diggle 2001, version1.7-4). First, we defined the spatial autocorrelation structure by using a Gaussian process with variance-covariance matrix C related to an exponential correlation function between unit locations:

$$C=\sigma_s^2\, exp\, (-d_{ij}/phi) \qquad \text{eqn 2}$$

where d_{ij} is the distance between grid units i and j, σ_s^2 is the threshold variance known as the sill (which we kept at a constant value) and phi is the range parameter that represents a fraction of the distance beyond which there is little or no autocorrelation (Diggle, Tawn &

Moyeed 1998). The strength of spatial autocorrelation was controlled by varying the range parameter; the larger the range, the stronger the autocorrelation because it persists over longer distances. To generate spatially autocorrelated survey counts, we then conditioned the outcome of the NBD on these spatially correlated random fields by affecting the actual realization of the distribution for each cell via the exponential link and the mean and aggregation parameters.

At the time of the counts, juvenile wildebeest are found within large nursery herds with their mothers, while older males remain in separate aggregations (Estes 1992). In the 2006 census in the Serengeti, juvenile wildebeest were more likely to be present in photos with higher total numbers of animals (Fig. 2; GLM with a binomial error structure: z=6.560, df=340, P<0.001). Empirical juvenile counts did not differ significantly from a NBD (χ^2=84, df=340, P>0.99), and 46% of the photos with wildebeest present had juveniles and adults, while the remaining only had adults (J.G.C. Hopcraft, unpublished data).

The distribution of juveniles was modelled for a range of juvenile proportions in the total population. Juvenile counts followed a NBD drawn separately from the previous one which simulated the total count of wildebeest per cell, incorporating both adults and juveniles. We assumed that juveniles occurred in half of the photos where wildebeest were found, with the probability of presence associated with higher total numbers of animals. Juveniles were thus redistributed according to total wildebeest counts per cell. To simulate the number of juveniles per cell, the desired proportion of cells without juveniles (i.e. zeros in the NBD; p'(0)) and mean number of juveniles per cell μ_{juv} were used to estimate the aggregation k_{juv} of juveniles (Perry & Taylor 1986):

$$p'(0) = \left(\frac{1 + \mu_{juv}}{k_{juv}}\right)^{-k_{juv}} \qquad \text{eqn 3.}$$

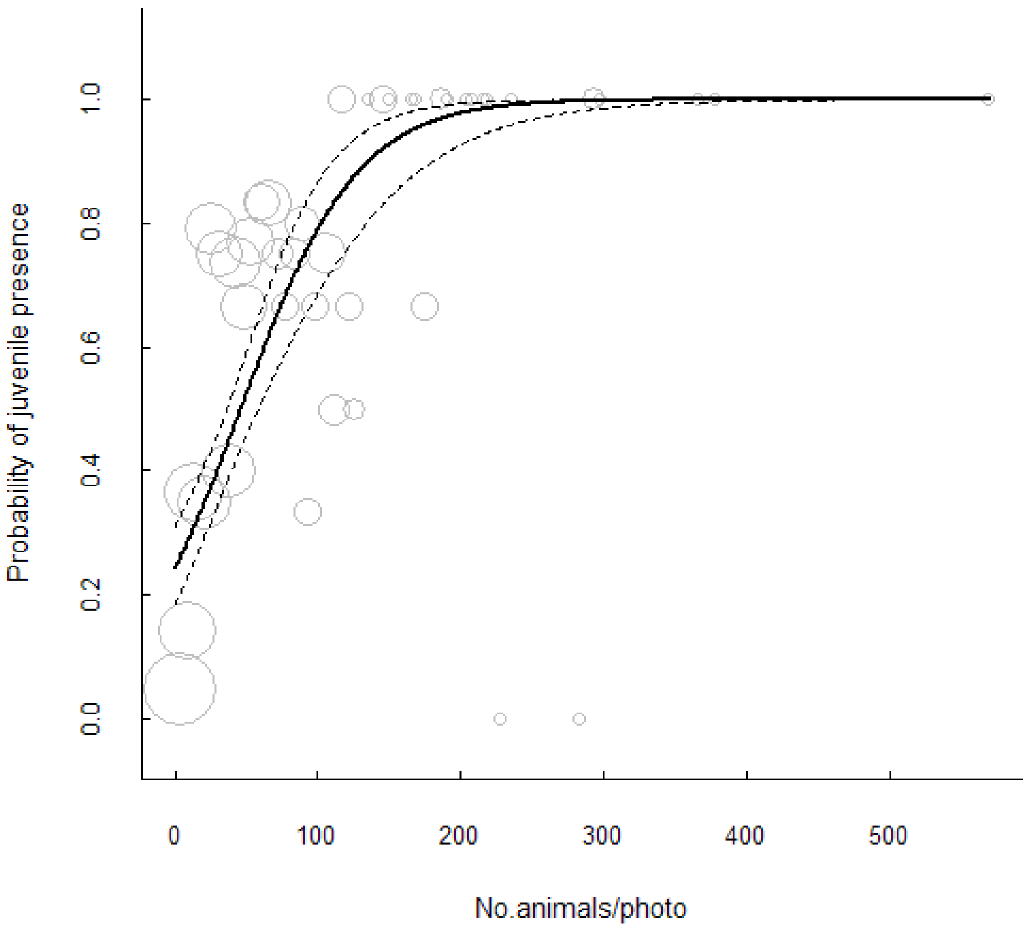

Figure 3.2. Estimated probability of juvenile presence according to total number of animals per photo. Original data on the presence of juveniles are superimposed as grey circles, with diameter proportional to the total number of animals. The trend line represents effect taken from model outputs (GLM with binomial errors, N=343 photos) and the dashed lines indicate 95% confidence intervals.

b) Impala

A range of "true" population sizes of impala was distributed in a virtual landscape with shape and area similar to the real survey area (around 1500km^2; Appendix A).

Impala form herds of two to hundreds of animals and are generally dispersed in a random or slightly aggregated pattern (Jarman & Jarman 1973; Stein & Georgiadis 2008). We were interested in modelling individual spatial locations while taking into account the abundance patterns related to herd distribution and size. Impala distribution was thus modelled using a 3-step clustering process: (1) a number of clusters ("herds") was situated randomly in the landscape (assuming a homogeneous landscape) according to a Poisson process, defining a "parent point" per herd; (2) herd size followed a lognormal distribution; and (3) animals within each herd were independently and uniformly scattered inside a circular herd home range centred on the parent point. Herd home range was obtained by multiplying herd size by the assumed "individual space" requirements, up to a specified maximum value ("maximum herd home range"). The lognormal distribution was parameterized with the mean and coefficient of variation of the observed scale, where the standard deviation of the lognormal variable (SD_{ln}) is given by:

$$SD_{ln} = \sqrt{ln(1 + CV^2)} \qquad \text{eqn 4}$$

and the mean of the lognormal variable ($mean_{ln}$) is given by:

$$mean_{ln} = \ln(mean) - 0.5\ln(1 + CV^2) \qquad \text{eqn 5.}$$

The lognormal distribution is commonly applied to describe multiplicative processes when mean values are low, variances large, and values cannot be negative, such as wildlife abundance (Matthiopoulos 2011). Impala monitoring does not provide counts of juveniles so population sizes were assumed to refer to adults only.

3.2.4. Wildlife monitoring

The observation procedure was modelled according to descriptions of monitoring in the Serengeti by Sinclair (1973), Norton-Griffiths (1973, 1978), Sinclair and Norton-Griffiths (1982), and Hilborn and Sinclair (2010). Therefore, we simulated monitoring of wildebeest in the Serengeti plains during the wet season when animals are aggregated in large numbers in a relatively small area. This timing increases the likelihood of good visibility and leads to a clear separation between migratory and resident wildebeest (only migratory animals are surveyed in this monitoring design). Migratory wildebeest are monitored through Aerial Point Sampling (APS; Norton-Griffiths 1978, 1988), which was first developed to characterize the land use of a region by interpreting a sample of aerial photos. We simulated monitoring of impala using Systematic Reconnaissance Flight (SRF) surveys, in which abundance data is collected within each sub-unit along several flight lines (i.e. transects; Norton-Griffiths 1978).

Sampling

The sampling steps simulated the process of taking aerial photos of wildebeest or conducting direct impala counts through selection of grid cells. We simulated a wide range of levels of sampling effort (measured by distances between transects and spacing between photos) in order to investigate the effects of sampling error on survey accuracy and precision. Detailed information about each specific step in this model component is provided in the supplementary material (Appendix A).

Observational procedures: flight and observer effects

These steps simulated flight and counting characteristics, namely variation in flight altitude and speed, and spatially autocorrelated miscounting of animals from photos or direct counts because of bad weather conditions, habitat or fatigue. For impala, observer effects also included herd and individual detectability and distance. This component allowed us to investigate the effects of observation error on survey accuracy and precision. Detailed information is provided in the supplementary material (Appendix A).

A summary of the modelled variables and range of values explored for each species is presented in Table 3.1.

Table 3.1. Description of variables and range of values explored for monitoring of: A) wildebeest and B) impala. The subscripts "wild" and "imp" refer to parameters regarding wildebeest and impala, respectively.

Parameters	Notation	Range	Sources
A. Wildebeest			
Population characteristics			
Population size	N_{wild}	200 000 – 2 000 000	Hilborn & Sinclair (2010)
Proportion of juveniles (%)	α	5 - 35	Estimated
Aggregation	k	0.01 - 2	Assumed
Spatial autocorrelation range	phi	0.1 - 0.5	Assumed
Spatial threshold variance (sill)	σ_s^2	Fixed (1)	Assumed
Sampling characteristics			
Distance between transects (km)	γ_{wild}	0.5-24	Hilborn & Sinclair (2010)
Time between photos (seconds)	δ	1-120	Hilborn & Sinclair (2010)
Flight characteristics			
Mean flight altitude (feet)	ε_{wild}	Fixed (1200)	Hilborn & Sinclair 2010
CV error altitude	ζ_{wild}	0 - 0.2	Estimated
Mean flight speed (km/sec)	θ_{wild}	Fixed (0.06)	Hilborn & Sinclair 2010
CV error speed	ι_{wild}	0 - 0.3	Assumed
Observer effects			
Minimum error counting juveniles (%)	Λ	0 - 0.2	Sinclair (1973)
Juvenile detectability (number of animals in a photo for which 50% juveniles are likely to be missed)	$\ddot{\imath}$	20 – 50	Assumed
CV error counting adults	$\ddot{\upsilon}$	0 - 0.5	Assumed
Counting error autocorrelation range	phi_{wild}	0-1	Assumed
B. Impala			
Population characteristics			
Population size	N_{imp}	1 000-15 000	Grumeti Fund (2010)
Median herd size	ξ	5-50	Jarman & Jarman (1973)
CV herd size	o	0-0.5	Stein & Georgiadis (2008)
Maximum herd home range (km^2)	π	0.5-3	Jarman & Sinclair (1979)
Individual space (km^2)	ς	0.05-0.2	Jarman & Sinclair (1979)
Sampling characteristics			
Distance between transects (km)	γ_{imp}	0.5-7	TAWIRI (2010)
Flight characteristics			
Mean flight altitude (feet)	ε_{imp}	Fixed (300)	TAWIRI (2010)
CV error altitude	ζ_{imp}	0-0.2	Assumed
Mean flight speed (km/sec)	θ_{imp}	Fixed (0.06)	TAWIRI (2010)
Observer effects			
Minimum herd detectability (%)	σ	0.05-0.5	Assumed

Herd size non-detectability (herd size for which there is a 50% chance of missing it)	τ	10-50	Assumed
Individual detectability at distance 0 (%)	υ	0.7-0.99	Assumed
Detectability by distance (distance for which there is a 50% chance of seeing animals; km)	φ	0.125-0.250	Assumed
Maximum individual detectability (%)	χ	0.7-0.99	Assumed
Herd size estimability (number of animals in a herd for which 50% are likely to be missed)	ψ	10-50	Assumed
CV counting error	ω	0-0.5	Assumed
CV counting error autocorrelation range	phi_{imp}	0-1	Assumed

3.2.5. Abundance estimation

The simulated survey data were used to estimate wildlife abundance, following procedures currently adopted in the study area.

a) Wildebeest

Simulated aerial photographs were treated as simple random samples from which juvenile and adult wildebeest were counted (Hilborn & Sinclair 2010). The estimated density per photo is the number of animals in a certain photograph divided by the photo area. The final estimate of the wildebeest population size is the area included in the survey (90x35 km^2) multiplied by the average density:

$$N = DA \qquad \text{eqn 6.}$$

b) Impala

Data from a simulated Systematic Reconnaissance Flight (SRF) were converted to estimates of animal density by dividing the total number of animals seen by both observers by the length of the sub-unit multiplied by their summed strip widths (Norton-Griffiths 1978). Sub-units were then combined within each transect and population estimates were calculated using transects as units of random sampling (Campbell & Borner 1995).

3.2.6. Analysis of sources of observation uncertainty

Analysis involved varying all model parameters simultaneously within the range considered (Table 3.1) and testing their effects on survey accuracy and precision. Survey precision was measured by the coefficient of variation (CV) and the normalized variance (CV is squared to the coefficient of variance, CV^2, which represents the total observed variance) but only CV results are presented (CV^2 results in Supplementary Information). The coefficient of variation (CV) was based on the simulated survey data, rather than statistically derived from each survey estimate, and expressed as:

$$CV = \frac{SD}{\bar{x}} \qquad \text{eqn 7}$$

where *SD* is the sample standard deviation of the population estimates from 50 simulations and $\bar{x}$ the mean estimate of population size. Accuracy was defined as the percent discrepancy between the mean estimated population size and the known population sizes for juveniles only or all age-classes together (for impala, only adult counts were conducted).

One thousand sets of parameter values were generated independently from uniform distributions for each species, and 50 simulations were carried out for each parameter set, from which mean values were obtained. All explanatory and dependent variables were scaled to have a standard deviation of unity, resulting in unit-less measures that can be used to infer the relative importance of parameters. Generalized linear models with Gamma (log link) and Gaussian error distributions were fitted to the simulation results to evaluate the sensitivity of survey precision and accuracy to parameters, respectively. A generalized linear model with quasibinomial error distribution (to account for overdispersion) and a logit link was fitted for juvenile wildebeest. Relevant two-way interactions were also considered. The linearity of the relationship between the parameters and the dependent variables and model residuals was examined graphically.

We also explored under which conditions (population characteristics and observation error) Systematic Reconnaissance Flights were adequate for impala monitoring. We assumed that at least one herd or 5 animals would have to be seen in order for the method to be considered adequate, and used a generalized linear model with binomial error distribution to evaluate the effects of potential drivers on survey adequacy, treated as a binary variable.

Finally, to illustrate the potential effects of different budget allocations on survey precision and accuracy, we ran 50 replicates for one thousand parameter sets under high and low budget scenarios. High or low budget scenarios assume parameters at their best or worst values, respectively (values presented in Appendix A). For example, the low budget scenario assumes only a few transects are conducted and that there is high counting variability (perhaps due to inexperienced or untrained observers). We obtained current unitary costs from itemized monitoring expenses in the study-area (J.G.C. Hopcraft, unpublished data) and then multiplied them by the simulated parameter values to estimate approximate budget costs for both scenarios.

3.3. Results

3.3.1. Effects of survey characteristics on precision and accuracy

Wildebeest

As wildebeest became more aggregated (i.e. lower *k* values) and more spatially autocorrelated (i.e. higher similarity between nearby cells), the surveys became less precise (higher coefficient of variation; CV). Higher sampling effort (i.e. smaller distance between transects or spacing between photos) increased precision in the wildebeest surveys but this effect was significantly weaker when spatial autocorrelation increased (Table 3.2).

The comparison between the population estimates from the surveys and known population sizes suggested that accuracy was lower for higher population sizes, when juveniles constituted a higher proportion of the total population, and for lower levels of juvenile detectability when counting from photos (Table 3.2). Accuracy of juvenile estimates was mostly affected by population size, juvenile detectability and aggregation.

Table 3.2. Results of a sensitivity analysis in which generalised linear models were fitted to precision (coefficient of variation) and inaccuracy (percent discrepancy between the mean estimated population size and the known population size) for wildebeest monitoring. All dependent and explanatory variables were scaled to have a standard deviation of unity for comparative purposes. The table shows the coefficients of all parameters and interactions from the full model. All β>0.10 are given in bold. Significance is coded as: ***=*P*<0.001, **=*P*<0.01, *=*P*<0.05.

Parameter	Relative importance (standardized regression coefficients; β)		
	Coefficient of variation (CV)	Inaccuracy	Inaccuracy (juveniles only)
Population size	-0.03	**0.40*****	**0.70*****
Proportion of juveniles	-0.02	**0.71*****	0.05***
Aggregation (*k*)	**-0.17*****	-0.08***	**-0.12*****
Spatial autocorrelation	**0.35*****	-0.04*	0.01
Distance between transects (km)	**0.13*****	-0.01	-0.09**
Time between photos (sec)	**0.14*****	-0.01	-0.08**
CV error altitude	0.02	0.04	-0.02
CV error speed	-0.01	0.01	-0.01
Minimum error counting juveniles (%)	0.02	0.05***	-0.01
Juvenile detectability	-0.02	**-0.16*****	**-0.29*****
CV of error counting adults	0.03**	0.01	0.02
Spatially autocorrelated errors	0.01	-0.03	-0.01

Spatially autocorrelated error* CV of error counting adults	-0.02	0.01	0.01
Spatially autocorrelated error* Juvenile detectability	-0.03	0.02	-0.01
Spatially autocorrelated error* minimum error counting juveniles	0.01	-0.01	0.01
Spatial autocorrelation*distance between photos	-0.07**	0.02	-0.01
Spatial autocorrelation*distance between transects	-0.09**	0.01	-0.01
Aggregation * Spatial autocorrelation	0.05	-0.02	-0.01

Impala

For impala monitoring through Systematic Reconnaissance Flights (SRFs), the surveys became less precise as distance between transects increased (i.e. lower sampling effort), for lower population sizes, higher mean herd sizes and lower herd size estimability. Accuracy in SRFs decreased when detectability at minimum distance and herd size estimability decreased and mean herd size and herd size non-detectability increased (Table 3.3).

The likelihood of detecting at least one herd or 5 animals using SRFs decreased for lower population sizes, lower sampling effort (measured as distance between transects), higher mean herd size, lower maximum individual detectability and lower herd size estimability (Table 3.3).

Table 3.3. Results of a sensitivity analysis in which generalised linear models were fitted to precision (coefficient of variation), inaccuracy (percent discrepancy between the mean estimated population size and the known population size) and survey adequacy (able to detect at least one herd or 5 animals) for impala monitoring. All dependent and explanatory variables were scaled to have a standard deviation of unity for comparative purposes. The table shows the coefficients of all parameters and interactions from the full model. All β>0.10 are given in bold. Significance is coded as: ***=P<0.001, **=P<0.01, *=P<0.05.

Parameter	**Relative importance (standardized regression coefficients; β)**		
	Coefficient of variation (CV)	**Inaccuracy**	**Adequacy**
Population size	**-0.32*****	0.05*	**0.36*****
Mean herd size	**0.15*****	**0.25*****	**-0.31*****
CV herd size	0.02	0.10***	0.01
Maximum herd home range (km^2)	-0.04	0.03	0.04
Individual space (km^2)	-0.03	-0.01	-0.01
Distance between transects (km)	**0.45*****	0.03	**-0.53*****
CV error altitude	-0.03	-0.02	-0.04
Minimum herd detectability (%)	-0.05	-0.07***	0.04
Herd size non-detectability	0.08**	**0.39*****	-0.03
Detectability at distance 0 (%)	-0.02	**-0.20*****	0.07
Detectability by distance	-0.03	-0.04*	0.02
Maximum individual detectability (%)	-0.01	-0.04	**-0.18****
Herd size estimability	**-0.11*****	**-0.62*****	**0.54*****
CV counting error	0.02	-0.01	0.01
Spatially autocorrelated errors	0.01	0.01	-0.01
Spatially autocorrelated errors*CV counting error	0.01	0.01	-0.01

3.3.2. Budgetary scenarios

High budgets produced more precise estimates for wildebeest and impala (Figure 3.3: b and d) though both monitoring techniques were likely to underestimate wildlife abundance (Figure 3.3: a and c). Mean underestimation for wildebeest monitoring from APS was around 15% and, although low and high budget scenarios produced similar values of mean underestimation, survey accuracy was much more variable for low budgets, producing estimates from 60% below the known population size up to 30% above (Figure 3.3a).

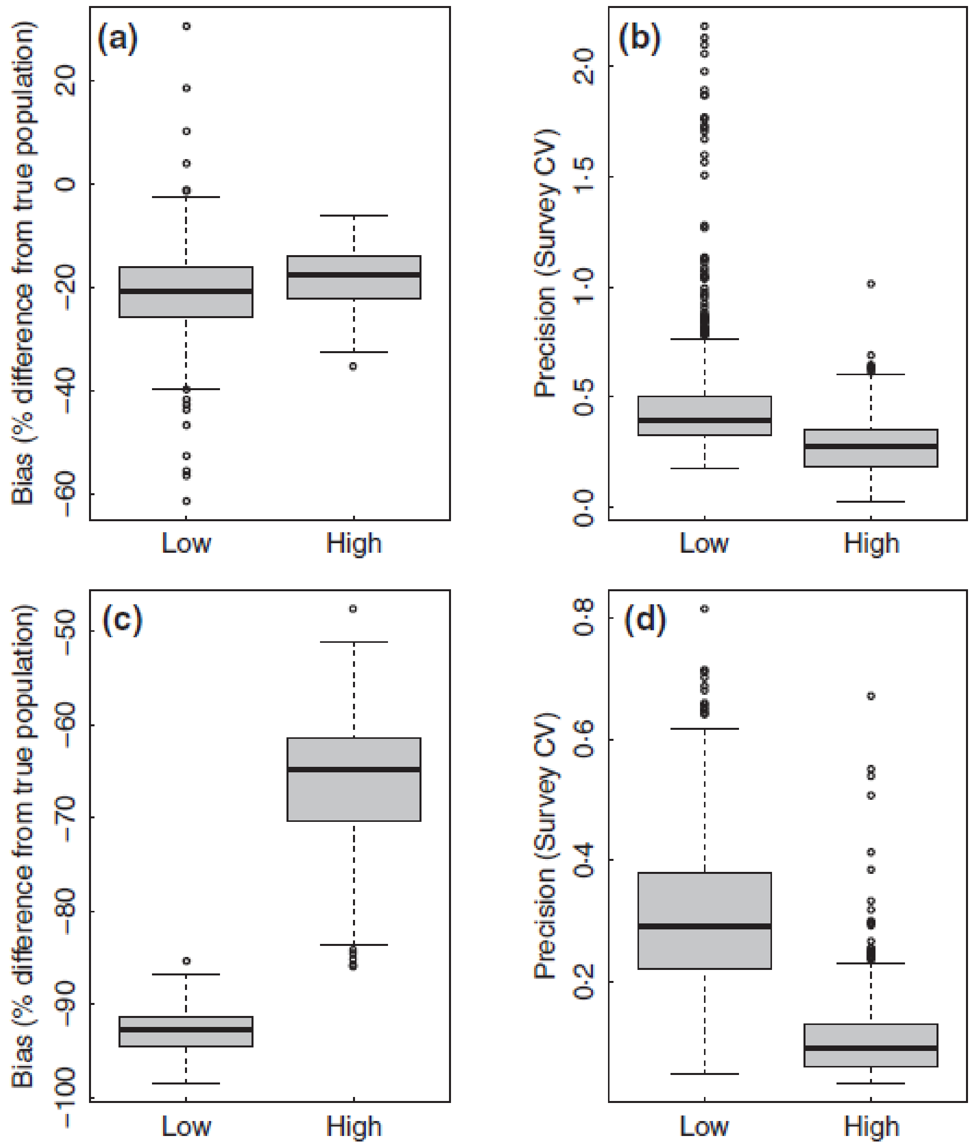

Figure 3.3. The potential effects of different budget allocations (low or high budget scenarios) on: a) survey accuracy for wildebeest monitoring; b) survey precision for wildebeest monitoring; c) survey accuracy for impala monitoring; d) survey precision for impala monitoring. High or low budget scenarios assume parameters at their best or worst values, respectively (see Table A1 in Appendix A). For example, the low budget scenario assumes conducting only a few transects and high counting variability.

For impala monitoring, the SRFs produced estimates generally 80% below the true value. Higher budget sizes produced a mean underestimation of around 65% and lower budget sizes produced a mean underestimation of around 90%, ranging from 80% to 100%. Higher budgets produced more variable bias, unlike for the wildebeest; this is due to variability being constrained by reaching zero herds detected in the low budget scenario.

For wildebeest monitoring, the simulated high and low budget scenarios were estimated to cost approximately US$6410 and US$3780, respectively. For impala, the high budget would require around US$8250 and the lower approximately US$4250. The higher budget scenario considered for wildebeest monitoring, which provides twice more precise estimates, would thus cost approximately 70% more to implement. The higher budget for impala monitoring, which increases accuracy by 30%, would increase costs roughly by 95%.

3.4. Discussion

In this study we have considered the multiple sources and effects of uncertainty in monitoring data obtained through wildlife surveys, focusing on the interactions between observation error and the spatial distribution of wildlife populations. Our results suggest that, under the simulated conditions, the relative importance of each process affecting precision and accuracy varies according to the survey technique and biological characteristics of the species. While survey precision was mainly affected by population characteristics and sampling effort, the accuracy of the survey was greatly affected by observer effects, such as juvenile and herd detectability. The adequacy of Systematic Reconnaissance Flights (SRFs), i.e. whether these surveys led to a minimum number of sightings, was mainly affected by population size, mean herd size, herd size estimability, maximum individual detectability and sampling effort. Our results also illustrate how budget size affects survey precision and accuracy, particularly for SRFs.

We extend previous work on causes of survey bias and imprecision (e.g. Norton-Griffiths 1978; Norton-Griffiths & McConville 2007) by developing a 'virtual ecologist' framework (Zurell *et al.* 2010) within which to carry out simulated tests of different monitoring strategies for different types of species. Elphick (2008) highlights the need for improved understanding of the effects of multiple sources of uncertainty on survey bias and precision, particularly errors due to observation uncertainty and its interaction with biological characteristics. However, compared to other aspects of monitoring such as sampling design, observation uncertainty is still the 'Cinderella' of monitoring, with little attention to the multiple potential sources of error involved. By decomposing observation uncertainty into components which may vary in magnitude and direction, we can make practical recommendations to managers concerning the priority issues that require attention. This would allow them to improve precision or accuracy of their counts, depending on the biology of the species concerned and budgetary constraints (Table 3.4).

The spatial distribution of a species is a major driver of variation in survey precision and accuracy (Table 3.4). Our findings chime with those of, for example, Blanchard, Maxwell & Jennings (2007) and Borkowski, Palmer & Borowski (2011), who also show the importance of aggregation (due to biological/social characteristics) and spatial autocorrelation (due to environmental/spatial characteristics) in determining survey precision. Counterbalanced variation due to changes in sampling effort, aggregation and spatial autocorrelation (for more aggregated species) and population size and mean herd size (for less aggregated species), suggests that sampling effort should be defined according to the spatial distribution in order to account for differences in precision. For monitoring highly aggregated species, such as wildebeest, we recommend that particular attention should be given to survey precision and that sampling effort should be defined according to previous estimates of aggregation in the monitored population. For example, in the Serengeti, sampling effort varies between years according to rough visual estimations of aggregation. This assessment could be formally considered in the monitoring protocol. The survey precision is most sensitive to spatial autocorrelation, which should be explicitly considered in abundance estimation procedures (e.g. confidence levels adjusted for “effective sample size” lower than actual sample size).

Table 3.4. Summary of the main issues considered in this study and our main recommendations for different types of species according to their spatial distribution, listed in priority order.

	Type of species according to spatial distribution	
	Highly aggregated (e.g. wildebeest)	**Random or slightly aggregated (e.g. impala)**
Aerial survey technique analysed	- Aerial Point Sampling	- Systematic Reconnaissance Flights
Main issues considered	- sampling effort - flight characteristics (variation in altitude and speed) - spatial distribution (aggregation and spatial autocorrelation) - population size and structure (proportion of juveniles) - observer effects (juvenile detectability and counting error of adult animals)	- sampling effort - flight characteristics (variation in altitude) - spatial distribution (herd size and home range) - population size - observer effects (counting error, herd detectability according to size, individual detectability within herd and distance effects)
Prioritized recommendations	1. Focus on survey precision 2. Obtain preliminary estimates of aggregation and spatial autocorrelation, and define sampling effort accordingly 3. Minimize, and obtain estimates of, counting errors of juvenile animals or obtain juvenile estimates from ground transects	1. Focus on survey bias 2. Maximize, and obtain estimates of, herd size estimability 3. Maximize, and obtain estimates of, herd detectability 4. Apply bias correction factor according to mean herd size

Similarly to other studies comparing estimates obtained through aerial surveys to known or presumed accurate population sizes (Goddard 1967; Jachmann 2002), our simulated surveys produced underestimates of considerable magnitude. Survey accuracy was greatly affected by multiple observer effects, particularly juvenile detectability when counting from photos, and herd size estimability and detectability when conducting direct counts during transects. Although the effects of distance and counting variability have been often mentioned as sources of inaccuracy (Buckland 2001), our results show that these commonly discussed types of observer error were comparatively less important in driving survey accuracy for these species in the range of conditions that occur in the Serengeti. This demonstrates the need for error minimization priority-setting based on comparative analyses. For example, McConville *et al.* (2009) explore the effect of herd detectability on accuracy, but we show that aerial survey accuracy is very much affected by detectability of individual animals within a herd. For random or slightly aggregated species monitored through aerial surveys, such as impala, we recommend that minimising potential bias should be a major consideration. Since accuracy is most sensitive to observer effects, monitors should be provided with appropriate training and their reliability evaluated before the actual survey to calibrate the final abundance estimates. For example, observers' estimates could be compared with photos of herds, obtaining correction factors. Other studies have shown that ground counts can provide more accurate estimates than aerial surveys, which are greatly affected by wildlife visibility for this type of species, but are generally more time-consuming and expensive, particularly for large survey areas (Jachmann 2002). When feasible, ground counts, or other better-performing techniques, should be conducted instead of or in addition to aerial surveys.

We also highlight the importance of considering which demographic group is subject to biases. In the case of wildebeest, juvenile detectability was a key driver of survey accuracy, while the effect of miscounting adults was negligible. Variation in juvenile survival can be used to make inferences about population trends (Gaillard, Festa-Bianchet & Yoccoz 1998), which further illustrates the importance of correctly counting juveniles. For highly aggregated populations, juvenile abundance could be obtained from other sources, such as ground transects, to avoid reducing accuracy of total population estimates. In other species, there may be different population components for which accurate and precise abundance estimates are crucial to management. For example, Katzner, Milner-Gulland & Bragin (2007) demonstrated the importance of collecting data on adult survival of Imperial eagles (*Aquila heliaca*) instead of territory occupancy to detect population trends.

This study took a static, spatially explicit approach to analysing monitoring uncertainties in the range of conditions that occur in the Serengeti, but there are also issues related to changes over time. For example, observer performance may improve or herd aggregation coefficients may change (cf McConville *et al.* 2009). Chee & Wintle (2010) have developed a dynamic cull control rule for overabundant wildlife where iterative culling can be used to update population parameters through Bayesian methods. Similarly, a dynamic monitoring strategy could update according to knowledge gained from the observation process.

Monitoring efficiency is of the utmost importance for conservation especially in the context of limited budgets and other priorities (Danielsen *et al.* 2003; Bottrill *et al.* 2008). Relating data quality to budgetary constraints for different survey techniques and prioritising approaches to error minimization are thus essential to investigate trade-offs and make informed decisions under uncertainty (Caughlan & Oakley 2001; Gaidet-Drapier *et al.* 2006) but these are rarely considered.

Monitoring and management decisions should be incorporated into conceptual and methodological frameworks which explicitly consider uncertainty, such as the Management Strategy Evaluation (MSE; Bunnefeld, Hoshino & Milner-Gulland 2011) and Adaptive Management (AM; Keith *et al.* 2011). MSE uses monitoring data to estimate trends and population size and then simulates decisions taking the degree of observation uncertainty into account, while AM implements strategies that incorporate uncertainty by testing multiple plausible hypotheses. Using a 'virtual ecologist' approach (Zurell *et al.* 2010), we provided insights into how to improve monitoring data and implement informed management actions that take monitoring uncertainty into consideration. This approach could easily be integrated into an MSE or AM framework. Explicit analyses of multiple types and sources of uncertainty are required, ensuring that conservation trade-offs are evaluated in a comprehensive, robust and transparent manner (Chee & Wintle 2010).

4. A novel approach to assessing the prevalence and drivers of illegal bushmeat hunting in the Serengeti

4.1. Introduction

Illegal behaviour, such as poaching and poisoning of wild animals, is common worldwide and threatens biodiversity in many terrestrial and aquatic ecosystems (Keane *et al.* 2008; Mateo-Tomás *et al.* 2012). The first step in devising effective strategies to reduce illegal behaviour is to assess its extent and nature and the identity of the noncompliers. However, the true extent of illegal activities is hard to quantify due to people´s fear of prosecution and the cryptic nature of the behaviour (Gavin, Solomon, & Blank 2010). Illegal behaviour is thus a frequent source of uncertainty that affects management decisions and compromises evaluations of conservation interventions (Mateo-Tomás *et al.* 2012). Effective conservation planning therefore requires use of methods that detect and quantify illegal activities accurately.

A number of methods have been used to measure and monitor illegal resource use, such as law-enforcement records, market surveys, and self-reporting (Gavin, Solomon, & Blank 2010). The choice of method depends on the type of information being sought, budget, capacity, and the nature of the illegal behaviour (Gavin, Solomon, & Blank 2010). Direct questioning is generally considered a cost-effective method to assess the harvest of natural resources. However, interviewees may not be willing to discuss participation in illegal and/or sensitive activities (e.g. taboo) and may refuse to answer survey questions, which leads to a nonrandom group of respondents, or lie to project a favorable image of themselves (social desirability bias) (St. John et al. 2010).

Indirect questioning techniques have been developed that minimize these sources of error in surveys. These techniques aim to increase respondent willingness to answer and reduce bias by making it impossible to directly link incriminating data to an individual (Warner 1965). They have been applied, for example, in surveys on racial prejudice (Blair & Imai 2012) and illegal immigration (GAO 2007). St. John et al. (2010) used randomized response technique (RRT) to estimate rule-breaking among fly fishers and has called for its wider application. Apart from RRT, applications of indirect questioning techniques are limited in conservation (but see St. John et al. 2010), and there is little understanding of their effectiveness at minimizing question sensitivity and increasing perceived anonymity. Trade-offs between question complexity and respondents' understanding deserve further consideration, particularly given that in developing countries conservation interventions often take place in predominately illiterate communities.

One of the illegal behaviours of concern, for which indirect questioning may be useful, is poaching. Quantifying poaching helps in targeting conservation interventions, assessing effects, and determining the costs of conservation (Mduma, Hilborn, & Sinclair 1998; Nielsen 2006), but its illegal nature makes this a particularly difficult task. For example, the Serengeti ecosystem encompasses some of the largest herbivore and carnivore populations in the world, and poaching is considered a major driver of changes in wildlife abundance (Hilborn *et al.* 2006; Sinclair *et al.* 2008). Bushmeat is widely consumed by local communities surrounding protected areas in the Serengeti, where hunting is conducted for subsistence and to generate cash (Loibooki *et al.* 2002; Johannesen 2005). People are generally aware of law enforcement and that hunting is conducted illegally (Bitanyi *et al.* 2012). Because of the sensitive nature of hunting in this area, given the potential repercussions, there is enormous uncertainty surrounding the prevalence and distribution of poaching, incentives to poach, and socioeconomic characteristics of the people involved. It is estimated that 8-57% of households in the western Serengeti engage in bushmeat hunting, and this percentage differs greatly among studies (Table 4.1).

The general drivers of poaching range from economic incentives and unawareness of laws to tradition and fairness (see Keane et al. [2008] for a review). Previous studies in the Serengeti report cultural, socioeconomic, seasonal, and spatial factors are associated with illegal bushmeat hunting (Table 4.2). The information about poaching households presented in these studies derives from interviews with arrested hunters, is self-reported through direct questions, or relies on dietary recall. Some of the information on who engages in hunting is contradictory. The potential relations between hunting and alternative sources of income and protein, as well as demographic variables, are particularly important to understand because this information should be used to design interventions to control bushmeat hunting.

Table 4.1. Estimated prevalence of bushmeat hunting by communities surrounding the Serengeti National Park in previous studies, obtained through direct questioning.

Prevalence (% of hhs hunting)	No. hhs surveyed	No. villages sampled	Comments by authors	Reference
8	590	8	*"hunting may well exceed the levels reported (…which can…) probably be attributed to the contentious nature of the issue and the fear of repercussion"*	Kaltenborn, Nyahongo, & Tingstad (2005)
9	421	8	*"Thirty-seven households admitted to poaching (…) Poaching households reported killing 4.8 wildebeest in the last 12 months compared to 0.4 wildebeest per non-poaching household"*	Knapp (2007)
10	477	10	*"the collected data needs to be treated cautiously, because we may have been lacking important information due to fear from respondents"*	Mfunda & Røskaft (2010)
27	297	6		Johannesen (2005)
29	715	24	*"individuals in households were asked if they were involved in hunting (…) many respondents chose not to answer (155 out of 715 responded)"*	Campbell et al. (2001)
32	300	10	*"Respondents were not asked whether they participated in illegal hunting, but many voluntarily claimed to be involved"*	Loibooki et al. (2002)
57	359 in 24 focus groups	12	*"More group respondents than individual respondents claimed to be hunters, demonstrating that results can be influenced by the methods"*	

Table 4.2. Summary of the explanatory variables used in this study and their reported effects in other studies of bushmeat hunting in the Serengeti.

Explanatory variable	**Reported effects**
Ethnic group	Arrested poachers are mainly of the Kurya and Ikoma tribes (Ndibalema & Songorwa 2008). No significant differences between ethnic groups (Mfunda & Røskaft 2010).
Household size	Larger households have less involvement in hunting (Johannesen 2005). Household size has no effect on hunting involvement (Mfunda & Røskaft 2010)
Household migration	Immigrants to the area are more frequently involved in hunting (Mfunda & Røskaft 2010).
Household employment	Poaching and non-poaching households equally likely to report seasonal employment but poaching households less likely to have full-time employment (Knapp 2007)
Season	Poaching occurs all year round but mainly during the dry season when the wildebeest are in the study area (Kaltenborn, Nyahongo, & Tingstad 2005; Holmern, Muya, & Røskaft 2007)
Hunting as source of cash	Most arrested hunters report hunting only for their own consumption (Holmern *et al.* 2002). The main reasons for hunting are economic rather than just subsistence (Loibooki *et al.* 2002; Johannesen 2005)
District	Higher proportion of hunters in the Serengeti district than in Bunda (Johannesen 2005)
Distance from village to protected areas	The number and proportion of hunters in a village is negatively correlated with distance (Campbell & Hofer 1995). Distance does not affect hunting involvement up to 17km from the PA (Johannesen 2005).
Access to alternative sources of protein and/or income	Lower hunting prevalence in villages close to urban areas and lake Victoria (Loibooki *et al.* 2002)

Using bushmeat hunting in the Serengeti as a case-study, we investigated the potential of indirect questioning techniques for studying non-compliant and sensitive harvest behaviour. First, we explored the feasibility of applying these techniques in the study area by testing the willingness of respondents to give sensitive information, and their understanding of the survey, depending on the technique employed. Then, we assessed the prevalence of illegal hunting using the best performing of these techniques (the unmatched-count technique), as well as identifying the socio-demographic characteristics of non-compliant households. We based our hypotheses concerning the likely characteristics of hunting and the households engaged in it on the findings of previous studies (Table 4.2). We extracted the variation explained by the fact that respondents came from different villages and related this to spatial characteristics, such as the distance to protected areas and nearest urban area. Finally, we considered the effectiveness of the technique at minimizing question sensitivity by analysing respondents' perceived anonymity and discomfort.

4.2. Methods

4.2.1. Study area

The local communities surrounding the protected areas in the western Serengeti (Figure 4.1) are traditionally composed of pastoralists, agropastoralists, and hunters, but current livelihood strategies consist of a combination of occupations (Sinclair *et al.* 2008). The villages are multiethnic, owing largely to immigration. Households are generally polygamous, and education is up to the primary level (Loibooki *et al.* 2002; Kaltenborn, Nyahongo, & Tingstad 2005). In 2002, there were approximately 0.43 million people living in the Bunda and Serengeti Districts that surround the Serengeti National Park (SNP) (NBS Tanzania 2006).

Bushmeat is, in theory, a state-controlled natural resource in Tanzania. Hunters must obtain a license, and quotas for harvest in hunting concessions outside the national park are set annually. However, there is a high rate of noncompliance, potentially owing to the legal complexity and high fees associated with obtaining a license, lack of benefit sharing, poor governance, and centralized control of resources (Nelson, Nshala, & Rodgers 2007). Bushmeat hunting in the Serengeti is mainly nonselective and conducted through wire snaring, although use of weapons and hunting dogs and night hunting with flashlights are also common (Holmern *et al.* 2002). The seasonally available migratory ungulates, such as wildebeest *(Connochaetes taurinus)*, represent the bulk of harvested wildlife, but poaching affects a wide range of resident ungulates, such as impala (*Aepyceros melampus*) and topi (*Damaliscus lunatus*), and nontarget species, such as spotted hyena (*Crocuta*

crocuta) (Hofer et al. 1996). In our study area, all forms of legal hunting effectively ceased in 2003, when all legal hunting rights were bought by a local nongovernmental organization (Knapp *et al.* 2010). Law enforcement is carried out by Tanzania National Park rangers and personnel of the Grumeti Fund.

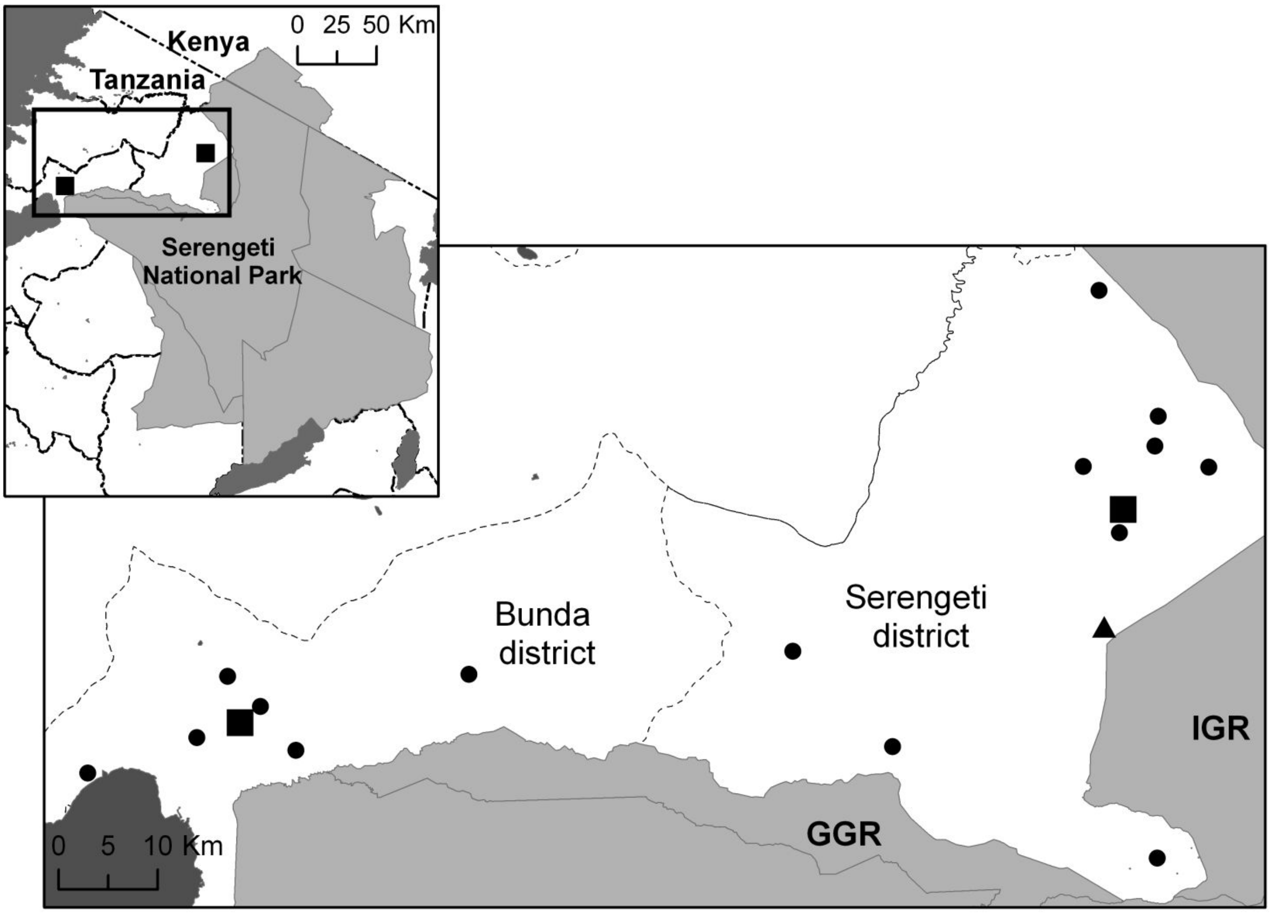

Figure 4.1. Protected areas (light grey), lake (dark grey), districts (boundaries represented by dashed lines) and study villages in the western Serengeti (indicated by circles). Triangle represents the village used in the exploratory study. Squares indicate urban areas (district administrative towns). GGR = Grumeti Game Reserve, and IGR = Ikorongo Game Reserve.

4.2.2. Survey techniques

We used the following questioning techniques in the exploratory study:

- unmatched-count technique (UCT): survey respondents are randomly allocated into a baseline group and a treatment group. Baseline group members receive a list of non-sensitive items (e.g. behaviours such as herding and trading) while the treatment group receives the same list but with the addition of the sensitive item (e.g. poaching). All respondents are asked to indicate how many, but not which, items apply to them (Droitcour *et al.* 1991). Differences in means between sub-samples are used to estimate the prevalence of sensitive behaviours;

- randomized response technique (RRT): respondents are presented with a randomising device (such as a die, coin or a bag of coloured balls) which they never show to the interviewer. They are instructed to give a “yes” or “no” response according to the randomly-drawn result; probabilities with which the questions are presented allow the estimation of the prevalence of behaviour (Warner 1965). The forced response version was used (Lensvelt-Mulders, Hox, & Heijden 2005): respondents randomly took one of four balls from a bag: one black, one red and two green. They were required to answer the sensitive question (e.g. have you poached in the last 12 months) truthfully if they got a green ball. Irrespective of the truth, respondents were asked to simply say the word “yes”, if they got the red ball, and to say “no” if they got the black ball;

- 2-card method: a list of items including the sensitive item (e.g. the person’s main employment) is divided into three mutually exclusive answer groups. The respondent is asked to say which group they belong to, but not which actual item applies to them (GAO 2007). The respondents are randomly allocated one of two treatments, which differ only in the answer group within which the sensitive item is placed. The prevalence of the sensitive item is then estimated by comparing the percentages of people from each of the two treatments who picked a particular answer group;

- Ballot box: respondents write their answers to the sensitive questions on a piece of paper, or put a cross against the appropriate answer, and place it into a sealed box, which is emptied later for counting.

The response cards are provided in Appendix B.

4.2.3. Data collection

The exploratory study was conducted in March 2010 and data collection for the main study was carried out from February to June 2011 in the western Serengeti, Tanzania. 15 villages (plus 1 for the exploratory study), located in the Serengeti and Bunda districts up to 15km from a protected area, were selected through random sampling with replacement from the 2002 official Tanzanian census data (Figure 4.1).

The interviews were conducted by local enumerators from the study village or neighbouring areas and the interviewers were trained to select one household in each village and then skip two households before approaching the next household to interview, making sure not to sample adjacent households. Approximately 1.7-5.6% of the households in each village were sampled. Interviews were conducted with the head of household or any other household member provided they were 18 years old or older.

For the exploratory study, each of 60 respondents was randomly allocated to one of the four techniques. Participation of any household member in bushmeat hunting was enquired about using the allocated technique preceded by socio-demographic questions and followed by questions assessing respondents' understanding of the survey technique and willingness to reply. Respondents' reactions and informal comments were also recorded.

Final surveys (Appendix B) were administered to, on average, 79 households per village. The questionnaire started with questions on individual and household socio-demographic characteristics. Next, the UCT was used to ask about the participation of any household member in bushmeat hunting and other livelihood activities over the last 12 months. Households were randomly allocated to baseline or treatment groups using a die. In the treatment group, bushmeat hunting was listed alongside 4 other livelihood activities and respondents were asked how many of these activities their household had engaged in. In the control group, bushmeat hunting was absent from the list. Respondents were asked separately about participation in these activities in the dry and wet seasons, as well as which ones they had obtained cash income from. Finally, the respondents' opinion was sought about the questioning technique itself, specifically their levels of understanding, feeling of anonymity and discomfort when answering the UCT questions.

The hunting UCT questions were preceded by a non-sensitive training question in which respondents were asked to say how many of a list of potential animals causing problems applied to them (e.g.

elephants, leopards). This was to put them at their ease and engender a positive attitude to the survey, check for the validity of the control and ensure that they understood the method. To minimize ceiling and floor effects, in which answer secrecy is removed because the respondent is engaged in all or none of the listed activities, non-sensitive items included at least one item whose prevalence was extremely low and one item with very high prevalence (Tsuchiya, Hirai, & Ono 2007). Non-sensitive items completely different from the target item may cause suspicion (Hubbard, Caspar, & Lessler 1989); therefore all items referred to livelihood strategies (or wild animals for training question).

4.2.4. Data analyses

For the exploratory study, respondents' reluctance to collaborate in the survey and their self-reported and/or observed difficulty in understanding the questioning technique were used as binomial dependent variables. The explanatory variables were sex, age and survey technique. Generalised linear models were fitted with a binomial error structure and logit link function.

For the main study, linear mixed models were fitted with village and card type (baseline or treatment) within village as random effects to account for spatial dependence of observations. A random effect for individual was also included to account for the grouping structure of the data, since every respondent answered multiple UCT questions. To estimate behaviour prevalence, models were fitted only with the random effects and question topic and card type as fixed effects. Then, UCT answers to bushmeat questions were fitted with card type, the demographics, and interactions of the card type variable with each demographic (Holbrook & Krosnick 2010); the interactions between socio-demographic variables and treatment status indicate differences between the reported number of behaviours in the two conditions for each predictor variable.

To analyse the spatial effects affecting hunting prevalence, best linear unbiased predictors (BLUPs) of the random effect of village were extracted from the top model, in which the random effect of treatment card within village measures unexplained deviance of each village from the mean hunting prevalence. A graphical inspection of the data showed a potential non-linear effect of distance to the national park. Generalised linear models were fitted with Gaussian error structure and identity link function, using district and logarithmic transformations of villages' population size and distance to urban area, squared and linear distance to the national park and Lake Victoria as explanatory variables.

We employed cumulative logit models to analyse respondents' self-reported levels of understanding, anonymity and discomfort when answering the UCT questions. Specifically, we evaluated the effect of age, sex, education level and status within household on respondents' perceptions as a multinomial response ("very much", "moderately", "a little" or "not at all") without making assumptions about the distance between ordered categories or their distribution. We were also interested in evaluating the effect of potential question sensitivity on perceived anonymity and discomfort, assuming that being shown a treatment card (which includes hunting) could be more sensitive, particularly if more activities were reported (respondents may feel less able to mask involvement in the sensitive item). A two-way interaction between UCT card (treatment or baseline) and number of reported activities (UCT answers) was included in the models fitted to anonymity and discomfort. Village was included as a random effect. These models were implemented using the clmm function in the ordinal package version 2012.01-19 (Christensen 2012) in R v.2.15.1 (The R Foundation for Statistical Computing 2012).

The corrected Akaike information criterion (AICc) was used to select and rank the most parsimonious models. When analysing the number of reported activities to identify characteristics of non-compliant households, only models with interactions were considered for comparison. We averaged estimates across models with ΔAIC < 4 (Burnham & Anderson 2002).

4.3. Results

4.3.1. Comparison of techniques

In the exploratory phase of our study, respondents' age ranged between 18 and 90 years (32±11.9 years; median ± semi-interquartile range), and 42% were men. 22 out of 60 respondents reported or exhibited difficulty in understanding the sensitive question while 8 respondents showed reluctance in answering.

Age was included in all the top models (ΔAICc <4) explaining variation in willingness to answer questions, but its confidence intervals overlapped with zero, decreasing confidence in its explanatory power. Survey technique and sex were also among the best models but had considerably less support (Appendix B: Tables B1 and B2).

The ease of understanding the question was best explained by survey technique while sex and age had smaller relative variable importance. The UCT was found to be easier to understand than the ballot box and the RRT (Figure 4.2), and older people and females were more likely to report the questions as difficult.

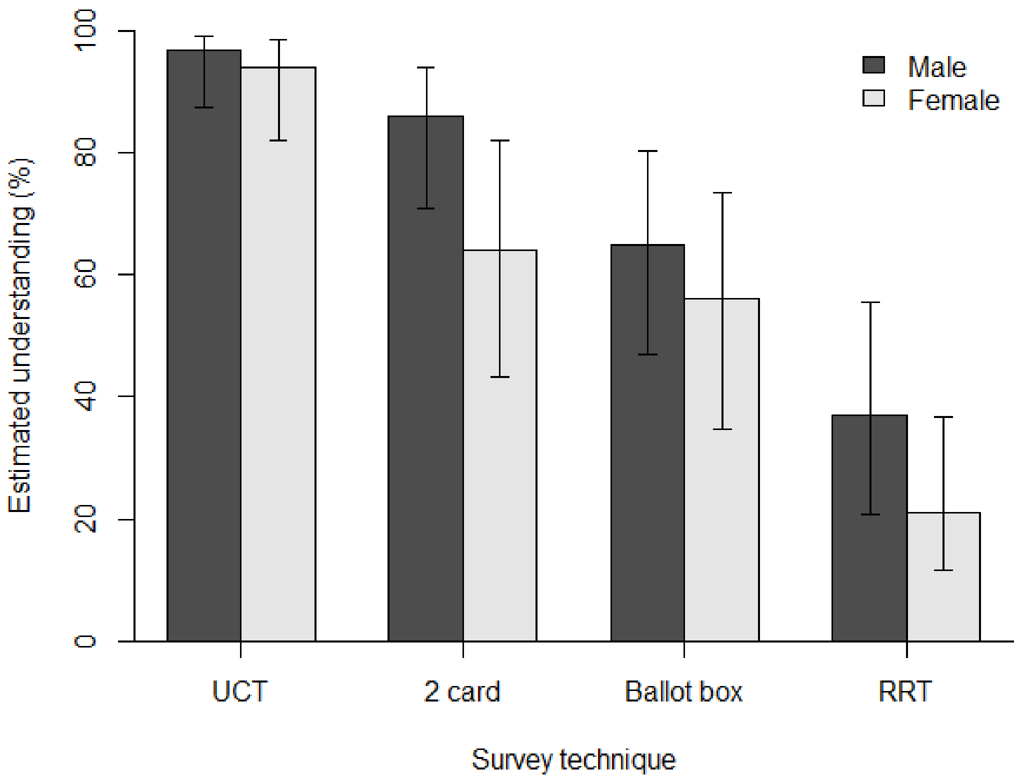

Figure 4.2. Estimates and standard error of the ease of understanding the questioning technique, obtained as multimodel averaged coefficients from GLMs with a binomial error structure and logit link function.

4.3.2. Estimating bushmeat hunting prevalence

Given the results of the comparison of techniques, we used the UCT for the estimation of hunting prevalence. We approached 1191 household members, of which only 28 refused to participate (non-response rate <2.5%). In all cases, this occurred at the start of the questionnaire before asking any questions. There was no difference between survey respondents and non-respondents in terms of their sex (χ^2=0.92, df=1, p=0.34) but older respondents (66+) were approximately 7% less likely to respond than the other age groups (age groups: 18-25, 26-45, 46-65, 66+; χ^2=13.05, df=3, p=0.01). Before analysis we discarded questionnaires with missing data, leaving a sample of 1093 individuals (summary in Appendix B: Table B3). Respondents allocated to baseline (n=551) and treatment (n=542)

UCT cards did not differ according to their socio-demographic characteristics (Appendix B: Table B4). Correlation between predictor variables was low (all<0.4).

The extent of illegal bushmeat hunting

Bushmeat hunting was conducted by approximately 18% (±5) of the households in the western Serengeti during the 12 months prior to survey administration. More households were involved in illegal hunting during the dry season than in the wet season, and hunting households predominately generate cash income from bushmeat, particularly in the dry season (Figure 4.3). However, the differences between season and the season:cash interaction are non-significant, with wide and overlapping standard errors.

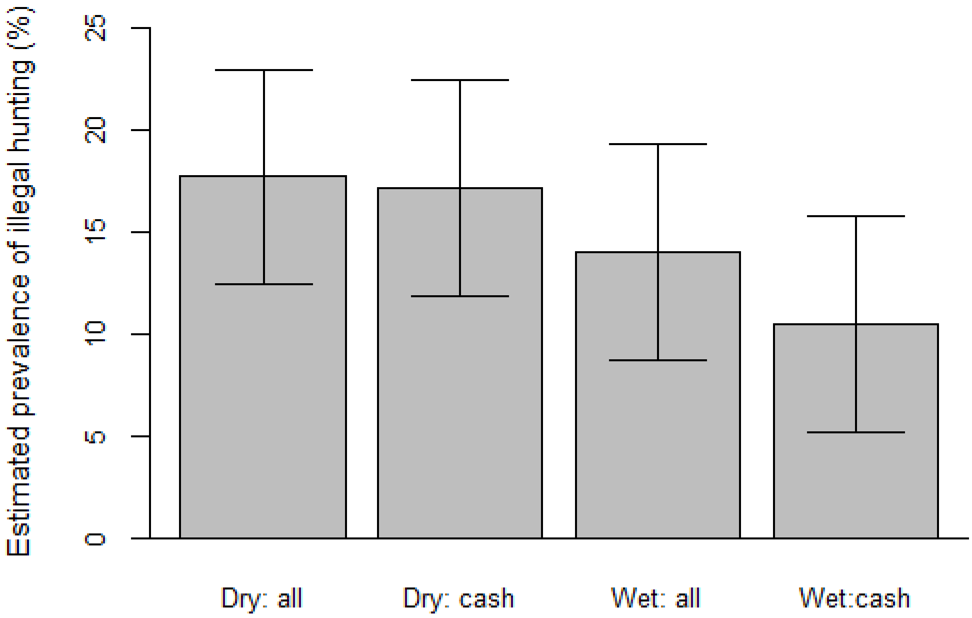

Figure 4.3. Estimated prevalence (SE) of illegal bushmeat hunting in the western Serengeti during the 12 months prior to the study. Estimates obtained from model fitted only with the random effects and question topic and card type (treatment or control) as fixed effects (dry, dry season; all, cash and other reasons; cash, cash income; wet, wet season).

Characteristics of poaching households

Illegal bushmeat hunting was more likely in households with seasonal or full-time employment, lower household size, longer household residence in the home village and where respondent had higher education levels (Figure 4.4). Hunting prevalence was also explained by question (poaching during the wet season for cash income was less common).

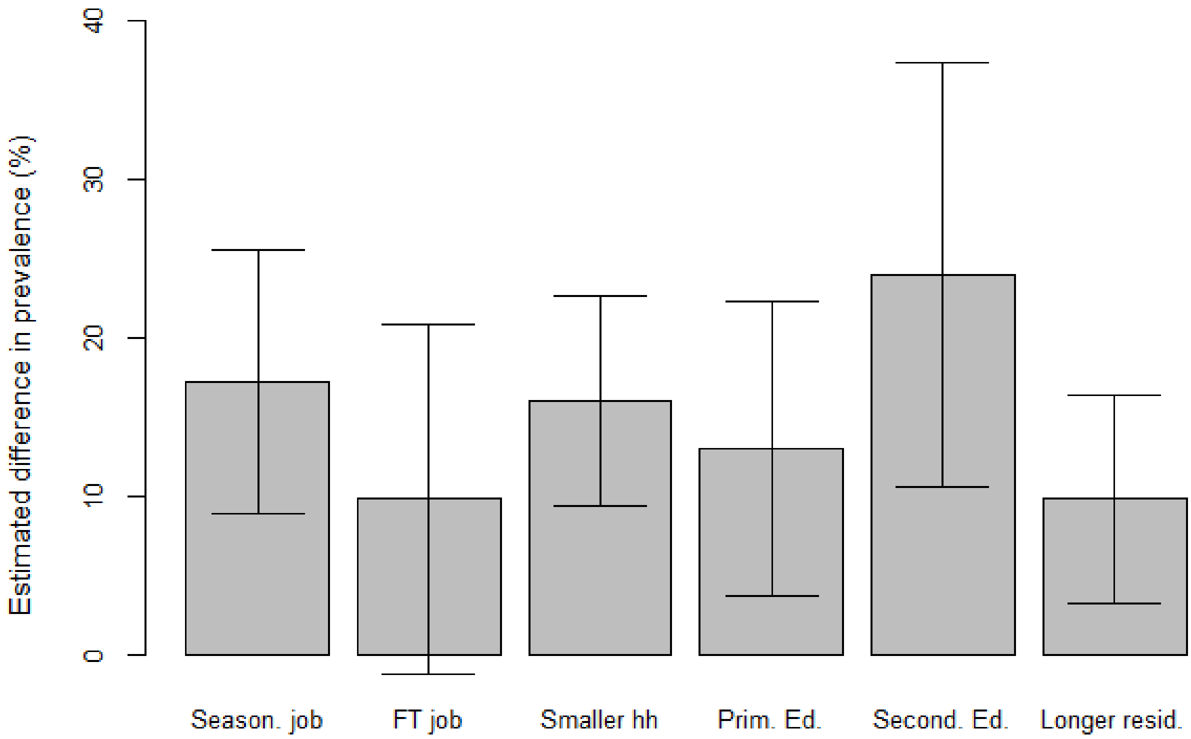

Figure 4.4. Main socio-demographic explanatory variables of estimated bushmeat hunting. All variables are categorical and the effects are presented as the estimated difference (and S.E.) in prevalence where each level is contrasted to a reference level. A baseline prevalence of 6.5% includes all reference levels: no seasonal job, no full-time job, larger households, respondent with no formal education and shorter residence in the village.

Other variables also included in the top models but with much less support were the number of children in the household, respondent sex and whether or not the respondent was the head of the household (Appendix B: Tables B5 and B6). Ethnicity was not retained in the top models.

Village random effects

The nesting factor of village explained 21.9% of the variance which was not explained by any of the fixed effects. This village-level variance was best predicted by the village's distance to the national park and to urban areas. After accounting for the socio-demographic effects analysed in the main model, distance to national park had a negative effect on hunting prevalence up to around 5km away, when the effect of distance became positive (Figure 4.5a), and villages further away from urban areas had higher hunting prevalence (Figure 4.5b). Villages with higher population sizes had lower unexplained hunting prevalence but this variable received little support for inclusion in the top models, while district and distance to Lake Victoria were not retained in the top models (Tables B7 and B8 in Appendix B).

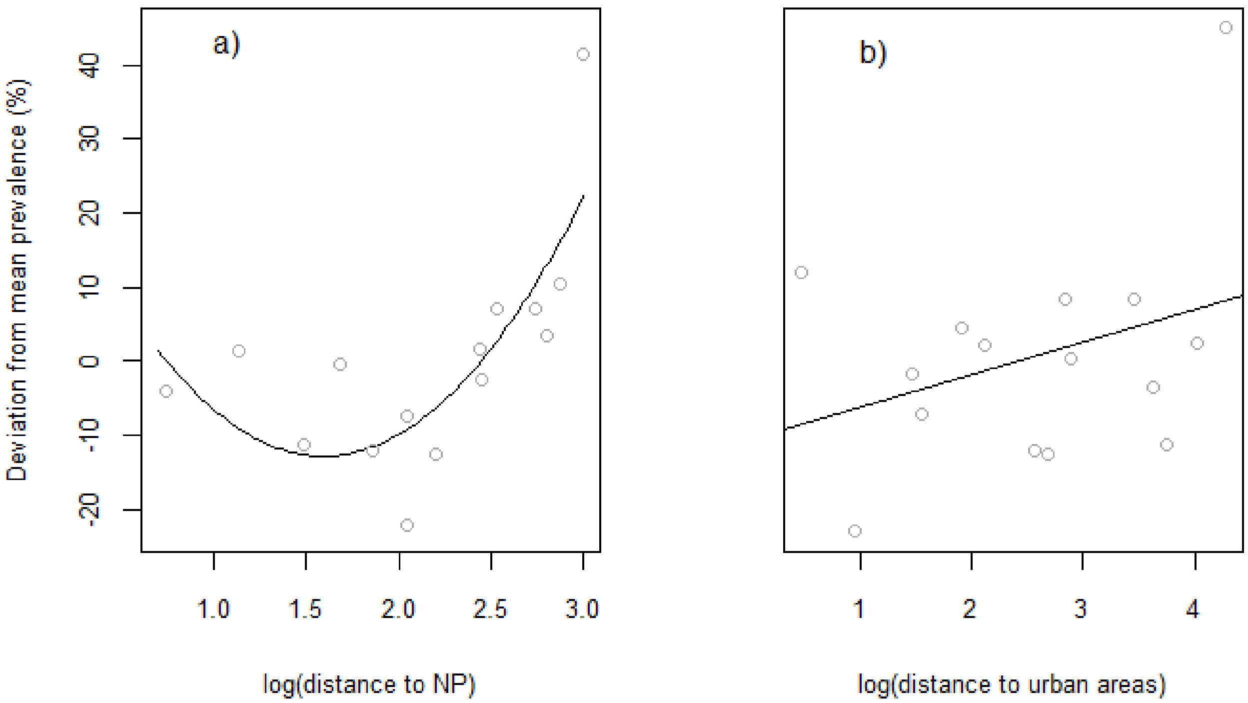

Figure 4.5. The effect of the logarithmic distance to: a) Serengeti National Park and b) urban areas on the hunting prevalence of each village (N=15, deviation from the estimated mean from a mixed effects model, also called best linear unbiased predictors, BLUPs). The circles show villages' data and the trend lines represent effects taken from model outputs.

Respondents' perceptions about the UCT

The majority (65%) of survey respondents found the UCT questions very easy to understand and only 9% reported them as difficult. Similarly, less than 10% of respondents said they felt very uncomfortable answering these questions and 77% said they were not uncomfortable at all. However, 70% of respondents said that they thought their answers were not anonymous (Appendix B: Table B9).

The model results suggested that there were no major issues with respondent perceptions that may have influenced the survey: the null model was the most parsimonious model explaining self-reported understanding of the survey technique. Age, sex, education level and status within household had low relative importance (<0.35; Table B11 in Appendix B). Reduction in perceived survey anonymity was explained by older age and being shown the treatment cards (which include the sensitive items). However, the variable importances were still low (0.66 for age and 0.59 for the treatment cards) and their small effect size and large standard errors reduce our confidence in the direction of their effects. Respondents' perceptions of increased discomfort were mainly explained by being shown the treatment rather than control cards (variable importance 0.89), reporting fewer UCT activities, particularly when being shown the treatment cards (importance 0.8) and not being the head of their household (0.53). Except for head of household status, the large standard errors for these variables decreases our confidence in whether the potential effect on discomfort was positive or negative.

4.4. Discussion

Effective conservation requires a better understanding and assessment of human behaviour and its drivers in order to motivate behavioural change (Milner-Gulland 2012). The true extent of natural resource exploitation is, however, difficult to ascertain, particularly if it is illegal in nature (Gavin, Solomon, & Blank 2010). Understanding the mechanisms behind responses to sensitive questions and separating out the confounding effects of the survey technique from the actual drivers of behaviour are thus of the utmost importance but rarely considered. We investigated how techniques developed in the social sciences may be applied to minimize survey bias and increase respondents' willingness to share sensitive information and considered their potential shortcomings.

Bushmeat hunting in the Serengeti has often been described as a conservation threat (Campbell & Hofer 1995; Sinclair *et al.* 2008) and several interventions, such as law enforcement, game-cropping schemes and microcredit access initiatives, have been employed in an effort to reduce poaching. The difficulty of quantifying harvest offtake and poaching involvement in the study area impedes the evaluation of intervention effectiveness. For example, estimates of the number of wildebeest hunted annually range from 40,000 (Mduma, Hilborn, & Sinclair 1998) to 118,000 (Campbell & Hofer 1995), and the reliability of estimates of hunting prevalence obtained through direct questions has often been questioned (Table 4.1). Eighteen percent of households admitted to being involved in hunting. Results from studies conducted elsewhere show that failing to include the effects of illegal behaviour in planning and evaluation undermines the success of conservation interventions, reduces their credibility in the eyes of policy makers, and limits the ability to target interventions (Mateo-Tomás *et al.* 2012; St. John *et al.* 2012).

Information about the characteristics of rule breakers can help managers focus resources on the least compliant groups (St. John *et al.* 2010, 2012). Previous studies in the Serengeti have provided sometimes contradictory evidence about who engages in bushmeat hunting and why, where, and when they engage in it (Table 4.2). For example, poverty is the most commonly cited reason people in the Serengeti poach bushmeat (Loibooki *et al.* 2002; Kaltenborn, Nyahongo, & Tingstad 2005), but

Knapp (2007) suggests the decision to poach may be more an issue of time availability than household wealth. Our results suggest households with seasonal or full-time employment were more likely to be involved in bushmeat hunting than households without any employment, supporting neither of the previous explanations.

Poaching in the Serengeti is generally considered to be mainly a seasonal activity used when ungulate migrations pass by the villages during the dry season (Loibooki *et al.* 2002; Holmern, Muya, & Røskaft 2007). Our results suggest that seasonal differences in engagement in hunting are not as clear as expected, indicating that households in the Serengeti hunt both for food and cash all year round. The migratory ungulates are partially protected from hunting by the protected areas (Thirgood *et al.* 2004) and during the wet season, when they are located in areas less accessible to hunters and less suited to the use of snares (Campbell, Nelson, & Loibooki 2001). However, poaching during all year may result in more drastic consequences for resident species, such as impala and topi, as suggested by low densities of resident wildlife in several areas in the Serengeti (Campbell & Hofer 1995).

Our results also suggest that, given the widespread involvement in hunting for cash, current alternative sources of income may not be sufficiently attractive to compete with the opportunities provided by hunting and availability of cash from employment may even facilitate hunting. Recent research in the area points to the strong role of women in encouraging hunting as they highly value the access to meat and instant cash (Lowassa, Tadie, & Fischer 2012) and, while wealthier households tend to attribute less utility to hunting than less well-off households, they also seem to be less concerned about the risk of being caught (Moro *et al.* 2013). In the Serengeti, despite the general awareness of the illegality of hunting and its repercussions, its monetary and protein-based benefits greatly exceed the costs (Bitanyi *et al.* 2012; Knapp 2012). Moreover, evidence from other areas shows that natural resource use is not restricted to the poorest people and may actually increase as other sources of income increase in generally poor communities. This evidence may indicate the existence of transition states out of poverty (Nielsen, Pouliot, & Bakkegaard 2012) and that the effect of increased income on hunter behaviour may be ambiguous. For example, increased income may facilitate a change to more effective or selective hunting techniques (Damania et al. 2005).

A number of potential drivers of and explanations for illegal bushmeat hunting have been proposed. Among these, we did not consider , for example, awareness of hunting regulations (Bitanyi *et al.* 2012), risk perceptions (Knapp 2012) and cultural reasons (Lowassa, Tadie, & Fischer 2012) for hunting.

Further studies that focus on understanding the multivariate causation processes driving poaching behaviour in the study area are essential. We also found that, as suggested by others (Campbell et al. 2001; Nielsen 2006), villages are less involved in hunting as the distance to protected areas increases. However, we found that hunting prevalence increased substantially as distance to the park increased for villages >5 km away from the park.

Although the indirect questioning techniques have been applied in a number of socio-demographic and cultural contexts (e.g. Solomon et al. (2007) in villages in Uganda and St. John et al. (2010) with fishers in the UK), relatively little attention has been given to the trade-offs between technique complexity and respondent understanding, discomfort and perceived anonymity. For example, similarly to our findings, Razafimanahaka et al. (2012) reported problems with understanding of the RRT in one of their study villages in Madagascar. By focusing on respondents' perceptions, we considered the interpretability of the questioning technique within our study's sociocultural context. Our aim was to increase the reliability of our results by using a technique that respondents felt comfortable with. Comparative studies between survey methods are however rare and our study is an exception in the way that it tests the feasibility of multiple techniques before conducting the main data collection. Pilot studies, such as ours, can provide essential information about the adequacy of different survey instruments and their importance cannot be overemphasized.

The UCT was developed to address some of the criticisms of RRT (i.e., that the technique may be constrained by belief in trickery or by respondents' feelings of confusion and education level [Hubbard et al. 1989; Landsheer et al. 1999]). The UCT has been more effective than direct questions for estimating prevalence of sensitive behaviours (Tsuchiya, Hirai, & Ono 2007) and produces similar or higher estimates of illegal behaviours than RRT (Wimbush & Dalton 1997; Coutts & Jann 2011). Work on improving UCT's statistical efficiency is ongoing (e.g., Blair & Imai 2012). Our results demonstrate the UCT is well suited to investigating noncompliance in conservation. The high levels of self-reported understanding, respondents' willingness to participate in the survey, and low reported levels of discomfort could be understood as signs of trust in the technique. Nevertheless, the respondents' education level affected their likelihood of reporting hunting and perceived anonymity was low, probably due to people being questioned face to face by interviewers from their own or neighboring villages.

The disadvantages in using indirect rather than direct questioning include the increased complexity of data analysis, requirement for higher sample sizes, potentially high standard errors, and the limited form that questions can take (questions that require a yes or no answer or questions that involve comparable, or mutually exclusive, options). Moreover, the results are still likely to underestimate actual noncompliance because there will still be participants who give evasive responses regardless of the survey instrument.

Most evaluations of conservation interventions are based on attitudes and behavioural intentions, but change in actual behaviour is a much more pertinent measure of conservation success (Holmes 2003). Part of the reason actual and reported behaviours are so rarely quantified may be the difficulty in measuring sensitive behaviours. We describe an approach to obtaining information on involvement in poaching that can be applied in mainly illiterate communities and administered by local interviewers, factors that may promote local participation in monitoring. This suggests the technique may have wider application in developing countries, where resources for conservation are especially scarce (Danielsen *et al.* 2003). Furthermore, transparent and robust conservation decisions require full consideration of multiple types of uncertainty including observation uncertainty (Bunnefeld, Hoshino, & Milner-Gulland 2011). Conceptual and methodological frameworks that explicitly consider uncertainty, such as adaptive management (Keith *et al.* 2011) and management strategy evaluation (Bunnefeld, Hoshino, & Milner-Gulland 2011), would benefit from approaches such as we used here, which explore the different sources of bias in the observed data and disentangle the survey processes from the actual effects of interest.

5. Trade-offs in effectiveness and efficiency when monitoring abundance trends under uncertainty

5.1. Introduction

Monitoring is an essential tool in natural resource management and conservation, used to trigger interventions, inform decisions, measure success against stated objectives, and learn about the system (Yoccoz, Nichols, & Boulinier 2001; Lindenmayer *et al.* 2012). Monitoring aims to draw inferences about changes in the observed system over time (Yoccoz, Nichols, & Boulinier 2001) and, in order to be useful, must be able to detect true trends over time while balancing cost-effectiveness and efficiency (Kinahan & Bunnefeld 2012). In some cases, time, budget and observational constraints may even mean that managers may be better off allocating resources to other interventions instead of monitoring (Field, Tyre, & Possingham 2005; McDonald-Madden *et al.* 2010). Monitoring effectiveness and efficiency are thus key considerations when planning and implementing conservation interventions (Nichols & Williams 2006).

The importance of detecting changes at appropriate spatial and temporal scales and with adequate confidence levels has often been emphasized (Field *et al.* 2004; Jones 2011) but a number of factors may affect monitoring effectiveness, ultimately affecting management decisions and their robustness to uncertainty. For example, the time frame over which change can reliably be detected might not match that required for management (Maxwell & Jennings 2005), monitoring effort may not be enough or appropriately targeted to detect trends (Brashares & Sam 2005; Katzner, Milner-Gulland, & Bragin 2007), sampling design may not be optimal (Blanchard, Maxwell, & Jennings 2008) and different estimates of population change might be obtained using different analytical methods (Thomas & Martin 1996). The degree of environmental and demographic stochasticity also affects the quality and reliability of monitoring data (Hauser, Pople, & Possingham 2006; Rhodes & Jonzén 2011).

In the face of limited resources in conservation, monitoring is generally constrained by budgets and varies with the manager's willingness to accept different error types (Field *et al.* 2004; Lindenmayer *et al.* 2012). For example, type I errors (α; rejecting the null hypothesis when it is true, such as when a species is reported to be declining but is actually stable) may cause unnecessary restrictions and waste resources, while type II errors (β; failing to detect a difference that is present, such as concluding that a species is stable when is actually declining) could mean failing to implement required management interventions and potentially cause irreversible damage by allowing the species to go extinct (Brosi & Biber 2009). Other potential types of error, rarely considered when planning and evaluating monitoring programmes, are: type III errors (correctly rejecting the null hypothesis but incorrectly inferring the direction of the effect; Morrison 2007), and misidentifying the shape of the population trajectory (e.g. by only fitting linear models when trends are non-linear) despite the potential use of shapes of trends to identify threatening processes (Mace *et al.* 2008; Di Fonzo, Collen, & Mace 2013).

While uncertainty is recognized as a feature of conservation and natural resource management (Regan, Colyvan, & Burgman 2002; Harwood & Stokes 2003), its multiple types and sources are rarely formally considered in decision-theoretic approaches for planning and implementing interventions. However, different monitoring decisions may be required under diverse types and degrees of uncertainty and these will ultimately affect the prevalence of different error types. For example, Hauser, Pople, & Possingham (2006) suggested that monitoring is only needed every second year when environmental conditions are similar to the average but that yearly monitoring is needed when the effect of extreme events (e.g. rainfall, drought) on population dynamics is less predictable. Thus, monitoring needs to be tailored in order to correctly detect trends not only when wildlife is subject to relatively deterministic processes due to poaching, but also when affected by highly uncertain processes, such as climate change, and unexpected processes. These different types of process are one reason for investing both in hypothesis-driven targeted monitoring and non-targeted surveillance monitoring (Wintle, Runge, & Bekessy 2010).

Long-term research in the Serengeti includes monitoring of a range of species, with wildlife censuses having been conducted since the 1950s (Sinclair *et al.* 2007). Poaching (Loibooki *et al.* 2002), encroachment (Mbano *et al.* 1995), climate change (Ritchie 2008) and development of infrastructures, such as a commercial highway (Holdo *et al.* 2011), have been suggested as current or potential threats to this system. Poaching by local communities and environmental variability have been described as major sources of uncertainty in the system and observation error affects wildlife abundance estimates (Pascual & Hilborn 1995, Chapters 3 and 5). Using monitoring of two contrasting ungulate species and multiple scenarios of population change in the Serengeti ecosystem as a case study, we used a 'virtual ecologist' approach (Zurell *et al.* 2010) to investigate monitoring effectiveness and efficiency under uncertainty. Specifically, we explored interactions between different types of error (I, II, III and shape) when monitoring changes in population abundance. We also explored how these interactions vary depending on budgetary, observational and ecological conditions.

5.2. Methods

5.2.1. Study area and species

We chose two ungulate species to investigate contrasting issues determining the effectiveness and efficiency of monitoring in savannah ecosystems. The migratory wildebeest population (*Connochaetes taurinus*), currently numbering around 1.3 million animals (Hilborn & Sinclair 2010), has been extensively studied over the last 60 years (Mduma, Sinclair, & Hilborn 1999). The wildebeest use the Serengeti plains during the wet season (mid-October to end of April), moving west and north at the beginning of the dry season (May to mid-October) and giving birth synchronously in February (Thirgood *et al.* 2004). The importance of the wildebeest migration has often been demonstrated, both for its ecological significance and as a source of tourism revenue (Norton-Griffiths 2007; Kaltenborn, Nyahongo, & Kideghesho 2011; Holdo *et al.* 2011). The resident population of impala (*Aepyceros melampus*) found in the Grumeti-Ikorongo Game Reserve (Figure A1 in Appendix A) has received considerably less attention, but represents a suite of resident ungulate species important both for local livelihoods as bushmeat, and as constituents of the Serengeti mammal fauna. Currently, there are around 12,000 impala in the game reserve (Grumeti Fund 2012).

5.2.2. Methodological framework

The modelling framework was divided into four main components (Figure 5.1): (a) an "operating model" which produced the “true” population dynamics under different scenarios of population change; (b) an “observation model” which simulated monitoring of wildlife populations over time; (c) the "assessment model" which simulated a manager's estimation of trends of wildlife abundance based on the simulated monitoring data,; and (d) an evaluation of monitoring effectiveness and efficiency, in which discrepancies between “true” and “observed” trends and their drivers were investigated.

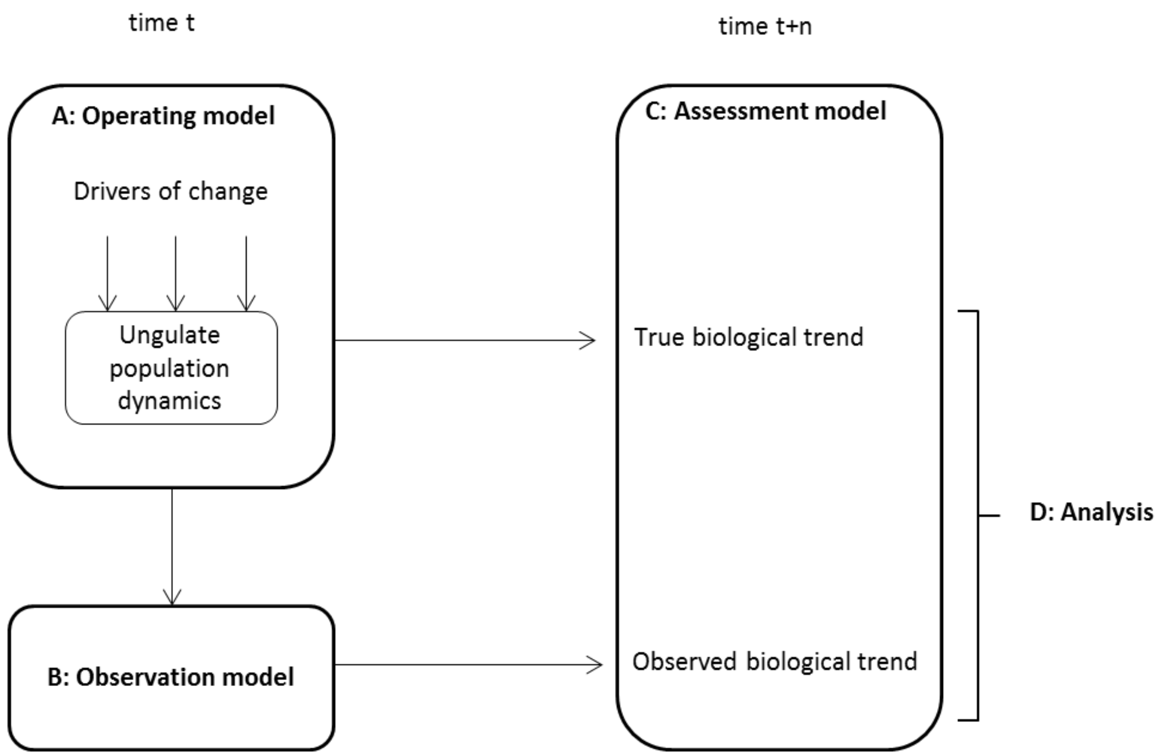

Figure 5.1. Conceptual description of the study's methodological approach. The "operating model" (A) produces the "true" population dynamics under different scenarios of population change; the "observation model" (B) simulates monitoring of wildlife populations over time *t* during *n* number of years; the "assessment model" (C) estimates trends of wildlife abundance from simulated monitoring data; and "analysis" (D) assesses monitoring effectiveness and efficiency.

5.2.3. Operating model

Ungulate population dynamics

We used post-breeding, age-structured two-sex matrix models to represent ungulate population dynamics (Caswell 2001). The models include juveniles (< 1 year old), yearlings (2nd year), adults (> 2 years old), and senescent adults (impala: ≥ 8 years; wildebeest: ≥ 14 years). The matrix model was parameterised using vital rates from studies on wildebeest (Mduma, Hilborn, & Sinclair 1998; Mduma, Sinclair, & Hilborn 1999; Owen-Smith 2006), impala (Jarman & Jarman 1973; Fairall 1983; Owen-Smith, Mason, & Ogutu 2005) and general ungulate life-history (Gaillard *et al.* 2000). The models account for polygynous mating behaviour (Caswell 2001) and the effects of dry-season rainfall and density-dependence on ungulate mortality (Gaillard, Festa-Bianchet, & Yoccoz 1998;

Mduma, Sinclair, & Hilborn 1999; Gaillard *et al.* 2000; Owen-Smith 2006). The structure and parameterization of these models is fully described in Appendix C.

Drivers of change

To investigate the ability of monitoring robustly to detect population trends under a number of types of threat, we considered that both ungulate populations were potentially affected by three types of process and used simplified scenarios to illustrate realistic conditions of change under which monitoring may be conducted:

1. Harvest

Illegal hunting occurs throughout the Serengeti (Loibooki *et al.* 2002) but its prevalence is highly uncertain (Chapter 4). Snaring is the main hunting method in the area (Holmern *et al.* 2006). Despite this technique being mostly non-selective, male bias in wildebeest offtake due to behavioural factors has often been suggested, with reported male selectivity ranging from 138% to 148% (i.e. the proportion of males in the harvest offtake is 38-48% higher than in the population; Georgiadis 1988; Hofer, East, & Campbell 1993; Holmern *et al.* 2006). The estimates of annual wildebeest offtake in the Serengeti range from 40 000 to 129 000 animals (Mduma, Sinclair, & Hilborn 1999; Rentsch 2011), corresponding to 3-10% of the current population size.

In the poaching scenario, we assumed a 10% harvest rate for wildebeest, to be precautionary, and a 5% rate for impala, which is less heavily targeted by poachers (Rentsch 2011). We assumed a rate of 143% male selectivity in wildebeest offtake, the median of the published estimates.

2. Climate change affecting rainfall trends and variability

In sub-Saharan Africa, the predicted primary effect of global climate change is on precipitation but there still remains much debate as to which areas will receive more or less rainfall (Hulme *et al.* 2001). Global climate models predict that annual rainfall will increase in East Africa but several studies have suggested that there will be a great deal of regional variation (Ogutu *et al.* 2008; Mango *et al.* 2011; Dessu & Melesse 2012). Ritchie (2008) suggested that the Serengeti will experience decreased and less variable rainfall and that overall rainfall has decreased by approximately 25% over the past 50 years.

In the climate change scenario, the dry-season rainfall mean (148mm) and the dry-season rainfall variability, expressed by its standard deviation (SD=69mm), were assumed to decrease exponentially (rate of annual change: -0.006), resulting in a cumulative 26% decrease over the 50 years of the simulation.

3. Changes to vital rates

Vital rates may be affected by a number of processes, such as encroachment and habitat fragmentation. For example, landscape fragmentation can lead to reduced population growth and a lower carrying capacity for migratory ungulates (Hobbs *et al.* 2008) and the proposed commercial highway in the Serengeti could affect the ability of migratory animals to effectively track high-quality forage resources across the landscape (Holdo *et al.* 2011). However, these processes often occur unexpectedly and their effects are poorly understood.

In this scenario, we used potential impacts of a proposed road crossing the Serengeti (Holdo *et al.* 2011) to illustrate change in vital rates. We assumed consecutive declines in juvenile survival, yearling fecundity, adult fecundity and adult survival (Gaillard *et al.* 2000) which started 3 years apart and then continued for the rest of the simulation at exponentially increasing rates (annual rate of change = -0.002), resulting in an approximately 10% decrease in vital rates over 50 years.

Changes to the parameters were applied after the initial transient dynamics in the baseline scenario (without any threats) and we ran 10,000 replicates of the operating model for each of the scenarios, producing estimates for “true” trends of population abundance, and their associated uncertainties, under the three different sets of conditions. Five pre-threat and 50 post-threat years of each simulation and iteration were used as outputs.

5.2.4. Observation model

We simulated the monitoring of the “true” wildlife abundance obtained from the operating model. In the Serengeti ecosystem, migratory wildebeest are monitored through Aerial Point Sampling (APS) and impala using Systematic Reconnaissance Flight (SRF) surveys (see Chapter 3 for a description of the monitoring procedure and wildlife observation model). Monitoring was assumed to be carried out using the current methods and we simulated the effects of low and high monitoring budgets as defined in Chapter 3.

Unstandardized estimates of precision (measured as the coefficient of variation; CV) and accuracy (percent discrepancy between the mean estimated population size and the simulated known population size) were taken from Chapter 3 (Tables A2 and A3). These estimates were obtained by fitting generalized linear models to simulated precision and accuracy as a function of multiple sources of observation uncertainty for wildebeest and impala monitoring, such as sampling effort, ecological features and animal detectability (see Chapter 3 for a full description). Values of bias and CV were then used to obtain “observed” abundance from “true” abundance for each simulation and iteration.

5.2.5. Monitoring scenarios

Monitoring was simulated under different conditions of survey frequency (every 1, 3 or 5 years), monitoring length (5, 10, 25 or 50 years), observation error (none, low or high as produced by monitoring budgets defined in Chapter 3 and starting point (how long before or after the threat started did monitoring begin; 5 years before, at the same time as the threat started, or 5 years after).

To minimize the influence of simulation variability on any comparisons between different monitoring options, we generated complete data sets under maximum monitoring frequency (yearly) and length (50 years) for each simulated scenario. All monitoring designs were then applied by subsetting the complete data set under specific conditions. We assumed that at least 3 data points would be needed for trend assessment so monitoring was annual if it was conducted only for 5 years and done annually or every 3 years if it was conducted for 10 years.

5.2.6. Assessment model

The assessment model simulated the process of trend estimation from wildlife abundance data. Generalized additive models with a normal error distribution and identity link were fitted to the observed and "true" data, smoothing the time series of abundance using the package mgcv version 1.7-22 in R v.2.15.2 (The R Foundation for Statistical Computing 2012). We modelled the year effect as a cubic smoothing spline with 3 d.f. (given the length of the time series and our interest in trends instead of short-term fluctuations), as a linear term or as a constant (null model). Gamma was set to 1.4 to include a penalty for each additional degree of freedom within the model and prevent model overfitting (Wood 2006). Selection of the most parsimonious model was performed using the Akaike Information Criterion corrected for small sample size (AICc). We considered that non-null models would be acceptable instead of null models, and non-linear instead of linear, only if $\Delta AIC \geq 4$; $\Delta AIC \geq 4$ indicates considerably less support for the alternative model (Burnham & Anderson 2002). We averaged model weights for each trend type over all the iterations and, based on the most parsimonious models, quantified how many of the 10,000 replicates showed decreasing or increasing trends for each trend type. To identify the direction of the trend, we used the sign of the slope if year was fitted as a linear term, or the sign of the mean annual change in smoothed population size if year was fitted as a smoothing factor (Collen *et al.* 2011).

5.2.7. Analysis of monitoring effectiveness and efficiency

We investigated differences between "true" and estimated trends as a function of different ecological and monitoring conditions by quantifying different types of error for each scenario. Type I errors (α) were quantified as the percentage of the 10,000 replicates in which a negative or positive trend was detected in the "observed" data but the trend from the "true" data was actually stable (i.e. the null model was the most parsimonious model). Type II errors (β) were quantified as the percentage for which no significant trend was detected in the "observed" data although this was present in the "true" data. A subset of the type II error (β_2) represented the worst case in which negative trends were not detected, despite their presence. Type III errors (γ) were quantified as the percentage of cases in which a trend in the "observed" data was identified in the opposite direction to that in the "true" data. "Shape errors" were quantified as the percentage of non-null cases in which we identified a linear trend as non-linear and vice-versa.

To investigate the effect of monitoring conditions on the prevalence of each type of error, we fitted generalized linear models with a quasibinomial error distribution (to account for overdispersion) and a logit link to the simulation results (i.e. the number of times a certain error type occurred out of 10,000 simulations). Relevant two-way interactions were included.

The monitoring budgets were calculated by multiplying current unitary costs from itemized monitoring expenses in the study area for wildlife surveys (J.G.C. Hopcraft, unpublished data). Inflation, technological advancements and discount rates are expected to affect future expenses but are generally unknown; thus, we kept current costs to simulate into the future. The total costs for each monitoring scenario were expressed relative to the baseline scenario.

5.3. Results

5.3.1. Baseline scenarios: "true" population trends under different threat conditions

Under the "no threat" scenario and the baseline parameterization of the biological models (Table C1 in Appendix C), wildebeest and impala generally stabilised at around 1.4 million animals and 14,000 animals, respectively. Other studies in the Serengeti have indicated similar carrying capacities for wildebeest (1.2-1.5 million; Mduma, Sinclair, & Hilborn 1999; Holdo *et al.* 2011) and the impala population in the game reserve has been stabilizing around 12,000 animals (Grumeti Fund 2012), suggesting that our biological model produces relatively realistic carrying capacities.

Declines were greatest in the scenarios of poaching and vital rate change, with both species declining, on average, by 43-69% in 50 years (Figure 5.2). On average, non-linear models had greater support than linear and null models for all the scenarios but impala and wildebeest populations showed differences in the prevalence of the shape and direction of abundance trends depending on the threat type (Table 5.2). The wildebeest populations generally declined non-linearly in response to all threats, although 37% of populations declined linearly in response to changes in vital rates. Most impala populations declined non-linearly in response to the effects of change in vital rates. In response to poaching, about half of the impala simulations showed non-linear declines and half linear declines. The shape and direction of the effects of climate change on impala were more uncertain; 15% of populations remained stable or increased while the others decreased, on average by 31% over the 50 years.

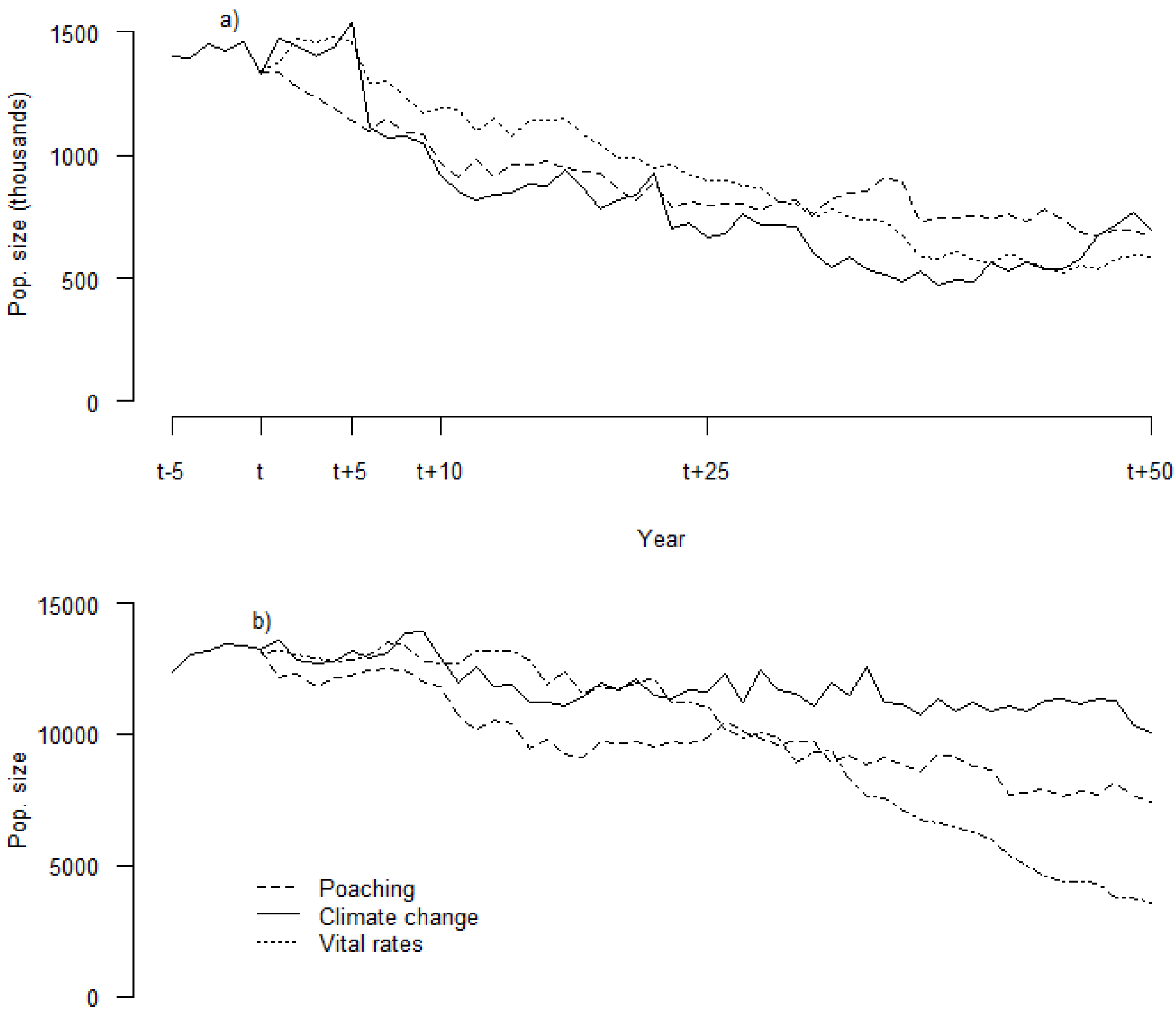

Figure 5.2. Mean population sizes (10,000 simulations) of: a) wildebeest and b) impala under each threat scenario. The starting point at which threat starts occurring is shown by *t*.

Table 5.1. Average Akaike model weights per trend type (N: null; L: linear; NL: non-linear), prevalence (percentage of 10,000 simulations) of best-fit models and trend direction (increasing ↑ or decreasing ↓), and average total change (%) per trend direction over 50 years for each threat scenario for the "true" abundance of wildebeest and impala.

Threat scenario	Ungulate species					
	Wildebeest			Impala		
	Average weights	Prevalence	Average total change	Average weights	Prevalence	Average total change
None	N: 0.22 L: 0.29 NL: 0.49	N: 57 L: ↑9, ↓23 NL: ↑9, ↓3	0	N: 0.03 L: 0.11 NL: 0.86	N: 7 L: ↑11, ↓11 NL: ↑48, ↓22	0
Poaching	N: 0 L: 0 NL: 1	N: 0 L: ↑0, ↓0 NL: ↑0, ↓100	↓50%	N: 0 L: 0.22 NL: 0.78	N: 1 L: ↑0, ↓50 NL: ↑0, ↓49	↓43%
Climate change	N: 0 L: 0 NL: 1	N: 0 L: ↑0, ↓0 NL: ↑0, ↓100	↓40%	N: 0.02 L: 0.15 NL: 0.83	N: 6 L: ↑4, ↓28 NL: ↑5, ↓57	↓27%
Effect on vital rates	N: 0 L: 0.15 NL: 0.85	N: 0 L:↑0, ↓37 NL: ↑0, ↓63	↓63%	N: 0 L: 0.03 NL: 0.97	N: 0 L: ↑0, ↓7 NL: ↑0, ↓93	↓69%

5.3.2. The prevalence of different error types according to threat scenario and species

Under the best monitoring conditions (i.e. 50 years of data collected annually with high monitoring budgets resulting in CVs around 0.15 for wildebeest and 0.23 for impala), the prevalence of different error types was affected by the specific threat conditions and their impacts on population abundance, structure and trajectory (Table 5.2).

The occurrence of type I errors, when a negative or positive trend is detected in the "observed" data but the trend in the "true" data is actually stable, was very low for all threat scenarios ($\alpha \leq 0.02$, Table 5.3). Similarly, type III errors (identifying a trend in the "observed" data with an opposite direction to that in the "true" data) were low ($\gamma \leq 0.03$) for both the impala and wildebeest populations, although 82% of type III errors related to the more serious situation in which a negative trend was observed as positive.

Type II errors, failing to find a significant trend in the "observed" data although this was present in the "true" data, were relatively low for wildebeest ($\beta \leq 0.34$) but higher for impala ($\beta \leq 0.76$), except in the scenario of change in vital rates in which both species had similar low levels (Table 5.2). Moreover, 90% of the type II errors involved negative trends being undetected. Reporting the wrong trajectory shape, i.e. identifying a linear trend as non-linear and vice-versa, was common for all threat scenarios; in average, 46% of the non-null trends were misclassified, 96% of which were identified as linear but were actually non-linear.

Table 5.2. Prevalence of different error types (out of 10,000 simulations) for each threat scenario from the "observed" wildebeest and impala data, monitored annually over 50 years with a high monitoring budget.

Threat scenario	Ungulate species	
	Wildebeest	**Impala**
None	α: 0.02 β: 0.34 β_2: 0.20 γ: 0.01 "shape": 0.16	α: 0 β: 0.76 β_2: 0.26 γ: 0.02 "shape": 0.51
Poaching	α: 0 β: 0 β_2: 0 γ: 0 "shape": 0.55	α: 0 β: 0.35 β_2: 0.35 γ: 0 "shape": 0.50
Climate change	α: 0 β: 0 β_2: 0 γ: 0.03 "shape": 0.15	α: 0 β: 0.66 β_2: 0.59 γ: 0.01 "shape": 0.58
Change in vital rates	α: 0 β: 0 β_2: 0 γ: 0 "shape": 0.52	α: 0 β: 0 β_2: 0 γ: 0 "shape": 0.68

5.3.3. The effect of monitoring conditions on the prevalence of different error types

The occurrence of type I and type III errors was unaffected by any of the monitoring conditions (frequency, length, observation error and starting point), given the threat scenarios considered in this study, generally remaining at very low levels (Table 5.3). Increasing monitoring length did not significantly affect the occurrence of different types of errors; changing the monitoring length tended to change the shape, direction and magnitude of the true trends, offsetting the expected benefit of increasing monitoring length. For example, if monitoring was conducted for only 5 years after the threat, virtually no errors were found because the "actual" trend, to which observed trends were compared, was identified as stable.

Type II and shape errors were more likely to occur when surveys were conducted with observation error or less frequently. The effects of the level of observation error were, however, strongly conditioned on survey frequency and length of the monitoring period (Table 5.3): as surveys were conducted more frequently or monitoring length increased, the importance of observation error in determining the ability of monitoring to detect trends correctly increased. For example, in order to detect true negative trends in wildebeest numbers more than 80% of the time over a 50 year period, one would have to monitor with no observation error every 3 years or with low error every 2 years (Figure 5.3). Starting monitoring 5 years before or after the actual threat started only affected the probability of occurrence of type II errors; fewer negative trends went undetected when monitoring started 5 years before, although this effect was less important as monitoring length increased.

Characteristics related to threat type and species explained some of the differences in the likelihood of type II and shape errors. Impala populations were 1-5% more likely to present these errors than those of wildebeest, while keeping all the other variables constant. Threat scenarios were only 4-5% more likely to have shape errors than the "no threat" scenario but the likelihood of failing to detect a negative trend (subset of the type II error; β_2) was 7-15% higher in threat scenarios than in the no threat scenario.

Table 5.3. Parameter logit estimates from the full generalised linear models with a quasibinomial error structure and logit link function. The table shows the coefficients of all parameters and interactions from the full model. Dependent variable is the presence or absence of a given error type (based on the most parsimonious model selected using AIC). Significance is coded as ***P < 0.001, **P < 0.01, *P < 0.05. [a] The intercept includes the "no threat" scenario for wildebeest, with monitoring conducted with low observation error and starting when the threat starts.

Independent variables	Error types				
	Type I	Type II	Type IIa	Type III	Shape
Intercept (Threat: none) [a]	-7.872	-2.051***	-3.274***	-8.919	-2.790***
Length	0.120	0.011	0.010	0.128	0.031
Frequency (years between surveys)	3.380	0.282***	0.318***	2.823	0.170**
Starting point					
5 yrs before	-0.442	-0.641**	-0.270*	-0.290	-0.047
5 yrs after	-0.222	0.455*	0.463	-0.644	-0.269
Observation error					
None	-4.107	-3.222***	-3.537***	-23.662	-1.777***
High	-0.154	0.137*	0.176*	0.121	0.110*
Threat					
Poaching	-1.190	0.139	1.339***	0.593	0.692***
Climate change	-0.810	0.073	1.166***	0.356	0.580***
Vital rates	-1.102	-0.010	1.072***	0.431	0.650***
Species					
Impala	0.887	0.393***	0.346***	0.368	0.169*
Length x Frequency	-0.139	-0.002	-0.003	-0.111	-0.003
Length x Observation					
None	-0.0701	-0.045***	-0.054***	0.402	-0.017**
High	-0.0003	0.015**	0.016**	0.003	0.002
Frequency x Observation					

None	3.709	0.894***	0.998***	2.592	0.453***
High	0.063	-0.100*	-0.116*	0.073	-0.041
Length x Starting point					
5 yrs before	-0.006	-0.017**	-0.008*	-0.009	-0.009
5 yrs after	0.002	-0.011*	-0.011	-0.002	0.004

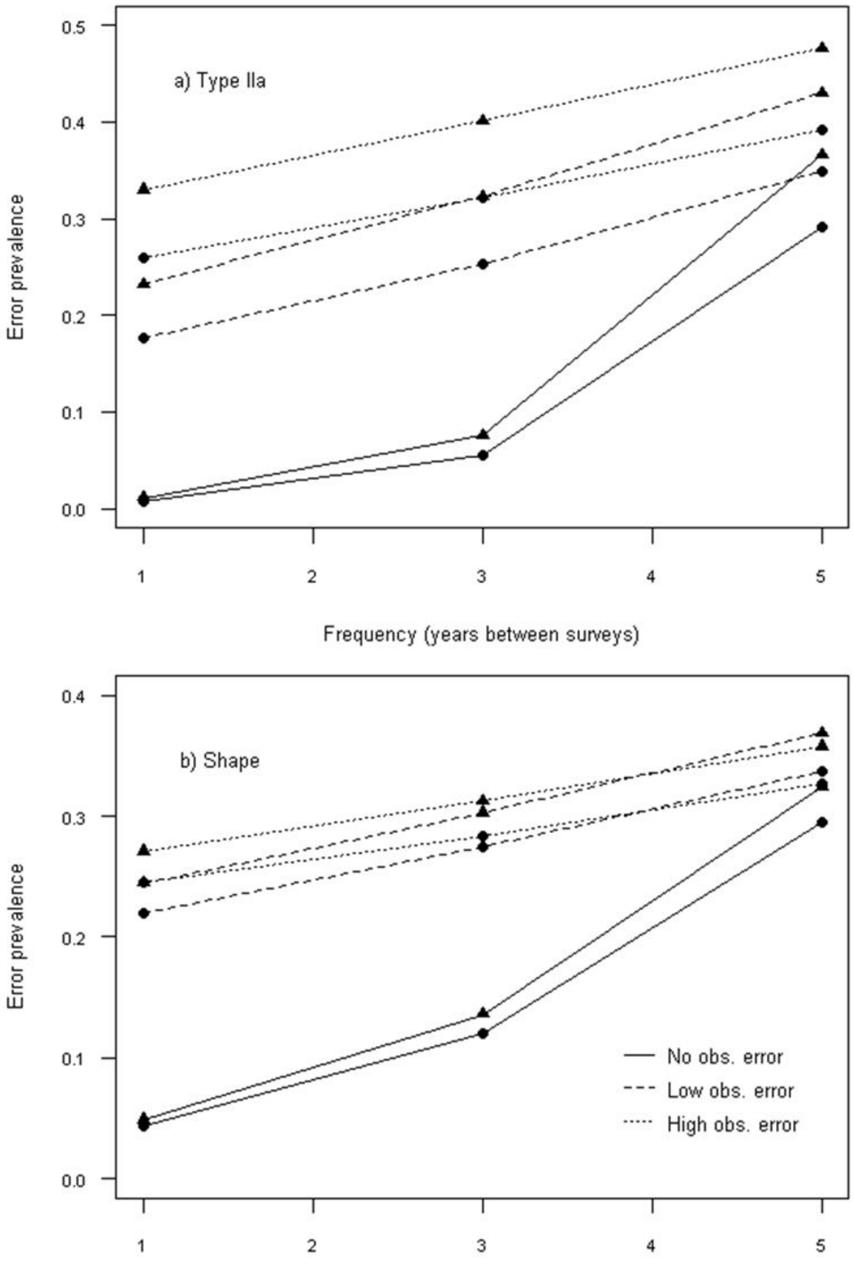

Figure 5.3. Effect of survey frequency and observation error on the occurrence of a) type IIa errors (negative trends being undetected), and b) shape errors for wildebeest (circles) and impala (triangles).

5.3.4. Trade-offs between monitoring effectiveness and efficiency

Negative trends would go undetected 32% or 2% of the time in impala and wildebeest populations, respectively, if conducting annual surveys over 50 years with a low observation error (Figure 5.4). A reduction in budget leading to reduced survey frequency and higher observation error would increase the likelihood of not detecting negative trends and misclassifying the shape of trends (Table 5.3). For example, when compared to the total costs of conducting annual surveys for 50 years with low observation error, conducting surveys only every 5 years and with higher levels of observation error would save up to 90% of the budget, but negative trends would not be detected more than 80% of the time (Figure 5.4).

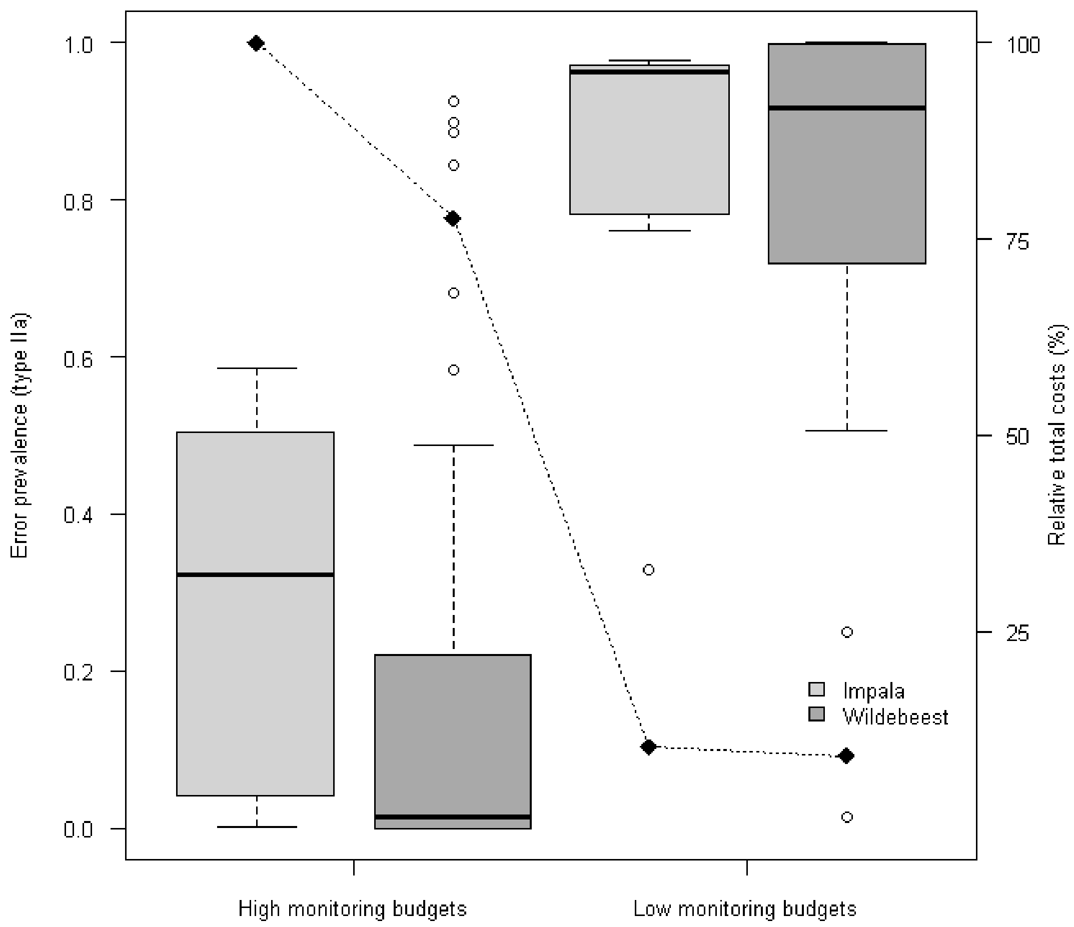

Figure 5.4. The potential effects of monitoring costs scenarios (high budgets: low observation error and annual surveys; low budgets: high observation error and surveys every 5 years) on the prevalence of type IIa errors (negative trends not being detected) and relative total costs (diamonds) when monitoring is conducted for 50 years for wildebeest and impala populations.

5.4. Discussion

In this study, we have considered the effects of budgetary, observational and ecological conditions on monitoring effectiveness and efficiency. We used population and observation models parameterised for two contrasting ungulate species in the Serengeti ecosystem, linked to realistic scenarios of population change and monitoring conditions to explore the impacts of these conditions on different types of error (I, II, III and shape) in detecting abundance trends. Under the simulated conditions, the occurrence of type I (a negative or positive trend is detected in the "observed" data but the trend from the "true" data is actually stable) and type III (identifying a trend in the "observed" data with an opposite direction to that in the "true" data) errors were generally very low for both populations. Higher observation error and conducting surveys less frequently increased the likelihood of not detecting trends and misclassifying the shape of the trend but the differences between multiple levels of observation error decreased for higher monitoring length and frequency. Greater investment in monitoring considerably decreased the likelihood of failing to detect significant trends, particularly for wildebeest.

Using a "virtual ecologist" approach, we have linked changes in population abundance and structure caused by simulated realistic conservation threats to specific monitoring effectiveness outcomes. Different types and rates of human pressure are likely to produce different shapes of declines in wildlife population abundance (Mace *et al.* 2008). For example, di Fonzo, Collen, & Mace (2013) showed that wildlife population declines curves can be used to distinguish between broad categories of pressure or threat types, although not for detailed threat attributions. Our results suggest the need to better understand the effects of monitoring conditions on our perceptions of observed trends before we can make any inferences about processes. Although we used a simple linear vs. non-linear distinction, we showed that misclassifying the shape of trends, particularly classifying non-linear trends as linear, was common under realistic ecological and monitoring conditions. As the prevalence of non-linear trends was affected by threat type and monitoring length, the linkages between specific conservation threats and their impacts on population abundance and structure must be better understood and taken into consideration when designing monitoring programmes. In addition, the trajectory and magnitude of the threats themselves may vary with time and location (Mace *et al.* 2008; Spangenberg *et al.* 2012), so it is critical to assess their impacts on specific populations across time and space, and integrate this information within monitoring design. Otherwise trends in abundance may be mistakenly assumed to represent underlying threat or biological processes, when in fact they are artefacts of the observation process.

Different factors might affect the monitoring of multiple species and groups within wildlife populations. In the Serengeti, monitoring of highly aggregated species, such as wildebeest, is improved by increasing survey precision by defining sampling effort according to wildlife spatial distribution, while for random or slightly aggregated species, such as impala, accuracy is the key factor, being most sensitive to observer effects (Chapter 3). By linking this information with two-sex age-structured models representing population dynamics of wildebeest and impala in the Serengeti, we are able to produce monitoring advice within an integrated modelling framework. For example, if monitoring in the Serengeti is conducted with the current survey frequency (approximately every 3 years; TAWIRI 2010) and low observation error, negative trends in wildebeest and impala populations might go undetected approximately 23% or 30% of times, respectively. A reduction in monitoring budgets by 66%, leading to higher observation error and surveys being conducted less frequently, could increase this likelihood up to 50%, in which case monitoring would simply be a waste of resources. Our results also suggest that the likelihood of not detecting negative trends would be particularly high in scenarios of climate change for impala, and that the implications of this change are also more uncertain for this species. These findings can be used to interpret the data on ungulate population abundance being currently collected in the study area and to aid decisions on budget allocation. This is particularly relevant given the internationally expressed importance of identifying robust and reliable monitoring targets, such as CBD Aichi targets, that can be used to infer declines in specific populations and biodiversity in general (Collen *et al.* 2009; Porszt *et al.* 2012).

While type II errors, failing to detect effects, may result in serious consequences to the environment, type I errors, incorrectly rejecting the null hypothesis, would result in unnecessary restrictions and waste of resources; much more attention is given, however, to type I errors (Field *et al.* 2004; Brosi & Biber 2009). Our results suggest that, when monitoring abundance of wildebeest and impala in the Serengeti under the simulated threat conditions, the type I error rate is low and unaffected by most forms of uncertainty. This means that reports of population decline in the system are very unlikely to be wrong, suggesting that this information should be promptly used to inform management decisions.

Linear models are commonly applied to population trend assessment (Thomas 1996) but most populations naturally exhibit complex non-linear dynamics (Clutton-Brock *et al.* 1997). Distinguishing these natural dynamics from impacts caused by multiple threats and how they interact in time and space is critical for assessing the actual effects of human activities on wildlife (Collen *et al.* 2011). In addition, decline shapes may be varied (e.g. linear, quadratic and exponential) and may be used to identify broad categories of pressure (Di Fonzo, Collen, & Mace 2013). However, our study shows that making a correct the distinction between linear and non-linear trends may be challenging.

We used simplified scenarios of population change to simulate conditions under which trends should be detected. The effects of different conservation threats, acting independently and together, on monitoring effectiveness should be further explored under a range of scenarios to investigate the sensitivity of population trends and trajectory shape between threat types. Additionally, an iterative decision-making model could be developed, in which monitoring decisions would be updated according to knowledge obtained from past monitoring. Applying the concept of "learning by doing" from adaptive management (Keith *et al.* 2011), this would allow us to narrow down the range of possible processes that could be producing the shapes and trends concerned. A process of adaptive monitoring in which multiple monitoring strategies are implemented and adapted in response to data collected during the monitoring programme itself could also be developed (Lindenmayer & Likens 2009). Finally, we could investigate the interactions between monitoring uncertainties and management decisions using a management strategy evaluation (MSE) framework, which tests the robustness of decisions to a range of uncertainties by modelling the whole system (Bunnefeld, Hoshino, & Milner-Gulland 2011).

Most biological surveys are constrained by observational and economic constraints which affect the way resources can be allocated (Field, Tyre, & Possingham 2005). The implications of monitoring under less than perfect conditions are, however, often unknown and given little consideration in the design of monitoring programmes worldwide. As shown in this study, the likelihood of not detecting negative trends and misclassifying shapes may be too high to be ignored. Addressing these monitoring issues may, however, be too expensive or not worthwhile within the broader management strategy for a species or system. Uncertainty mitigation efforts must be focused on the kinds of information which are most valuable and make a meaningful difference to our understanding of processes, and to the way we manage threats (Wintle, Runge, & Bekessy 2010; Runge, Converse, & Lyons 2011; Runting, Wilson, & Rhodes 2013). Decision-theoretic approaches which incorporate these trade-offs are essential to support more effective conservation interventions, providing clear and transparent advice for conservation decision-making (McDonald-Madden *et al.*

2010; Chee & Wintle 2010), and ultimately promoting the efficient use of the scarce conservation resources available (Mackenzie 2009).

6. Managing social-ecological systems under uncertainty: implementation in the real world

6.1. Introduction

Traditional approaches to natural resource management and conservation often assume that managers can accurately predict system responses to their actions and to external drivers (Walker *et al.* 2002). However, social-ecological systems behave as complex adaptive systems composed of multiple interacting agents (Walker & Janssen 2002) and uncertainties might be large and diverse (Harwood & Stokes 2003; Fulton *et al.* 2011). The implementation of successful actions is, thus, challenging; the achieved outcomes are sometimes very different from those expected (Armsworth *et al.* 2006) and, despite the widespread biodiversity loss and threats to many ecosystems (Cardinale *et al.* 2012), planned interventions are often not even implemented (Arlettaz *et al.* 2010). The translation of science and policy into practice still lags behind conservation needs and expectations (Knight *et al.* 2008) and understanding what constrains conservation implementation is an essential step towards achieving successful outcomes.

A "great divide" between science and action has often been described as a major barrier to achieving successful conservation outcomes (Pullin *et al.* 2004; Knight, Cowling, & Campbell 2006). Several reasons have been suggested for the existence of this research-implementation gap, such as the lack of communication and engagement between researchers and practitioners, absence of commitment by researchers themselves to engage in conservation implementation and insufficient consideration of social dimensions (Knight *et al.* 2008; Arlettaz *et al.* 2010). However, even when researchers and practitioners work together, challenging institutional settings, lack of economic, social and political support, and poor governance (referring to the processes and institutions through which societies make decisions; Armitage et al. 2012), may jeopardize implementation (Young 1998; Arlettaz *et al.* 2010). For example, institutional complexity has been suggested as a driver of inefficient use of resources and intervention ineffectiveness when addressing desertification in Mediterranean countries (Briassoulis 2004). These institutional and implementation uncertainties, related to the translation of policy into practice and arising from interactions between different groups and the different sets of rules governing their behaviour (Cochrane 1999; Bunnefeld, Hoshino, & Milner-Gulland 2011), may greatly affect conservation outcomes and managers' ability to design effective strategies (Young 1998; Harwood & Stokes 2003; Fulton *et al.* 2011).

To better understand and improve conservation implementation, it is necessary to assess the social-ecological structure and dynamics of the systems under consideration, as well as eliciting the perspectives of multiple actors (Knight, Cowling, & Campbell 2006; Ban *et al.* 2013). There can be several people undertaking conservation actions, often with divergent or only partially overlapping objectives, and individual differences in perspectives are often one of the reasons for conflict impeding successful interventions (Adams *et al.* 2003; Redpath *et al.* 2013). Identifying areas of agreement and disagreement between actors helps in understanding and overcoming obstacles between them; it provides insights about the perceived probability of particular outcomes from ongoing and potential interventions, and people's willingness to accept these outcomes (Biggs *et al.* 2011). Additionally, assessing the way these actors perceive institutional interactions may provide insights into how the system works, decision-making processes and the potential constraints to successful conservation action.

This understanding is at the core of the development and implementation of more holistic approaches to conservation, such as management strategy evaluation (MSE; Butterworth and Punt 1999, Bunnefeld et al. 2011) and adaptive management (AM; Walters 2007, Keith et al. 2011). Both take into account the relationships between and within system components in a more integrated and comprehensive way than traditional approaches to natural resource management, explicitly considering uncertainty, feedbacks between components and trade-offs between decisions. MSE tests the robustness of potential management strategies to a range of uncertainties by modelling the whole management system: the dynamics of the natural resources and their harvest ("operating model"), their monitoring ("observation model"), how this information is used to inform management decisions ("assessment model") and how these decisions are implemented ("implementation model"). MSE conceptual frameworks can be designed to emphasise the perspectives of different groups within the system (e.g. "resource users", "managers" and "monitors"; Figure 6.1). Despite having been used primarily as a modelling approach within fisheries science, MSE has potential as a flexible and intuitive conceptual framework for analysing the interactions between stakeholders (Milner-Gulland 2011; Bunnefeld, Hoshino, & Milner-Gulland 2011; Plagányi *et al.* 2013).

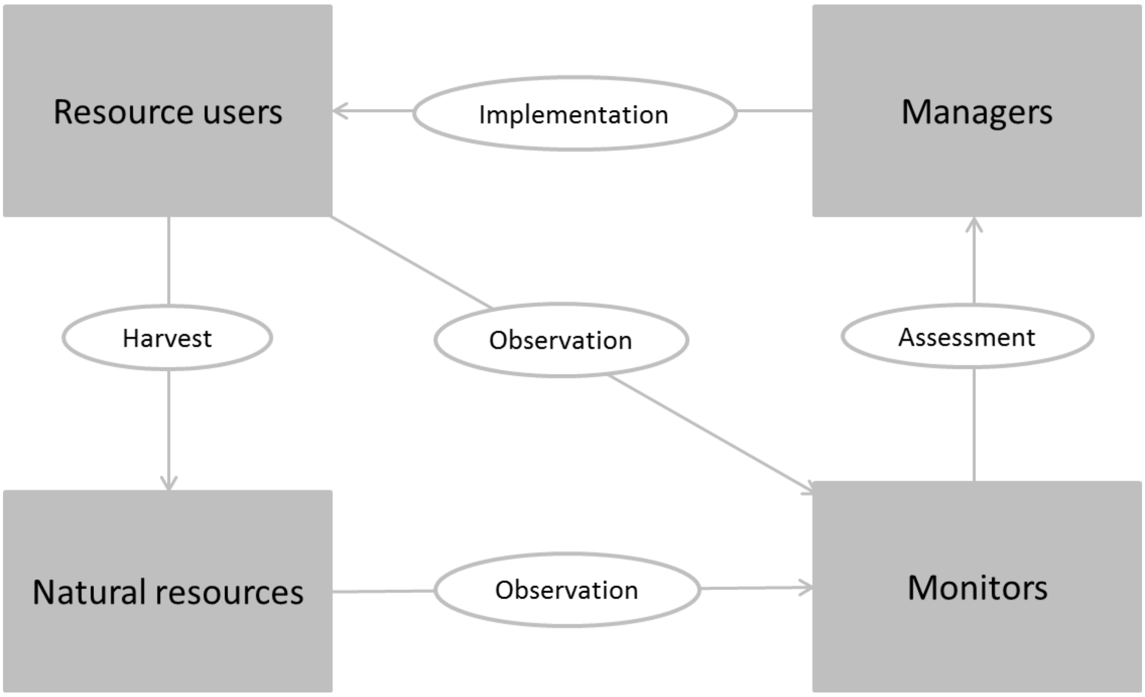

Figure 6.1. A conceptual diagram of the management strategy evaluation (MSE) framework used in this study.

While MSE has been developed as a simulation-based tool to test alternative management strategies in fisheries (Smith 1999), AM tests alternative strategies in the real world; it implements two or more strategies in a comparative experimental setting, monitors them and then uses information on system dynamics to improve management outcomes (Keith *et al.* 2011). Despite being widely advocated, AM has been relatively little used in practice (Walters 2007). Institutional barriers are among the major impediments to its implementation (Keith *et al.* 2011). Lack of leadership, unwillingness to embrace uncertainty and lack of a long-term vision are also often suggested as causes for the failure to implement AM (Walters 2007; Allen & Gunderson 2011).

In complex social-ecological systems, where adaptive conservation approaches such as MSE and AM are most needed, a range of personal, capacity and institutional barriers might reduce conservationists' capacity to achieve their expected outcomes with high predictability, potentially playing an important role in explaining the failure to implement successful conservation interventions. Using the bushmeat hunting system in the Serengeti as a case study, we used a MSE framework as a conceptual model to investigate the challenges and potential barriers to successful conservation implementation. First, we obtained insights into the constraints and opportunities for fulfilling stakeholder aspirations for the social-ecological system. Then, we analysed the multiple roles played by different institutions in the system, described the interactions between different actor types and summarized the main challenges to implementation of conservation action. Finally, we provide recommendations for the development and implementation of conservation interventions within long-term integrated and adaptive frameworks.

6.2. Methods

6.2.1. Study system

Well known for its charismatic wildebeest (*Connochaetes taurinus*) migration and for having some of the largest herbivore and carnivore populations in the world, the Serengeti ecosystem is one of the most emblematic social-ecological systems and has attracted the attention of explorers, missionaries, hunters, researchers and tourists over the last 150 years (Sinclair 2012). The Serengeti national park (SENAPA) was proclaimed in 1951. In 1959, the boundaries of the national park were realigned to include the area of what was assumed to be the migratory route of the wildebeest, which acts as a keystone species of the Serengeti ecosystem (Sinclair 2003; Thirgood et al. 2004). People living inside the park were evicted by 1960 (Shetler 2007). In 1981, SENAPA was internationally recognized as part of a World Heritage Site and a Biosphere Reserve. SENAPA is nowadays one of the most visited protected areas in the world (UNDP 2012) and its importance for biodiversity conservation, development and cultural heritage is widely acknowledged (Shetler 2007; Sinclair *et al.* 2007). The Serengeti ecosystem is one of the most intensively studied systems in Africa; monitoring and research have been conducted since the 1950s, producing several long-term biological datasets and hundreds of scientific publications and reports (Sinclair *et al.* 2007; Sinclair 2012).

All natural resource use within SENAPA has been prohibited since the park's establishment. The Tanzanian side of the ecosystem, the focus of our study, also includes protected multiple-use areas and village areas with agricultural and livestock systems, and with a range of different restrictions on hunting and settlement (Figure 6.2; MNRT 1998, Polasky et al. 2008). The establishment and enforcement of these restrictions has not been without difficulties; they have been debated since the establishment of the national park and characterized by a history of conflicts and power struggles over the use, control, and management of lands and resources, influenced by international interests (Nelson & Makko 2005; Shetler 2007). For example, a recently proposed highway crossing the Serengeti generated controversy about trade-offs between different development pathways and their ecological impacts (Dobson *et al.* 2010; Homewood, Brockington, & Sullivan 2010). This attracted the attention of international media (over 1000 press articles published in 48 countries over 8 months after its announcement; Sinclair 2012) and catalysed interventions by the World Bank and the German government.

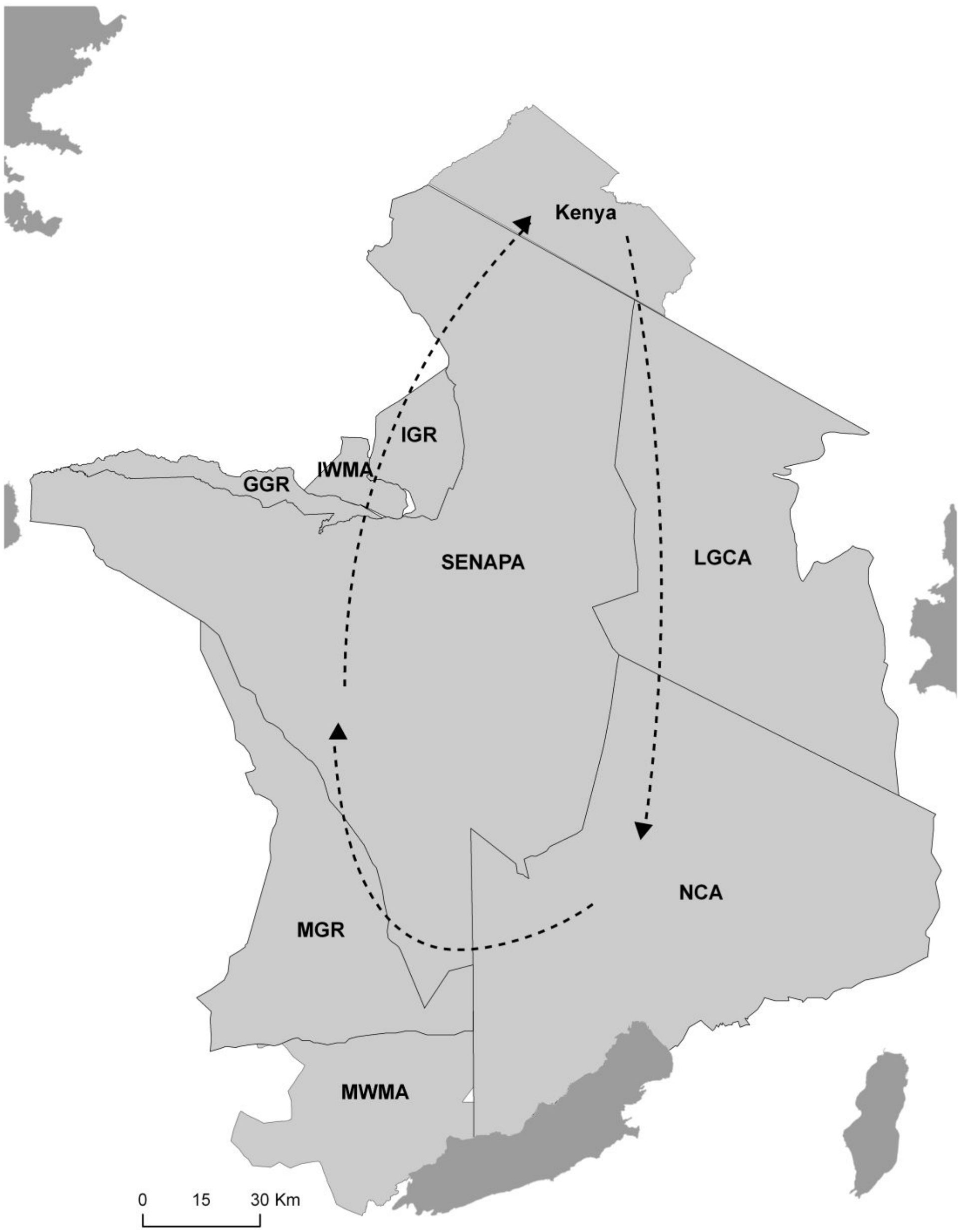

Figure 6.2. Protected areas and lakes (darkest grey) within and surrounding the Serengeti ecosystem. SENAPA= Serengeti National Park, LGCA = Loliondo Game Controlled Area, NCA = Ngorongoro Conservation Area, MGR = Maswa GR, GGR = Grumeti Game Reserve, IWMA= Ikona Wildlife Management Area, MWMA= Makao Wildlife Management Area, and IGR = Ikorongo Game Reserve. Dashed arrows indicate broad wildebeest migration patterns.

When making decisions about the Serengeti, a great number of interests are at stake; 106 groups of institutional stakeholders were identified in a study by the Serengeti Ecosystem Management Project (SEMP 2006). The protected areas are managed by a range of governmental, non-governmental and private sector organizations. Tanzania National Parks (TANAPA) is a parastatal organization responsible for managing and regulating national parks while the Ngorongoro Conservation Area Authority (NCAA) oversees wildlife conservation in the Ngorongoro Conservation Area (NCA). The Wildlife Division (WD) of the Ministry of Natural Resources and Tourism (MNRT) has oversight of game reserves (GRs), game-controlled areas (GCAs) and wildlife management areas (WMAs). The Tanzania Wildlife Research Institute (TAWIRI) is a parastatal organization under the MNRT responsible for conducting and coordinating wildlife research and advising the government and wildlife management authorities. Private tourism and hunting companies, such as Singita Grumeti Reserves, manage the GRs and enter into contracts with communities within other multiple-use areas. Frankfurt Zoological Society (FZS) is one of the most prominent international non-governmental organizations operating in the Serengeti, active in the system since the 1950s. A number of international donors and national and international research projects provide financial support and advice for park management and conservation interventions, complementing the main source of revenue from tourism (Thirgood *et al.* 2008).

With roughly 2.3 million people in the districts surrounding the national park and a population growth rate of approximately 3% (NBS Tanzania 2006), conflicts over land and natural resources are substantial and expected to grow (Polasky *et al.* 2008). Bushmeat is, in theory, a state-controlled natural resource in Tanzania and hunters must obtain a licence for hunting according to quotas set annually by the WD. However, illegal hunting is widespread throughout the Serengeti (Loibooki et al. 2002, Chapter 4) and has been perceived as a threat to wildlife for several decades (Watson 1965; Arcese, Hando, & Campbell 1995; Hilborn *et al.* 2006). In the past, game cropping schemes have been used, without success, in an attempt to reduce bushmeat hunting (Holmern *et al.* 2002). The main ongoing initiatives aimed at controlling illegal hunting, which vary in temporal and spatial scale, include: Law enforcement carried out by TANAPA rangers and personnel of the GRs; Community Conservation Banks (COCOBAs; facilitated by FZS and based on a lending model that provides access to micro-credit for environmentally-friendly enterprises); WMAs; Community Conservation Services (CCSes; program conducted by TANAPA to share benefits with communities surrounding SENAPA); and several outreach and environmental education programs (e.g. one conducted by Grumeti Fund, a local NGO associated to Singita Grumeti Reserves). Nevertheless, the high levels of poaching estimated in the area (estimated as being part of the livelihoods of 18% of households) suggest that bushmeat hunting remains an issue to be addressed (Chapter 4) while the effectiveness of these interventions has been difficult to ascertain and potentially limited to localized areas (but see Hilborn et al. (2006) on the positive effects of anti-poaching activities on wildlife abundance in the national park).

6.2.2. Study design

Using the bushmeat hunting system in the Serengeti as a case study, we investigated the challenges and potential barriers to successful conservation implementation according to main actors in the monitoring and management components of the MSE framework (Figure 6.1). We used key-informant interviews to elicit potential and desired scenarios for the study system (scenario-building exercise), to understand the actual and perceived roles of different organizations within the system and how they fitted in the MSE framework (institutional analysis exercise) and to analyse institutional interplay, social network composition and complexity (social network analysis).

6.2.3. Study participants

Given the institutional complexity and number of stakeholders involved in the Serengeti, we chose to interview actors from the four main organizations operating in the Serengeti, who are responsible for making or influencing rules affecting bushmeat hunting in the Western Serengeti; FZS, TAWIRI, TANAPA and Grumeti Fund, and actors from collaborating universities. Local people were not interviewed because, although some members of local communities are involved in WMA decisions, this process is still incipient and at a very local scale. Targeted sampling was used to select respondents, who were invited to participate if they were directly involved in management, monitoring or research in the Serengeti and connected to ongoing conservation actions. The number of interviews per organization is not proportional to its size; it represents the number of people familiar with the topics under discussion, ensuring coverage of different roles within the organizations and their availability to be interviewed.

Nineteen interviews were conducted. The average age of the respondents was 44 years and half had more than 5 years of experience working in the Serengeti. A summary of the study participants is presented in Table 6.1.

Table 6.1. Summary of the main characteristics of study participants (n=19).

Characteristics	Level	Count
Organization	FZS	7
	TAWIRI	6
	Universities	3
	TANAPA	2
	Grumeti Fund	1
Main type of role [a]	Research	11
	Coordination/management	9
	Fieldwork	3
	Administration	2
Area of work [a]	Livelihoods & engagement with communities	12
	Wildlife monitoring and management	9
	Academic	7
	Anti-poaching	2
Disciplinary background	Mainly ecological (e.g. Wildlife management)	13
	Interdisciplinary	4
	Mainly social (e.g. Applied economics)	2
Nationality	Tanzanian	12
	Other countries	7
Sex	Male	14
	Female	5

[a] Each respondent could choose more than one option so total count exceeds sample size.

6.2.4. Data collection and analyses

All exercises were carried out with individual respondents in private. Study participants were presented with a few questions about their role within the study system, academic background and socio-demographic characteristics, followed by the three exercises (scenario-building, institutional analysis and social network analysis). Then, semi-structured interviews were conducted to promote further discussion around the MSE framework and its components. Consent for participation and audio recording were obtained before each discussion. Total interview time ranged from 36 min to 1h40 min. All interviews were conducted by A.N.

A. Scenario-building

Scenario-building is a useful tool to ask respondents to consider different futures and assess their desirability and achievability given certain conditions (Peterson, Cumming, & Carpenter 2003). This exercise aimed to assess expected and desired scenarios for the study system according to multiple actors. This allowed us to identify the main areas of agreement, disagreement and uncertainty between actors, as well as gather information about potential threats and management strategies in the future and investigate how goals for the system were set by each respondent. First, the respondents were asked to describe scenarios for the overall Serengeti ecosystem, and then to focus specifically on scenarios for bushmeat hunting, the ecosystem's ecological value and poverty, as we were interested in knowing how these key issues, and potential trade-offs between them, were considered by different actors. After describing these scenarios, the respondents were asked what constrained movement from the expected to the ideal situation in order to obtain their overall opinions about key challenges to the system, particularly with respect to implementation issues (Appendix D).

B. Institutional analysis

Institutional analysis is often conducted to identify and represent stakeholders' perceptions of key institutions inside and outside a system and their relationship and importance, allowing researchers to understand how different participants perceive institutions differently (Holland 2007). This exercise aimed to identify key institutions operating in the system, how they overlap with each other in each MSE subcomponent and their perceived importance. Participants were asked to list the institutions operating in the bushmeat hunting system, indicate the subcomponents of the MSE framework in which they were involved (Figure 6.1) and if they played a weak, medium or strong role (scored as 1, 2 or 3, respectively) in decision-making and intervention implementation in the study system.

The institutions listed by different actors in the institutional analysis exercise were ranked according to their role in decision-making and implementation by weighting them based on their perceived importance for each process. Not being mentioned by a specific actor was scored as 0.

C. Social network analysis

Social networks can be used to characterize collaborations and social relations, to facilitate conservation and to identify potential challenges to its implementation (Bodin & Crona 2009; Guerrero *et al.* 2013). This exercise aimed to identify the role and influence of different actors and their organizations according to their positions within the network, as well as to obtain a measure of system connectivity. Each respondent was asked to list up to 10 collaborators in projects about the Serengeti and to indicate the frequency and nature of the collaboration (Appendix D).

Social network analyses were conducted using the igraph package version 0.6.5-1 in R v.2.15.2 (The R Foundation for Statistical Computing 2012). The analyses were conducted separately for the overall network (including all collaborators listed in the exercise), and for each of the subset networks obtained by asking the participants to indicate the main reasons for collaborating with each person ("advice and support network", "policy network" and "implementation network"). The intensity of the links in the social networks was measured using the frequency of interactions. To describe the structure of the networks, we measured the number of links, edge connectivity (also known as group adhesion; minimum number of directed links needed to remove all directed paths between two individuals), density (number of reported links as a percentage of the total possible links) and the mean geodesic distance (the shortest path through the network from one individual to another). To assess individual positions in the networks, we measured actor degree (the number of direct connections a person has), eigenvector centrality (based on the number of direct connections a person has but also on the centrality of those nodes) and betweenness centrality (how many times an actor rests on a short path connecting two others who are themselves disconnected) as indicators of centrality and influence (O'Malley & Marsden 2008; Prell, Hubacek, & Reed 2009).

D. Semi-structured interviews

To promote further discussion, open-ended questions were used to gather information about the personal experiences and perceptions of each respondent while working in the Serengeti. These questions focused on the overall study system and its multiple subcomponents according to the MSE framework (topic guide available in Appendix D). In particular, we aimed to gather information about the main issues characterizing and constraining conservation implementation.

After interview transcription, all texts were analysed and managed in NVivo10 using principles of thematic analysis (Bernard 2011), in which categories (codes) are identified, compared and grouped in order to create a typology of the main issues.

6.3. Results

6.3.1. Actors' perspectives about the Serengeti ecosystem

During the description of expected and desired scenarios for the Serengeti, the respondents expressed generally similar views about the current and future status of the Serengeti ecosystem and its multiple functions and value for biodiversity, local livelihoods and tourism. The respondents also shared similar views about the overall functioning of the ecosystem and the need to address bushmeat hunting and poverty in local communities. When asked to list the top threats to the Serengeti, increasing human population growth, land-use conflicts and poaching were the most frequently mentioned (Table D1 in Appendix D). Ten out of 19 participants listed bushmeat hunting as a top threat. Poor management and governance (e.g. dependence on unstable funding; institutional complexity; instability in policies) was mentioned as a top threat by 6 respondents. The listed top threats can be broadly grouped into the following, often interrelated, categories: human population growth; land-use conflicts and encroachment; poaching; climate change and environmental stress; development, infrastructures and tourism; poor management and governance; poverty and lack of opportunities; diseases; habitat degradation and water scarcity; invasive species; human-wildlife conflict; and mining.

The main areas of disagreement and uncertainty were related to how exactly issues of conservation concern should be addressed. For example, the respondents had differing opinions about the type and amount of human engagement that should be allowed in the system, either through management or resource use. Also, while some respondents suggested the need to emphasise the instrumental reasons for conserving the Serengeti (e.g. tourism revenue and its importance for national economy), others suggested that conservation actions should be driven only by its intrinsic value. Additionally, the role of international bodies was generally described as advisory but some respondents suggested that only through the pressure and action of these bodies will the Serengeti be maintained in the future. A key area of uncertainty discussed by all respondents was the need to identify and develop sustainable models of development which maximize, or at least do not jeopardize, biodiversity. For example, some respondents suggested that wildlife-related activities (e.g. tourism) are essential for community development, while others mentioned that other approaches should be used instead, in which communities are not dependent on wildlife at all. Disagreement between participants did not seem to be related to their institutional affiliation. Scenarios and the main areas of agreement, disagreement and uncertainty are presented in Table 6.2.

Table 6.2. Summary of the expected and desired scenarios described by the respondents, indicating main areas of agreement, disagreement and uncertainty.

<table>
<tr><th rowspan="2">Discussion topic</th><th colspan="3">Expected scenarios</th><th colspan="2">Desired scenarios</th></tr>
<tr><th>Agreement</th><th>Disagreement</th><th>Uncertainty</th><th>Agreement</th><th>Disagreement</th></tr>
<tr><td>Overall Serengeti ecosystem</td><td>• Population growth, land-use conflicts and poaching as major threats to the system
• Significant changes expected at the long-term</td><td>• The role of international bodies (“saviours” Vs. advisors)</td><td>• Climate change
• Potential multiplicative effect of multiple threats
• Technological advancements and development of infrastructure
• Tourism fluctuation and satisfaction
• Identification of model to be followed for achieving balance between conservation and development</td><td>• Serengeti preserved as unique and iconic ecosystem
• Maintain tourism, biodiversity and supporting livelihoods as key goals of the system
• Integrated holistic management approach achieved for its effective conservation</td><td>• Acceptable levels of human engagement (management and resource use) in ecosystem
• Role of intrinsic Vs. instrumental reasons for its conservation</td></tr>
<tr><td>Bushmeat hunting</td><td>• Prevalence generally increasing or, at least, not decreasing
• Done for both subsistence and commercial reasons
• Difficulty in defining and</td><td>• Timeframe over which bushmeat hunting will be controlled</td><td>• Link between hunting and poverty
• Intervention effectiveness
• Observation uncertainty
• Role of urban demand as</td><td>• Mosaic of areas with different protection status (with hunting not allowed inside the NP) should be kept
• Acceptability/tolerance of bushmeat hunting in the ecosystem, if at sustainable</td><td></td></tr>
</table>

	achieving sustainable offtake		driver • Effect of social change in the future	levels	
Ecological value	• Change is inevitable in dynamic ecosystem • Significant changes not expected in the short-term (5 years)		• Environmental uncertainty • Non-linear dynamics (tipping points) • System resilience	• Wildebeest migration kept as key driver of system function	• Type and magnitude of acceptable change
Poverty	• Improvements unevenly distributed within communities and between areas • Lack of opportunities for local communities surrounding PAs	• Direction of the expected general trends of poverty change	• Intervention effectiveness • Link between gradually increasing wealth and natural resource use • Effect of poverty alleviation in communities surrounding PAs on immigration	• Consensus about the need to decrease poverty • Equitable use of resources	• Role of wildlife-related activities (e.g. tourism) for community development

6.3.2. Constraints to reaching preferred scenarios

During the interviews, implementation was identified as the main gap that should be addressed for successful conservation of the Serengeti ("*However good a plan is, if something else doesn't go properly, the plan will just be there*"), followed by doing more research on topics such as climate change, invasive species, diseases and social dynamics, and disseminating research findings to wider audiences, particularly the implementers and end-users. While a few respondents were relatively optimistic about the success of different ongoing interventions in controlling bushmeat hunting in the Serengeti, several participants were sceptical about the effectiveness of any of these interventions. However, according to the respondents, issues of spatial and temporal scale, baseline definition, data availability and observation uncertainty hinder the measurement of actual intervention effectiveness.

The study participants mentioned a number of challenges preventing or limiting the effectiveness of ongoing conservation actions aimed at controlling bushmeat hunting and, more generally, preserving the Serengeti ecosystem. While these issues are mainly related to the implementation part of the MSE framework, several affect the observation and assessment components as well. These issues can be broadly grouped in the following categories (see Table D2 in Appendix D for examples):

- Multiple goals and lack of integrated approaches

Trade-offs between conservation, development and tourism were often described as a major consideration when implementing management interventions ("*at the same time, conservation projects need to maintain wildlife and improve livelihoods*"), but also as a potential limitation to their effectiveness ("*One solution could be a problem to another objective*"). The lack of integrated approaches that consider these multiple goals together was identified as a major barrier to successful implementation ("*There are development actors who are really pushing for a development scenario…and there are conservation actors who are pushing for a conservation scenario…it has to be some hybrid between these two*"). According to the respondents, a common vision for the Serengeti is lacking, requiring more coordination between actors ("*The management of the system itself…should sit together…because we have just a common goal but each one taking a different route*").

- Adaptive responses to change under uncertainty

The need for approaches that consider changes in system function over time was identified as a key requirement for the better management of the system, both for understanding its current dynamics and being able to plan effective strategies under uncertainty, particularly due to effects of climate change ("*Climate change… that's an unpredictable one*"), development ("*this road issue came out of the blue…we have to be prepared that things like this might happen*"), technology ("*poachers are using new ways of communications. 5 or 10 years, there were no cell phones… Now, everyone uses it to escape rangers*") and social change ("*political, cultural and economic issues…the more they change, the more they tend to affect*").

- Poor governance

Poor governance was described as an important barrier to effective implementation in the Serengeti. The interviewed actors mentioned that improvements were required in several of its components, namely: participation ("*local people should be central…not just being told what to do*"), performance ("*levels of bureaucracy that are completely unnecessary*"), transparency ("*there should be more transparency… revenues increasing but also being spent … more invested back into conservation*"), equity ("*the way people are benefiting from conservation… is not really evenly distributed*"), and rule of law ("*livestock in protected areas… that is prohibited by law but the enforcers are getting blockages*"). According to the respondents, poor governance has been responsible, for example, for the lack of sustainability of interventions ("*local people should have information so that, even if the project developers leave, they still own the process and will make it go on…but this is not happening*"), implementation error ("*the law is there…the judicial, the police and whatever… the setup is there but they are not functioning the right way*") and lack of trust of potential donors ("*too corrupt and donors don't want to waste money*").

- Institutional barriers

Issues related to interactions between different groups and institutional processes were often described by the respondents as an important consideration. All participants were involved in ongoing collaborations across, and within, institutions. Many benefits arising from, and driving, these collaborations were listed, such as; exchange of knowledge and expertise, sharing resources, achieving common goals, and facilitating buy-in by other stakeholders. The respondents also identified a number of main challenges related to the institutional setting and interplay: lack of a common and long-term vision in both the regulations and interventions ("*the regulations…this* *ecosystem is too big and managed by different guidelines…one regulation might affect the others*"); difficulty in data access ("*Accessing data not easy… all seems confidential to an organization*"); difficulty in bringing together and reaching consensus with many stakeholders ("*by the time you gathered everyone together and agreed on something, the budget is gone*"); and mistrust between institutional actors ("*during a presentation, there's sometimes doubt of the things they're presenting*"). The effects of institutional complexity include, for example: inefficient use of resources ("*you probably lose a lot of money in solving and tackling a single problem by different managers*"); contradictory regulations ("*you find laws are contradicting each other*"); competition for external recognition ("*everyone wants to take credit of the work…they want do it themselves*"); and contradictory advice being given to local communities ("*The forest officer goes to village and says you should protect an area…then goes the agricultural officer and says it's the most fertile and should be used for farming…without knowing the overall policies for forest conservation*").

- Individual characteristics

The specific individuals involved in the interventions and their personalities and other individual characteristics play an important role in the way projects develop. For example, commitment ("*People usually come for 2-3 years, they get sick of it, they get disillusioned, they leave*"), diverse personalities ("*conflicts between different types of personality…this can be disastrous if we fail to understand each other*") and reluctance to learn and adapt ("*even if they don't have the knowledge to do it, they prefer to do it alone instead of integrating with others that know*") were described as essential considerations in conservation implementation. One of the respondents described the importance of "conservation heroes" for successful conservation collaborations ("*Those people sacrifice a huge amount of their other types of lives…Sacrifice the opportunity to live a life they're used to. You have to give these people credit.").*

- Perceived value and use of scientific information

Several respondents mentioned the abundant amount of research conducted in the Serengeti ("*the Serengeti ecosystem is over-researched*"), while most considered that there is a need for more information, given the ongoing changes in social and environmental conditions ("*there's a lot to be studied and learned because context changes with time*"), as well as the uncertain nature of the system and the scientific process ("*Probably one of the best studied ecosystems but there are some things we just don't know*").

The link between scientific information, both from research and monitoring, and management decisions in the Serengeti is, however, considered weak. According to the respondents, this might be due to: a) researchers not sharing their findings widely ("*we failed in sharing information with other audiences and so impact has been minimal*"); b) researchers not addressing questions of management interest ("*not many researchers go into management-oriented kind of research*"); c) data quality not being adequate for management decisions ("*estimates with wide confidence limits... they are not a very good thing to set your hunting quotas*"); d) information not being perceived as valuable or trustworthy ("*monitoring...it's just an academic exercise*"). The recent use of long-term information about wildebeest population trends for informing decisions about the potential impacts of a road crossing the Serengeti was, however, occasionally mentioned as an example of scientific information influencing management decisions ("*when there's emergency, things are more linked...like with this road issue...suddenly people started to think what's going to happen*").

- Lack of proper incentives

Inadequate incentives were mentioned as a key factor explaining discrepancies between expected and obtained outcomes from conservation interventions. According to the interviewed actors, these inadequate incentives affect the effectiveness of these interventions at the local community, decision-maker and implementer levels. Targeting interventions at the individual versus household or community level was one of the most frequently mentioned required improvement for implementation effectiveness in the area ("*We need to use incentives... and not general incentives like construction of schools... tangible incentives that go directly to individuals*").

- Relationships with local communities

Lack of community participation during the planning of conservation interventions was frequently reported as a source of implementation error ("*We, as managers, sometimes sit and think for people... maybe we bring them food because they are going there for meat...maybe we bring them chickens... this is not what they want!*"). Most respondents agreed that the local communities were more considered, and engaged, in the ongoing conservation interventions than in the past, but were sceptical about the actual level of engagement ("*it has improved in policy but in reality not much*"). Despite the need for improvements, most respondents emphasised that these approaches are essential for the sustainable future of the Serengeti ("*The basic philosophy behind empowering communities to use wildlife is a very good approach*").

6.3.3. Institutional complexity

Institutional complexity was identified as a major barrier to conservation implementation in the scenario exercise. In the institutional analysis exercise, the study participants listed 13 institutions operating in the bushmeat hunting system in the Serengeti, of which FZS, TANAPA, TAWIRI, Grumeti Fund and WD were the most commonly mentioned. Wildlife and social monitoring are mainly conducted by TAWIRI and FZS, although the respondents listed 8 other institutions involved in these activities (Figure 6.3). Twelve of the institutions (all except the universities) were listed as involved in the management of the system, both in terms of decision-making and intervention implementation, of which TANAPA and WD were the most frequently mentioned. Based on the importance scores given by each respondent, TANAPA was the highest ranking institution for decision-making and implementation, with respect to controlling bushmeat hunting, but obtained only 21% of the total importance score. The summed weighed score of the three highest ranking institutions (TANAPA, FZS and TAWIRI) was 53% (Table D3 in Appendix D), suggesting that although the decision-making and implementation processes are shared mainly between these three organizations, responsibilities are also more broadly distributed among a number of institutions.

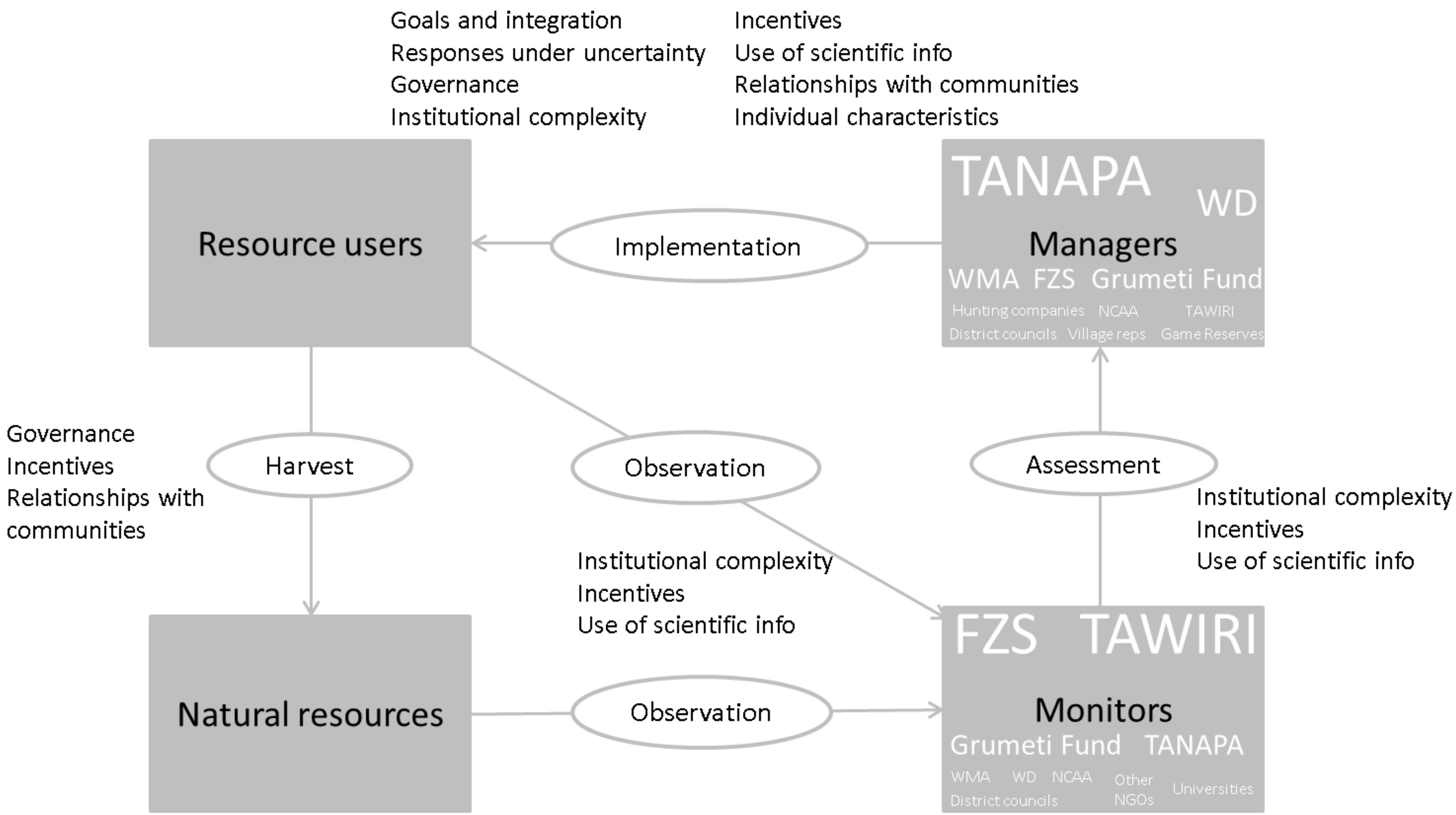

Figure 6.3. Main management challenges and institutions operating in the bushmeat hunting system, where they fit within the MSE framework and their perceived roles (font size is proportional to the number of respondents indicating a certain role for a specific institution.

6.3.4. Conservation networks

As expected given the number of institutions involved in the system, a large number of individuals from nine institutional groups (FZS, government – district level, government – national level, government – village level, other NGOs, TANAPA, TAWIRI, universities and WMAs) were listed by the study participants as collaborators in projects related to conservation in the Serengeti. Of a total of 110 links between 66 people in the network, 30% were connections to people working at FZS, followed by 21% to government (district and national levels) and 15% to TANAPA. 18% of the total links were intra-institutional, suggesting that most collaborations occur across institutions.

When looking at subsets of the overall network, obtained by asking the participants to indicate the main reasons for collaborating with each person (advice, influencing policy or implementation), the policy network was the smallest (35 links), followed by the one for advice (52 links). The policy network had the lowest proportion of intra-institutional links and the advice network had the highest (6% and 23% respectively), suggesting that collaboration has different functions between and within institutions. Additionally, the policy and advice networks were more disconnected than the implementation and general networks, with larger distances between actors (Figure 6.4).

A few actors were consistently more influential and central than the others, particularly actors (14), (4) and (10), all of whom were from FZS (Figure 6.4, Table D4 in Appendix D). Actors from FZS play a central role in all network types, suggesting a key role played by this organization in multiple steps of the decision-making and implementation processes. As expected by the different nature of the work done by different institutions, the policy network was mainly composed of links to TANAPA and other governmental institutions, such as WD (63% of total links), and the advice network was predominantly composed of links to NGOs and researchers from TAWIRI and universities (81% of total links). In the implementation network, 42% of the links were to NGOs and 25% were to TANAPA and other governmental institutions, suggesting an important role played by non-governmental bodies.

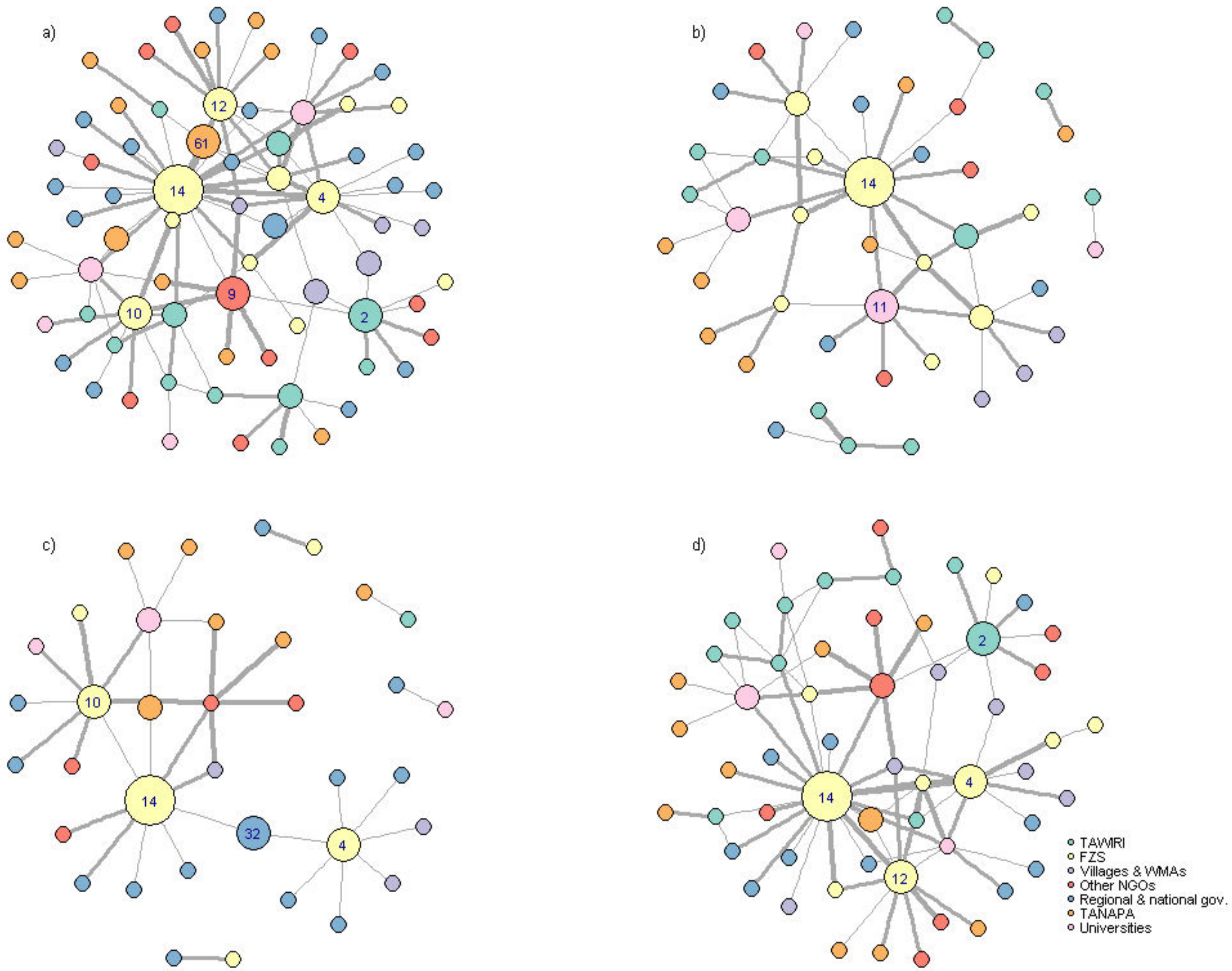

Figure 6.4. Social network of respondents for: a) overall conservation activities; b) advice and support; c) influencing policy; and d) implementation. For illustrative purposes, only one measure of influence (betweenness centrality) is shown. Each node (circle) represents an actor, node size is proportional to betweenness centrality (a measure of power/influence based on how many times an actor rests on a short path connecting two others who are themselves disconnected), width of lines represents frequency of interactions and colours represent organizations (see legend). Numbers represent the codes for the most influential actors as measured by their betweenness centrality.

6.4. Discussion

Managing for resilience of a social-ecological system is only possible if both social and ecological dynamics and feedbacks are understood (Folke 2006; Holling and Meffe 1996). Social considerations are essential for understanding the feasibility of alternative actions and identifying the scope of conservation problems (Raymond & Knight 2013) but, in traditional approaches to conservation and natural resource management, it is often assumed that the "managers" and "monitors" are outside the system (Walker *et al.* 2002). The MSE framework is helpful in highlighting the relationships between actors, and enabling reflection on the potential blockages in implementation of effective policy.

It is often assumed that natural resource management bodies can be modelled as unitary, rational and well-informed actors (Young 1998) but our study suggests that this might be unrealistic and misleading; in the Serengeti, the relationships between institutions and individual actors involved in policy implementation are complex and diverse. Our studies in the Serengeti indicate that understanding the complexity of behaviour of key actors within management institutions is also important for implementation. These individuals affect the decision-making processes leading to implementation, as well as the effectiveness of the actual implementation. For example, if regulations are not properly enforced, there is little hope that they will be abided by (Rowcliffe et al. 2004). Addressing implementation uncertainty will thus require not only a better understanding of the factors driving resource user behaviour and how resource users might react to different management strategies, but also of the institutional setting and how interactions between actors increase uncertainty and inertia in the system. The respondents in our study described contradictory regulations and advice as some of the negative effects of institutional complexity, while trade-offs between conservation, development and tourism were often described as a potential limitation to intervention effectiveness.

Given that a lack of functional integrated approaches to natural resource management was identified as a main challenge to implementation, enhancing collaborative management is fundamental to promoting future sustainable strategies in the Serengeti. Co-management involves shared responsibilities and rights, recognizing the plurality of institutions in governance structure (Plummer & Fitzgibbon 2004). Management decisions and implementation in the Serengeti are conducted by a number of institutional actors and, while there is no universal solution to the problems of resource management, governance features and institutional linkages affect conservation effectiveness (Acheson 2006; Armitage, de Loë, & Plummer 2012). Moreover, group size and heterogeneity influence prospects for collective action, often in non-linear ways; for example, resources (such as time, money and skills) may not be available in small groups but the levels of interaction that generate trust and facilitate action decrease in large groups (Poteete & Ostrom 2004). Additionally, the respondents had generally similar views about the current and future status of the Serengeti but disagreed about how to address issues of conservation concern and were more uncertain about the effectiveness and actual outcomes of management interventions. Patterns found in fisheries can inform the design of governance structures; De Nooy (2013) found that centralized systems, such as found in the Serengeti, have more disagreement overall, and especially within stakeholder groups, whereas co-management systems have more disagreement between groups.

Similarly to this study, difficulties in achieving multiple goals (e.g. conservation, development and tourism) in social-ecological systems have been frequently described as challenges to implementation (Salafsky & Wollenberg 2000). It is important to identify and analyse the potential trade-offs involved in conservation initiatives (Hirsch *et al.* 2011), which can be done by applying tools such as MSE and AM. For example, MSE has been used in situations in which several stakeholders had conflicting interests to identify objectives and alternative management strategies and then help them choose between multiple options (e.g. Mapstone et al. 2008, Smith et al. 2008, Dichmont et al. 2013). A similar approach could be used to promote consensus within a co-management committee, such as the Serengeti Ecosystem Community Conservation Forum (SECCF). This has been recently created to promote collaboration between diverse stakeholders throughout the system and has the potential to be an effective platform for stakeholder participation and management, although some financial, institutional and governance challenges remain (Randall et al. in press).

A key requirement for the development and implementation of adaptive approaches to natural resource management, such as MSE and AM, is the collection and use of information to learn about the system, which is then used to update conceptual models and to inform decisions about system management, closing the adaptive loop (Keith *et al.* 2011; Bunnefeld, Hoshino, & Milner-Gulland 2011). However, this study shows that the links between system components and actors (monitoring, assessment, implementation), despite being essential for the adequate functioning of the management system, are currently not well established and fully functional in the Serengeti. Improving implementation (rather than research, monitoring or assessment) was perceived as the priority, particularly given the amount of research already conducted in the area. This suggests that actually applying the knowledge accumulated over the last decades is still challenging. This is not unique to the Serengeti, having been described for a range of conservation projects as the "research-implementation gap" (Knight *et al.* 2008). Given the weak linkages reported between science and management decisions in the Serengeti, increasing the perceived value and use of scientific information should be a key priority for improving the management of the system (Pullin *et al.* 2004). The lack of monitoring and evaluation, leading to the uncertainty about the effectiveness of particular interventions aimed at reducing the exploitation of bushmeat species by local people (patrolling, micro-credit schemes) highlighted by the respondents, makes it difficult to learn from previous and ongoing interventions, potentially creating conflict and mistrust between actors (Redpath *et al.* 2004). Implementing integrated monitoring programmes encompassing both wildlife and resource users, and robustly evaluating ongoing interventions, would provide much-needed information of direct relevance to management decisions.

Although there were several areas of major difficulty in implementation of policies identified by respondents, the current management and monitoring system has the potential to work in a more integrated way. This was shown when a specific and easily identifiable threat to the system, a highway crossing the Serengeti, was proposed by central government. A swift and relatively coordinated response by international organizations and scientists was launched, based on a foundation of long-term research, which led to international concern and the identification of alternative options (Sinclair 2012). When faced with decisions about other more indirect or less easily measurable threats, such as climate change, the responses suggest that decision-making may be more difficult and prolonged, and research insights may be harder to marshall in support of management.

There is an increasing recognition that the analysis of the structure of social networks can enhance understanding of natural resource governance (Bodin & Crona 2009). Network measures may be used to quantify structural characteristics and link them to a number of features, such as information dissemination, leadership and trust (Bodin, Crona, & Ernstson 2006). Our results demonstrate the importance and centrality of an international NGO, FZS, in the conservation of the Serengeti, and in particular the importance of very few individuals within FZS in bridging a range of institutions in all three arenas of interaction. Despite not having actual authority in the management of the system, FZS has been fundamental to the past and ongoing interventions, being present in the ecosystem since the late 1950s. Local social and political capital are, however, fundamental to local ownership of the processes, empowerment, fairness and, ultimately, system resilience (Adger, Brown, & Tompkins 2005); capacity building should be further promoted in the Serengeti, to reduce reliance on expatriate expertise. Reliance on very few individuals means that they potentially have a powerful influence and the ability to bind different groups together. However it also reduces the robustness of the network. Adaptive governance of systems requires a large number of key people with different skills, who perform different leadership functions, enhancing the system's capacity to cope with uncertainty (Adger *et al.* 2005). Assessing and understanding the actual roles played by different individuals and institutions is essential for improving resilience of governance structures.

The need for decision tools for the quantitative description of the causal relationships and interactions between the various components of social-ecological systems has been increasingly recognized (Heinonen *et al.* 2012). These are, however, complex and data demanding tasks. Quantitative models may be based on little empirical information and may be perceived by decision makers as of little use in real world decision-making (Cooke *et al.* 2009). A qualitative investigation such as ours, that has MSE as the underlying framework, could form the starting point for a quantitative model that couples social and ecological dynamics and would be more relevant to decision-making than standard models rooted in a single discipline. For example, information about how different stakeholders interact (obtained from our network analysis), and how these interactions influence the decision-making process, could be used in an agent-based model of decision-making, producing emergent behaviour at higher levels (Rounsevell, Robinson, & Murray-Rust 2012). MSE has a good track record of promoting participatory modelling (Röckmann *et al.* 2012), although to date the treatment of implementation uncertainty has lagged behind that of process uncertainty in the biological models (Bunnefeld, Hoshino, & Milner-Gulland 2011). The many and diverse challenges to conservation implementation are multidisciplinary and complex, and require that findings from psychology, sociology and economics be integrated (St. John, Edwards-Jones, & Jones 2010), informing conservation in a more holistic way. Only by bringing these fields together and integrating them into unified frameworks, such as MSE and AM, will we be able to understand and provide tools for addressing the current conservation challenges.

7. Discussion

The Serengeti is one of the most famous protected areas in the world and one of the best studied systems in Africa. In terms of information and resource availability, and international interest and pressure for its conservation, the Serengeti stands in a privileged position when compared to many of the protected areas worldwide, particularly in developing countries. The long history of research and conservation in the Serengeti has produced many of the long-term studies conducted in Africa (e.g. Mduma et al. 1999, Packer et al. 2005, Durant et al. 2007) and several conservation success stories. For example, greater investment in anti-poaching activities since the mid-80s has resulted in the recovery of buffalo (*Syncerus caffer)*, elephant (*Loxodonta africana)* and black rhinoceros (*Diceros bicornis)* populations (Hilborn *et al.* 2006), the abundance and species richness of avifauna in native vegetation inside the national park is higher than in non-protected agricultural areas adjacent to the park (Sinclair, Mduma, & Arcese 2002) and the Serengeti cheetah project expanded into a national program, developing capacity for carnivore conservation in Tanzania (Durant *et al.* 2007). The challenges to the sustainability of the Serengeti, however, have never been greater since the national park was formed in 1951. This represents a unique opportunity to explore the complexities and challenges of managing social-ecological systems (SESs), giving special attention to the issues of observation and implementation uncertainty.

Using a multidisciplinary approach to gain a better understanding of the role and implications of different sources and types of uncertainty for the management of SESs, the research reported in this thesis follows relatively recent trends in conservation and natural resource management that highlight the need to consider the role of people as influential components within SESs in order to promote effective interventions (Adams *et al.* 2004; Ferraro & Pattanayak 2006; Ostrom 2009; Milner-Gulland 2012; Ban *et al.* 2013). To further improve conservation outcomes, processes such as monitoring and implementation must be understood as dynamic features of the system, instead of merely acting upon it, and the multiple sources of uncertainty must be fully considered in conservation planning, requiring the development and application of tools to aid management decision-making under uncertainty. This thesis contributes to progress in both these areas.

7.1. Monitoring social-ecological systems

While monitoring should allow the identification of changes in the biological and social components of SESs, as well as about their evolving relationships (Redman, Grove, & Kuby 2004; Miller, Caplow, & Leslie 2012), the challenges to reliably detecting those changes are plentiful. Monitors often have limited abilities to collect reliable data (Chapters 3 and 4), changes in system conditions may not immediately or linearly translate into effects on target populations (Chapter 5) and social components are generally given less attention than those of an ecological nature despite their importance for conservation implementation (Chapter 6). Moreover, monitoring programmes often lack management-oriented hypotheses, raising questions about their usefulness and efficiency (Nichols & Williams 2006).

What, and how, should we monitor?

Plenty of attention has been given to the issues of survey design and detectability in the scientific ecological literature but many practical issues challenge the effectiveness of monitoring programmes (Buckland 2001; Yoccoz, Nichols, & Boulinier 2001; Danielsen *et al.* 2003; Legg & Nagy 2006; Nichols & Williams 2006; McDonald-Madden *et al.* 2010). Moreover, the issues of non-response and social desirability, and how they may affect the reliability of data obtained through questionnaires, have been widely considered in the social sciences but often remain unaddressed in conservation and natural resource management (Warner 1965; Gavin, Solomon, & Blank 2010; St. John *et al.* 2010). Through the observation of the system, monitors collect data that can then be used to inform decisions but the findings from this thesis highlight the importance of observer effects in explaining survey accuracy (Chapter 3) and the need to consider how survey technique, ecological conditions and differences between species affect data quality (Chapter 3) and the ability to detect changes in population abundance (Chapter 5). Given the reported effects of observation uncertainty in data quality, trend detectability and subsequent management decisions, more attention should be given to its impacts to make sure observed trends actually represent underlying threats or biological processes, instead of being artefacts of the observation process. This is particularly relevant when conducting social surveys about sensitive topics, such as illegal resource use (Chapter 4).

The application of specialized questioning techniques to survey topics of sensitive and/or illegal nature is particularly novel, and Chapter 4 reports the first application of the unmatched-count technique (UCT) to investigate behaviour of conservation concern. This research contributes to a better understanding of the mechanisms behind responses to sensitive questions and demonstrates that UCT may be a useful tool to apply elsewhere. UCT data could be collected in the study area in addition to dietary and socio-demographic information in order to complement more in-depth information, being used for triangulation or to calibrate other tools; however, the effectiveness of the UCT as a long-term monitoring tool still remains to be investigated, specifically its involved costs and how effective it is in detecting changes over time. Other similar types of method have been developed in the political and health sciences, such as the nominative technique and crosswise model (St. John *et al.* 2010; Jann, Jerke, & Krumpal 2011). Most have not been applied within a conservation and natural resource management context, suggesting unaddressed potential to ask about sensitive topics using novel survey techniques. Comparative studies are also particularly limited and deserve further attention; only through robust comparison of several monitoring techniques (both for wildlife and resource use) will we be able to assess their inherent biases and evaluate how, and when, to minimize them.

The relatively little attention given to social data when compared to ecological data in the Serengeti is common elsewhere (Polasky 2008; Wilder & Walpole 2008); monitoring of socio-economic variables and natural resource use is often neglected in areas of conservation concern. The monitoring of institutions, governance structures and social networks over time has been given even less attention in the natural resource management literature (Cundill & Fabricius 2010; McAllister et al. 2013 are some exceptions) but may provide essential information, particularly when linked to specific conservation outcomes. Given their importance in explaining conservation implementation (Chapter 6), monitoring social structures and human behaviour deserves further consideration and should provide insights into how shifts in social, political and economic institutions affect livelihoods and natural resource use. These monitoring programmes would be particularly informative when designed to evaluate what works and when using, for example, randomized experimental designs or matching (Ferraro & Pattanayak 2006).

While population abundance across time is a commonly used indicator of population change (Mace *et al.* 2008), monitoring effectiveness might be improved by targeting specific demographic parameters, measures of habitat or threat indicators. For example, Katzner et al. (2007) demonstrated the importance of collecting data on adult survival of Imperial eagles *Aquila heliaca* instead of territory occupancy to detect population trends, while Jenkins et al. (2003) synthesized all estimates of trends in habitat extent to assess global change in nature, and Salafsky & Margoluis

(1999) used threat reduction assessment to evaluate conservation success and infer changes in biodiversity trends. While some variables may be easier to collect than others, not all are similarly valuable to measure conservation success. For example, attitudes are generally used as a behavioural proxy despite evidence of often weak links to actual behaviour (Heberlein 2012). Relatively little attention has been given, however, to how different monitoring targets compare in providing robust information about changes, particularly when collecting information on people's behaviours of conservation concern or other behavioural proxies. The modelling framework described in Chapter 5 could be expanded to provide a comparison of trends obtained from different monitoring targets, such as those of ecological and social nature, similarly to a management strategy evaluation framework in which both social and ecological processes are monitored. This would provide much needed information about the effectiveness and efficiency of different types of monitoring for SESs.

When is it worth monitoring?

The assumption that more information is always useful for conservation is often flawed, particularly given the limited resources available and trade-offs between different potential actions (Nichols & Williams 2006; McDonald-Madden *et al.* 2010). Furthermore, monitoring may create the illusion that something useful has been done (Legg & Nagy 2006), while the actual outcomes may be null or even worse than before. The value of obtaining additional data in the Serengeti and the usefulness of different kinds of information must be compared in terms of achieving specific objectives, following applications of the expected value of information in decision theory (Runge, Converse, & Lyons 2011). While there are many reasons for conducting monitoring, such as learning about the system, audit management actions and inform management decisions (Jones *et al.* 2013), all should require an assessment of how monitoring actually contributes to achieving them. Such an approach is currently lacking in the study area, at least formally, and would provide support for the continuation (or not) of those programmes, assessing trade-offs between several interventions (e.g. monitoring vs. management) and identifying conditions under which monitoring is worth conducting.

If the detection of declines to trigger conservation interventions is assumed as the main monitoring objective in the Serengeti, survey frequency and monitoring length are important factors in explaining monitoring effectiveness, particularly the power to detect true negative trends (Chapter 5). In addition, the findings from Chapter 5 show that, under current monitoring conditions and realistic levels of population change, the probability of reporting stable wildlife populations as nonstable (type I error) is very low. Similar analyses for other systems would contribute to greater accountability and transparency, allowing decision-makers to link outcomes to specific monitoring decisions and reducing the prevalence of situations in which decisions are unnecessarily postponed. In addition, data quality (i.e. accuracy and precision) is affected differently by multiple sources of uncertainty and priorities for minimizing observation uncertainty should be set according to the survey technique and biological characteristics of the species (Chapter 3). This implies that not all uncertainty is reducible or worth minimizing. For example, in highly aggregated species of savannah ungulates, the main focus should be on survey precision but accuracy is the key factor for random or slightly aggregated species. Investing in the sources of uncertainty to which data quality is most sensitive in a particular location should then be the recommended strategy.

To contribute to evidence-based management decisions, monitoring must also be carefully tailored to specific management requirements. For example, while quotas for hunting in the games reserves in the Serengeti are produced annually (although trophy hunting is currently not active in the Western Serengeti), the monitoring data being collected by the governmental agencies is generally not adequate to make decisions at that spatial scale. The findings from Chapter 5 show that trends in impala populations are very likely to be undetected, even when using high monitoring budgets. While harvest quotas should be based upon the available monitoring data, the data available would most likely not produce reliable harvest decisions under the current monitoring conditions, at least for some species.

7.2. Conservation implementation

Minimizing discrepancies between plans and realised action in natural resource management and conservation is one of the most important priorities for improving the effectiveness of interventions. Yet it is one of the most challenging and least addressed issues in the scientific conservation literature (Knight *et al.* 2008; Biggs *et al.* 2011). While the success of conservation interventions may be affected by unexpected environmental and ecological effects, implementation uncertainty primarily arises from social components of the systems under consideration. The findings from this thesis indicate that implementation uncertainty in the Serengeti is greatly affected by illegal bushmeat hunting by local communities and associated difficulties in quantifying and addressing that rule-breaking behaviour (Chapter 4) and social processes within and between management institutions (Chapter 6). Improving implementation (rather than research, monitoring or assessment) is generally perceived by managers and researchers working in the Serengeti as the key priority that should be addressed to improve conservation outcomes (Chapter 6).

How to reduce implementation uncertainty?

Illegal hunting by local communities has remained a notoriously difficult issue to address in the Serengeti. Anti-poaching enforcement has been one of the main activities of the national park since its creation, costing approximately 15% of its annual budget (Watson 1965; Arcese, Hando, & Campbell 1995; Holmern, Muya, & Røskaft 2007; Thirgood *et al.* 2008). Although rule non-compliance has been little addressed in conservation, there is a vast literature on rule-breaking from the social, psychological and economic sciences (Keane *et al.* 2008). In the Serengeti, despite the general awareness of the illegality of hunting and its repercussions, its monetary and protein-based benefits greatly exceed the expected costs perceived by local people (Bitanyi *et al.* 2012; Knapp 2012). Given the considerable amount of research already devoted to understanding the socioeconomic and cultural factors associated with hunting in the Serengeti (e.g. Loibooki et al. 2002; Johannesen 2005; Nyahongo et al. 2006; Knapp 2012; Moro et al. 2013; Chapter 4), the priority is not for further research. Instead there is a need for integration of existing theoretical and empirical understanding of the incentives for non-compliance in the study area into approaches to reducing rule-breaking behaviour, allowing managers to more realistically account for natural resource user behaviour. This understanding has already been gradually translating into a more community-centred approach to conservation in the Serengeti instead of law enforcement alone, with increasing attention being given to the impacts of protected areas on local communities and their livelihoods. The extent to which this has been successful is, however, still limited, due to poor governance, lack of proper incentives and conflicting relationships between managers and local communities (Chapter 6).

Flexible and transparent decision-making, enhancing collaboration, accommodating a plurality of values, perceptions, and beliefs, and identifying common goals and a shared vision among stakeholders are key priorities to addressing the "implementation crisis" (Reed 2008; Biggs *et al.* 2011). This demands a multifaceted toolkit combining qualitative and quantitative techniques and will require different solutions according to the specific context and study system, such as mental models to incorporating multiple sources of knowledge (Biggs *et al.* 2011) and choice experiments (Moro *et al.* 2013) to investigating how people may respond to different conservation interventions. To further explore social processes and interactions, simulation models may be useful to integrate ecological information with human decision-making processes; for example, agent-based modelling has been shown to be a powerful way of incorporating agent behaviour, producing emergent behaviour at higher levels (Matthews 2007; Rounsevell, Robinson, & Murray-Rust 2012).

7.3. Decision-making under uncertainty

Uncertainty is often used as an excuse for inaction and for decision makers to question the overall usefulness of science (Polasky *et al.* 2011; Kujala, Burgman, & Moilanen 2013). Uncertainty may have important implications for management decisions, relationships between stakeholders and conservation outcomes and, while it is not completely reducible, innovative tools that deal with uncertainty are much needed. For example, one of the most recent and controversial threats in the Serengeti has been a recently proposed highway crossing the national park. This generated an ongoing controversy about trade-offs between different development pathways and their ecological impacts, with questions being raised about the uncertainty surrounding the expected ecological impacts, the relative importance of this threat when compared to others such as climate change, and potential cumulative effects on other threats, such as poaching (Dobson *et al.* 2010; Homewood, Brockington, & Sullivan 2010; Holdo *et al.* 2011; Fyumagwa *et al.* 2013). For science to be increasingly used to inform management decisions in situations like this, further work must be done on assessing, minimizing and improving communication of multiple types of uncertainty, while integrating information about multiple system components, considering trade-offs and also acknowledging the psychological processes behind reactions to uncertainty (e.g. risk-averse vs. risk-prone people).

How to aid management decision-making under uncertainty?

Accounting for multiple types and sources of information and carefully weighting the risks involved in each alternative strategy are key requirements for a robust and transparent approach to decision-making under uncertainty. Experimentation is often difficult, not only due to terrain, lack of capacity and the financial and time costs involved, but also due to ethical and logistic limitations to the ability to manipulate experimental settings. Decision-theoretic approaches within simulation models, such as those used in this thesis (Chapters 3 and 5), are thus particularly useful to aiding decisions about conservation interventions. For example, the notion that monitoring should start in the office, by considering survey design, power, capacity, funding sustainability and specific management requirements before actually implementing the monitoring programmes is obviously not new, but still overlooked in practical terms. Models are often perceived as oversimplications and mistrusted. Therefore in order to enhance their contribution to problem-solving in conservation, scientists should work with stakeholders from the beginning to make sure their contribution is relevant, addressing questions that the practitioners really want to know about, improve communication and build trust (Addison *et al.* 2013).

Theoretical applications and simulation modelling, however, do not remove the importance of conducting field experiments, actively testing the effects of alternative actions and discriminating among competing hypotheses. The exchange between models and field experiments should be such that both benefit and evolve as more knowledge is gained, following the elements of adaptive management (Keith *et al.* 2011). For example, the ability to adequately link changes in system dynamics, structure and composition with the actual processes causing them is often poor. An adaptive management and monitoring process (Lindenmayer & Likens 2009; Lindenmayer *et al.* 2011) would be useful to provide insights into how specific threats may affect systems, how do changes translate into monitoring and how to better detect, predict and prevent changes in biodiversity. Integrated frameworks such as management strategy evaluation would be particularly useful to bridging the gap between field data, modelling and adaptive management in the real world, supporting decision-making under uncertainty.

7.4. Management strategy evaluation

"In preparing for battle I have always found that plans are useless, but planning is indispensable."
(Dwight D Eisenhower)

Management strategy evaluation (MSE) has been used in this thesis as a conceptual framework to illustrate the composition and dynamics of SESs, making explicit the linkages between monitoring and management decisions and potential sources of multiple types of uncertainty. When used as a quantitative tool, MSE provides information about the relative performance of each alternative management strategy to achieve set criteria, given the uncertainty inherent in the system being managed (McAllister *et al.* 1999; Sainsbury 2000). Applying MSE as a quantitative decision-support tool involves the following steps: 1) specification and quantification of the management objectives in the form of performance measures; 2) development and parameterization of "operating models"; 3) identification and simulation of candidate strategies; 4) summary of performance of each alternative strategy; 5) selection of the management strategy that best meets the previously defined criteria (McAllister *et al.* 1999; Rademeyer, Plaganyi, & Butterworth 2007). Through an iterative process of testing and development, this approach may be used to identify strategies that are capable of balancing multiple goals (e.g. economic, social and biological).

MSE: a powerful tool for conservation in the Serengeti?

Using MSE as a quantitative tool in the Serengeti would be most constructive if used to investigate the implementation of conservation policies developed to affect hunter decisions. This would require the development of a dynamic model of natural resource user behaviour to explore potential changes in hunter decisions according to multiple alternative management strategies, such as investing in law enforcement or livelihood enhancements. In terms of potential future applications, this approach would be particularly useful for its integration of social-ecological considerations into an integrated framework aimed at improving conservation outcomes. Conservation planning and implementation would greatly benefit from a more realistic consideration of how local communities will react to different conservation interventions, in order to provide decision-makers with robust tools for investigating trade-offs between economic, social and ecological objectives. Given the ethical and logistic implications of experimenting on wildlife and local communities, approaches such as MSE should be recommended as a first step to actual implementation in the study area. In practice, the following key issues would have to be addressed for this approach to be of real use for the conservation of hunted ungulate species in the Serengeti:

(1) feedback between monitoring and management actions to control bushmeat hunting

The minimum requirement for MSE to be appropriate is that there are links between monitoring and management decisions. However, the findings from Chapter 6 show that the links between system components (monitoring, assessment and implementation) are currently not well established and fully functional in the Serengeti. The lack of evaluation from monitoring also makes it difficult to learn from previous and ongoing interventions. Increasing the perceived value and use of scientific information, implementing integrated monitoring programmes encompassing both wildlife and resource users, and robustly evaluating ongoing interventions, should be key priorities for improving the management of the system, providing much-needed information of direct relevance to management decisions.

(2) defining socioeconomic and ecological objectives and performance measures

The first step in applying a MSE approach is specifying and quantifying management objectives in the form of performance measures. While there are broad socioeconomic and conservation objectives shared by stakeholders in the Serengeti (Chapter 6), further work must be done on setting specific management targets. The main associated challenge is, however, finding clear representatives; 106 groups of institutional stakeholders were identified in a study by the Serengeti Ecosystem Management Project (SEMP 2006) but reaching a consensus about specific management targets in such a large stakeholder pool would be extremely challenging. Finding a suitable spatial scale where decisions would be more tractable would be recommended, while having in mind the wider scale and dynamics of the Serengeti.

(3) modelling hunter decisions

A resource user model would require, for example, developing a household utility model to investigate trade-offs between livelihood options, such as farming and hunting, to maximizing wellbeing. These choices would be modelled in function of alternative management strategies, such as increased law enforcement, access to microcredit schemes and availability of other protein sources. Given the recent work on potential economic effects of policies to mitigate bushmeat hunting and consumption in the Serengeti (Rentsch & Damon 2013; Moro *et al.* 2013) and previous work on the trade-offs between farming and hunting in the area (Barrett & Arcese 1998; Johannesen 2005), this would be a logical next step to expand the research presented in this thesis. Using data from random utility models to specify human decision making would allow a better linkage between MSE outputs and the study area but one of the biggest challenges to realistically model human behaviour in the study area would be incorporating intertemporal choices, i.e. how individuals trade-off costs and benefits in function of time, which is still generally poorly understood (Keane *et al.* 2008) and for which no empirical data is available in the Serengeti.

(4) institutional flexibility and collaborative work

Practical applications of MSE and adaptive management are often challenged by a lack of stakeholder engagement, not using learning to modify policy and management, lack of leadership, unwillingness to embrace uncertainty and lack of a long-term vision (Payne 1999; Walters 2007; Allen & Gunderson 2011). For MSE to have practical use in the Serengeti, relationships within stakeholder forums, current platforms for data sharing and collaboration across institutions must be strengthened. This is when institutional barriers, personal characteristics and relationships with local communities may play a greater role in hindering or facilitating efforts to use MSE. The Serengeti already has a number of these collaborative initiatives, such as the Serengeti Ecosystem Community Conservation Forum and the Serengeti-Mara database, so it would be mainly a case of making these already available tools more sustainable and operational. This could actually be where using MSE could reveal particularly useful, providing a framework for interaction with stakeholders, synthesizing available information and prompting clearer thinking about long-term and short-term objectives, system dynamics and linkages.

The Serengeti has many critical issues and challenges that need to be addressed for its better management and full functionality as a resilient SES. Instead of focusing on MSE as a quantitative modelling tool, its potential as a conceptual framework and approach to conservation is even greater. For example, while applying MSE to conservation in the Serengeti may be complex and challenging given its institutional complexity, poor governance, number of stakeholders involved and controversial trade-offs between poverty and conservation, the exercise alone of engaging stakeholders around discussion about, and planning for, MSE could reveal useful if applied at a larger scale within the Serengeti. MSE as a robust operational model to conservation implementation should be given special consideration, particularly in case studies where management decisions are hindered by the need to consider multiple conflicting objectives and many types of uncertainty.

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Appendix A – Supplementary information for Chapter 3

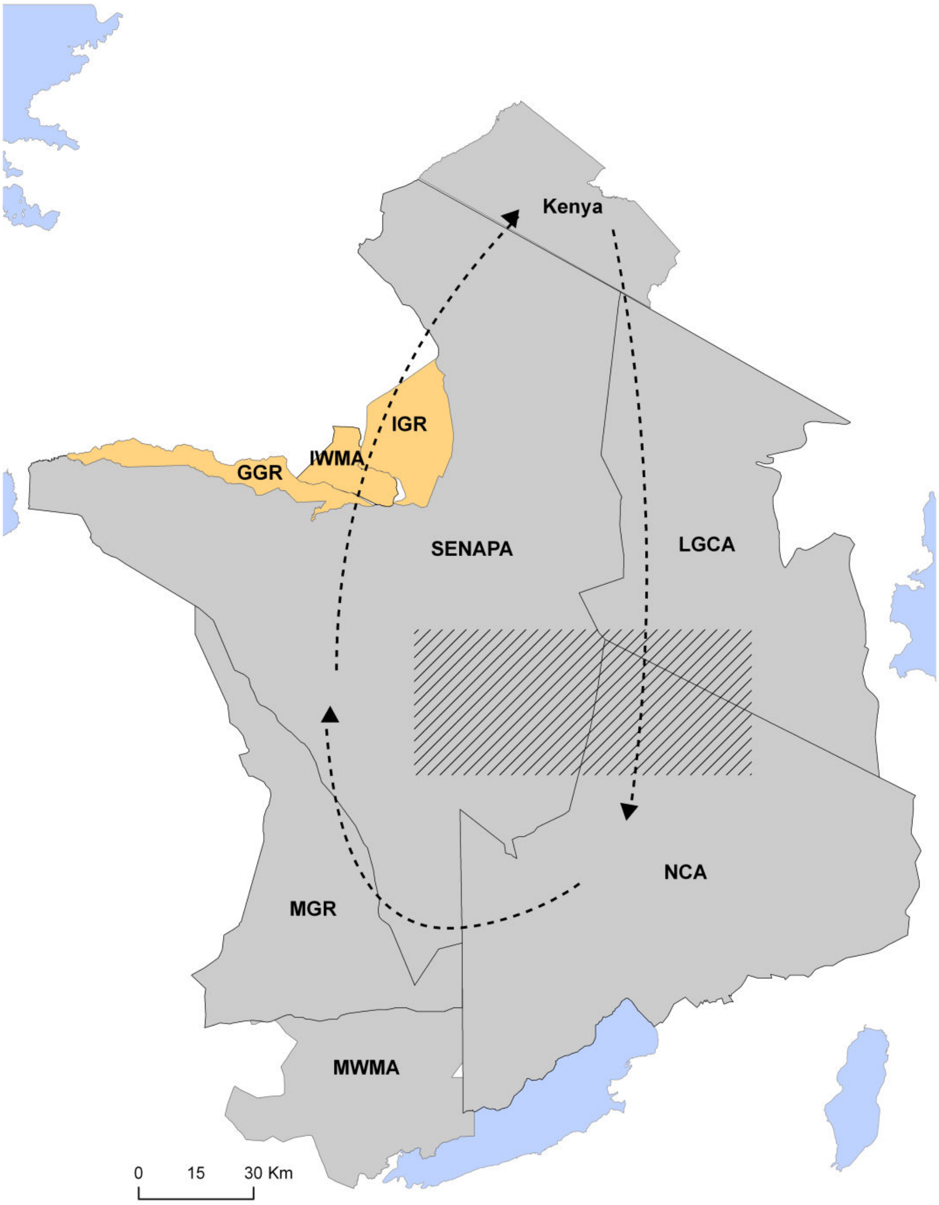

Figure A1. Protected areas and lakes (blue) within and surrounding the Serengeti ecosystem. SENAPA = Serengeti National Park, LGCA = Loliondo Game Controlled Area, NCA = Ngorongoro Conservation Area, MGR = Maswa GR, GGR = Grumeti Game Reserve, IWMA= Ikona Wildlife Management Area, and IGR = Ikorongo Game Reserve. Dashed arrows indicate broad wildebeest migration patterns. Yellow protected areas show impala monitoring area (around 1500 km^2) and filled rectangle represents area of wildebeest monitoring in 2009 (around 2900 km^2).

Description of the sampling steps in the wildlife monitoring model

A) Wildebeest

The broad distribution of the wildebeest population in a given year is defined by an initial reconnaissance survey; transects along this area are then flown with starting points on a systematic pattern, spaced at either 5km or 2.5km. Each transect is sub-sampled by taking vertical aerial photographs every 5-30 seconds using a camera with a 35 mm focal length lens. Altitude is recorded at the same time (Hilborn & Sinclair 2010).

In the model, each row of the spatial grid corresponded to a "potential transect" while each cell corresponded to a "potential photo" (Figure A2).

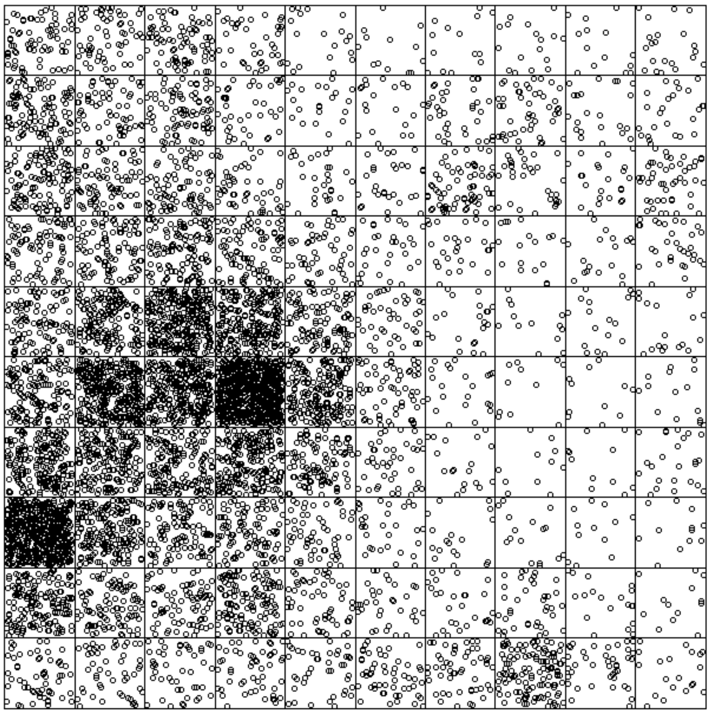

Figure A2. Example of wildebeest distribution plot in which animals are distributed according to specific parameters of aggregation and spatial autocorrelation range. Quadrats represent "potential photos" and dots represent individual animals.

To test the effect of sampling intensity on precision and accuracy, we varied the distance between transects and time between photos. Transects were systematically started 0.5-24 km apart with the first transect corresponding to the first row of the grid and aerial photos within each transect were taken every 1-120 seconds (maximum distance and time were defined in order to produce at least 5 transects per survey and 5 photos within each transect); time between photos was estimated from simulated flight speed.

B) Impala

Large-scale monitoring of resident species in the area is conducted through aerial sampling. East-west transects are flown, spaced 2.5km apart, and subunits are defined as 30 seconds of flying time, when altitude and wildlife counts are recorded (Campbell & Borner 1995). Rear seat observers record the sub-unit identification and counts of large animals within each sub-unit. Strips are defined by pairs of fibreglass rods attached to the wings of the aircraft defining inner and outer boundaries (Norton-Griffiths 1978; TAWIRI 2010).

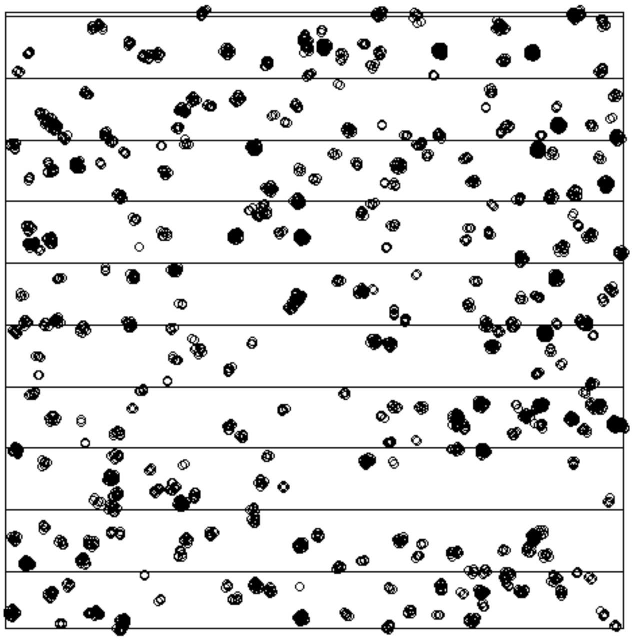

Figure A3. Example of spatial distribution of impalas within a section of the simulated survey area. Lines represent "survey transects" and dots represent individual animals.

To test the effect of sampling intensity on precision and accuracy, in the model, transects were conducted 0.5-7 km apart, producing at least 5 transects per survey and guaranteeing no overlap between transects. As in the real aerial surveys of resident species in the study area, transects had variable lengths due to the shape of the virtual landscape and only adult animals within strip boundaries were recorded.

Description of the observational procedures (flight and observer effects) in the wildlife monitoring model

A) Wildebeest

Mean flight speed and mean altitude were considered to be fixed (assumed to be related to technical flight characteristics). Simulated flight speed and altitude were assumed to have a lognormal error distribution; lognormal distributions are commonly applied to model multiplicative random processes (Hilborn & Mangel 1997).

Flight speed affects spacing between photos, while flight altitude affects actual area covered by each photo. The area of each photograph varies with the physics of the camera, the altitude and the angle of the camera relative to the ground (Campbell & Borner 1995). The best fit curve to the data, estimated by Hilborn & Sinclair (2010) by comparing actual areas measured by photographs of a runway with markers of known length, is:

$$area = \frac{(0.2506alt)^2}{15056} \qquad \text{eqn A1}$$

where *area* is area of photograph in hectares and *alt* is altitude above the ground in feet.

The behaviour of juveniles makes them less detectable in visual surveys. For example, Gonzalez-Voyer, Smith & Festa-Bianchet (2001) showed that the magnitude of the counting errors differs between age-classes in mountain goats and Sinclair (1973) suggested that wildebeest calves hidden behind other animals were an additional source of counting error. To simulate miscounting of animals in each photo, we assumed different error distributions for juvenile and older wildebeest. We assumed that juveniles are more likely to be miscounted, especially in large aggregations due to their higher probability of being hidden behind other animals; the proportion of missed juveniles (p) followed a logit distribution according to the total number of animals in the photo:

$$logit\ (p) = \ln\left(\frac{p}{1-p}\right) \qquad \text{eqn A2}$$

The assumed minimum undercounting error and the number of animals in a photo for which 50% juveniles are missed (juvenile detectability; Table 3.1) were used to calculate the slope and intercept for the linear predictors for the logit distribution:

$$\ln\left(\frac{p}{q}\right) = a + bz \quad \text{eqn A3}$$

where p is proportion of missed juveniles, q is proportion of non-missed juveniles, z is total number of animals per photo, and a and b are the intercept and slope of the linear predictor. The proportion of missed juveniles was then simulated using an inverse transformation for a logit function:

$$logit^{-1}(x) = \frac{e^x}{1 + e^x} \quad \text{eqn A4.}$$

For older wildebeest, we used a lognormal error distribution; this is a standard distribution to model measurement error when errors follow a normal distribution and variance increases with increasing sample size (Hilborn & Mangel 1997, Crawley 2007).

To incorporate spatial autocorrelation into juvenile and adult counting errors, for example due to habitat or weather conditions, we conditioned the outcome of the error distribution on the spatial effects defined by a Gaussian process with variance-covariance matrix C related to an exponential correlation function between unit locations:

$$C=\sigma_s^2\, exp\,(-d_{ij}/\rho hi) \quad \text{eqn A5}$$

where d_{ij} is the distance between grid units i and j, σ_s^2 is the threshold variance known as the sill and ρhi is the range parameter that represents a fraction of the distance beyond which there is little or no autocorrelation (Diggle, Tawn & Moyeed 1998). We assumed that the same spatial patterns affected juvenile and adult counting errors.

b) Impala

Similarly to wildebeest, mean altitude was assumed to be constant, while actual altitude incorporated lognormal distributed errors. Altitude affects the actual transect width and the size of the "blind spot" under the aircraft (Norton-Griffiths 1978). Flight speed was kept at a constant mean value; although flight speed affects the number of sub-units for each transect, sampling intensity is not affected (sub-units are consecutive and without gaps, covering complete transect). Assuming the virtual aircraft was calibrated to conduct transects of 282m (141m each side) with a 250m blind spot at an height of approximately 92m (300 feet; calibration values commonly used in aerial surveys; Khaemba et al. 2001), the simulated variation in altitude was assumed to produce directly proportional variations in width of the transect and blind spot.

Distance of each impala to the nearest transect line and herd size were used to simulate the effects of: (1) herd detectability (bigger herds are more likely to be seen); (2) distance (animals further away are less likely to be seen); (3) individual detectability (animals in bigger herds are less likely to be seen). Similarly to the juvenile wildebeest undercounting errors, each of these processes was simulated using an inverse transformation for a logit distribution parameterized with their assumed minimum (or maximum) detectability and assumed values for which the likelihood of detecting herds or individual impala is 50% (Table 3.1).

Visible animals were identified in the model after applying each of these effects. Simulated counts per observer were obtained, assuming subunits of 30 seconds for which visible animals are summed. Observers' ability to provide reliable counts may vary; counting error for each observer (2 per survey) was assumed to be lognormal and applied independently to each observer's transects. Similarly to wildebeest, spatial autocorrelation was incorporated into these errors. Simulated counts from different observers were then summed for each transect and mean counting error variability was estimated.

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Table A1. Description of modelled variables and range of values explored for low and high budget monitoring scenarios of: A) wildebeest and B) impala.

Parameters	Notation	Low budget	High budget
A. Wildebeest			
Population characteristics			
Population size	N_{wild}	200 000 – 2 000 000	
Proportion of juveniles (%)	α	5 - 35	
Aggregation	k	0.01 - 2	
Spatial autocorrelation range	ρhi	0.1 - 0.5	
Sampling characteristics			
Distance between transects (km)	γ_{wild}	15.7-24	0.5-8.3
Time between photos (seconds)	δ	80-120	1-40
Flight characteristics			
Mean flight altitude (feet)	ε_{wild}	Fixed (1200)	Fixed (1200)
CV error altitude	ζ_{wild}	0.14-0.2	0 - 0.07
Mean flight speed (km/sec)	θ_{wild}	Fixed (0.06)	Fixed (0.06)
CV error speed	ι_{wild}	0.2-0.3	0 - 0.1
Observer effects			
Minimum error counting juveniles (%)	Λ	0.14 – 0.2	0-0.07
Juvenile detectability (number of animals in a photo for which 50% juveniles are likely to be missed)	$\ddot{\imath}$	40 – 50	20-30
CV error counting adults	$\ddot{\upsilon}$	0.33 - 0.5	0-0.16
Counting error autocorrelation range	phi_{wild}	0-1	0-1
B. Impala			
Population characteristics			
Population size	N_{imp}	1 000-15 000	
Median herd size	ξ	5-50	
CV herd size	o	0-0.5	
Maximum herd home range (km²)	π	0.5-3	
Individual space (km²)	ς	0.05-0.2	
Sampling characteristics			
Distance between transects (km)	γ_{imp}	4.3-7	0.5-2.7
Flight characteristics			

Mean flight altitude (feet)	ε_{imp}	Fixed (300)	Fixed (300)
CV error altitude	ζ_{imp}	0.14-0.2	0-0.07
Mean flight speed (km/sec)	θ_{imp}	Fixed (0.06)	Fixed (0.06)
Observer effects			
Minimum herd detectability (%)	σ	0.05-0.20	0.33-0.5
Herd size non-detectability (herd size for which there is a 50% chance of missing it)	τ	37-50	10-23
Individual detectability at distance 0 (%)	υ	0.7-0.8	0.9-0.99
Detectability by distance (distance for which there is a 50% chance of seeing animals; km)	φ	0.125-0.167	0.21-0.25
Maximum individual detectability (%)	χ	0.7-0.8	0.9-0.99
Herd size estimatibility (number of animals in a herd for which 50% are likely to be missed)	ψ	10-23	37-50
CV counting error	ω	0.33-0.5	0-0.16
Error autocorrelation range	phi_{imp}	0-1	0-1

Table A2. Results from generalised linear models fitted to precision (coefficient of variation and normalized variance) and inaccuracy (percent discrepancy between the estimated mean population size and the known population size) for wildebeest monitoring. The table shows the coefficients of all the parameters and interactions obtained from the full model. Significance is coded as: ***=P<0.001, **=P<0.01, *=P<0.05

Parameter	Standardized regression coefficients (β)	Unstandardized regression coefficients			
	Normalized variance (CV^2)	Coefficient of variation (CV)	Normalized variance (CV^2)	Inaccuracy	Inaccuracy (juveniles only)
Population size	-0.05**	-6.15×10^{-8}***	-1.37×10^{-7}***	3.817×10^{-6}***	8.75×10^{-7}***
Proportion of juveniles	-0.03	-4.54×10^{-3}***	-9.49×10^{-3}***	0.52***	-2.74×10^{-3}**
Aggregation (*k*)	**-0.33***	-0.63***	-1.30***	0.28	-0.17***
Spatial autocorrelation	**0.58***	0.70***	1.20*	6.91**	0.34**
Distance between transects (km)	**0.21***	0.01***	0.02**	0.07*	-4.42×10^{-4}
Time between photos (sec)	**0.24***	3.31×10^{-3}***	7.02×10^{-3}***	5.23×10^{-3}***	-1.85×10^{-4}
CV error altitude	0.03	-0.08	-0.13	1.21	-0.01
CV error speed	-0.01	-0.28*	-0.48	1.36	-6.67×10^{-3}
Minimum error counting juveniles (%)	0.03	-0.71*	-1.05	15.40***	0.96***
Juvenile detectability	-0.03	-0.02***	-0.05***	-9.85×10^{-3}	-0.02***
CV of error counting adults	0.04*	-0.18	-0.20	4.57**	0.52***
Spatially autocorrelated errors	0.02	-1.46***	-2.62***	8.47***	1.06***
Spatially autocorrelated error* CV of error counting adults	-0.05**	0.39	0.49	-7.68**	-0.66***
Spatially autocorrelated error*	-0.02	0.03***	0.06***	-0.15***	-0.02***

Juvenile detectability					
Spatially autocorrelated error* minimum error counting juveniles	**-0.11***	1.37*	2.12	-15.04*	-1.37**
Spatial autocorrelation*distance between photos	**-0.11***	-2.24×10^{-3}	-4.68×10^{-3}	-0.02	-1.72×10^{-3}
Spatial autocorrelation*distance between transects	-0.07***	2.06×10^{-3}	0.01	-0.22	-5.12×10^{-3}
Aggregation * Spatial autocorrelation	**0.13***	1.23***	2.47***	-3.98**	-0.13**

Table A3. Results from generalised linear models fitted to precision (coefficient of variation and normalized variance), inaccuracy (percent discrepancy between the estimated mean population size and the known population size) and survey adequacy (able to detect at least one herd or 5 animals) for impala monitoring. The table shows the coefficients of all the parameters and interactions obtained from the full model. Significance is coded as: ***=P<0.001, **=P<0.01, *=P<0.05

Parameter	**Standardized regression coefficients (β)**	**Unstandardized regression coefficients**			
	Normalized variance (CV^2)	**Coefficient of variation (CV)**	**Normalized variance (CV^2)**	**Inaccuracy**	**Adequacy**
Population size	-0.58***	-6.85×10^{-5}***	-1.35×10^{-4}***	3.90×10^{-4}***	1.48×10^{-4}***
Mean herd size	0.29***	9.56×10^{-3}***	0.02***	0.21***	-0.04***
CV herd size	0.03	6.64×10^{-4}***	0.02	12.1***	-0.06
Maximum herd home range (km^2)	-0.07***	-0.06***	-0.12***	1.72***	0.07
Individual space (km^2)	-0.05*	-0.86***	-1.75***	28.8***	0.03
Distance between transects (km)	0.74***	0.18***	0.34***	0.50***	-0.49***
CV error altitude	-0.04	-0.50**	-0.92**	11.4*	-1.42
Minimum herd detectability (%)	-0.11***	-0.41***	-0.85***	0.73	0.47
Herd size detectability	0.14***	4.13×10^{-3}***	8.34×10^{-3}***	0.35***	-7.00×10^{-3}***
Detectability at distance 0 (%)	-0.06**	-0.80***	-1.57***	22.4***	1.11
Detectability by distance	-0.04*	-1.33***	-2.51***	43.8***	0.62
Maximum individual detectability (%)	0.03	-0.47***	-0.83***	38.9	-3.96***

Herd size estimability	-0.30***	-0.01***	-0.02***	-0.39***	0.08***
CV counting error	0.04	0.06	0.13	4.5*	-0.16
Spatially autocorrelated errors	0.02	-6.99×10^{-3}***	-0.03	-0.68	-0.08
Spatially autocorrelated errors*CV counting error	0.04*	0.07	0.19	-1.66	0.33

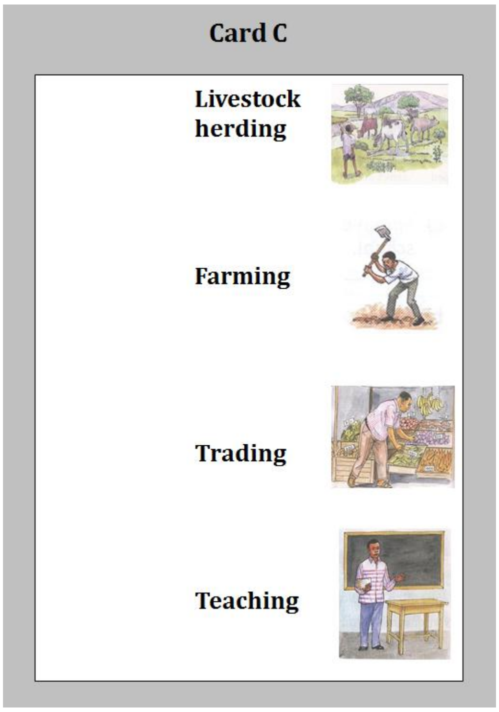
Appendix B – Supplementary information for Chapter 4

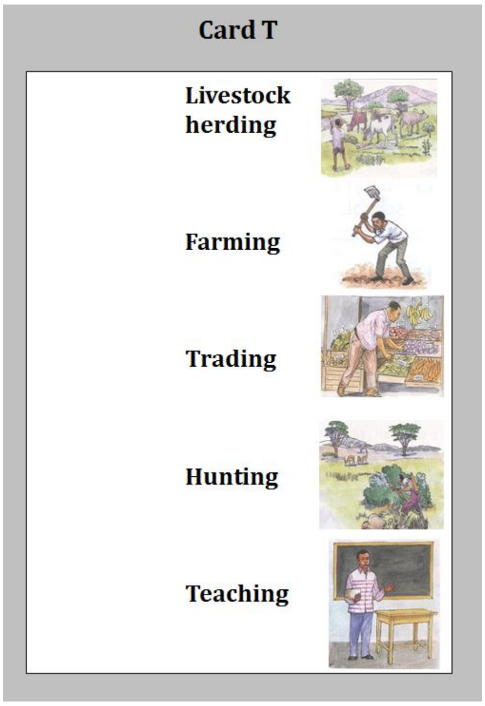
Sample cards: UCT (Unmatched Count Technique)

INTERVIEWER, PLEASE READ THE FOLLOWING EXPLANATORY TEXT:

I have one more question for you. I will show you a card with several answers and I need you to tell me how many of these answers apply to your household.

Do not tell me your answer because I just want to know how many.



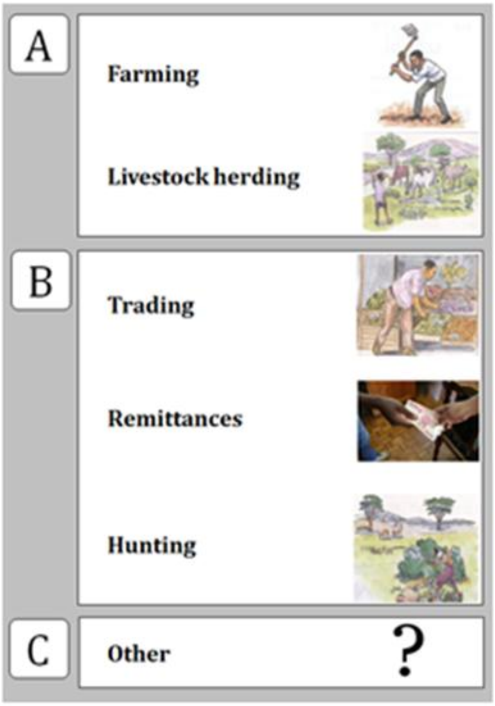


Sample cards: 2 cards method

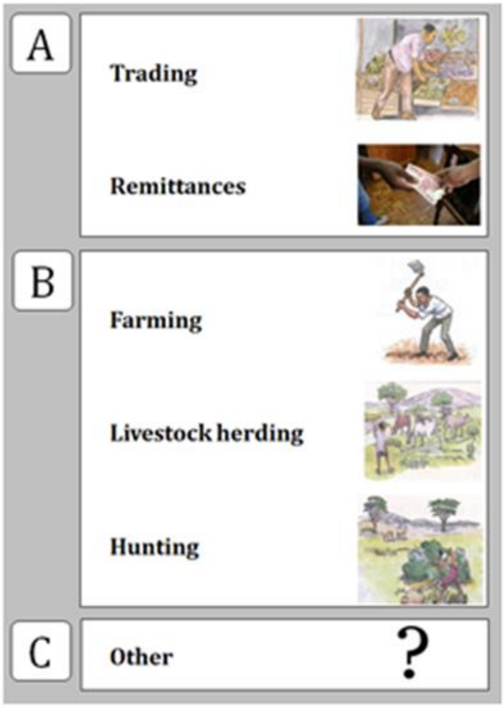
INTERVIEWER, PLEASE READ THE FOLLOWING EXPLANATORY TEXT:

I have one more question for you. I will show you a card with several answers and you just point to the box where is your answer. Do not tell me your answer because I just want to know <u>in which box of this card it is</u>.

CARD 1



CARD 2



Sample cards: RRT (Randomized Response Technique)

INTERVIEWER, PLEASE READ THE FOLLOWING EXPLANATORY TEXT:

I have one more question for you but for this we are going to play a game.

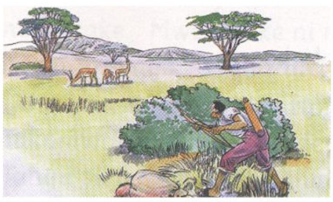
In this bag I have balls of different colours (SHOW). You will take one ball from this bag, look at the ball and memorize the colour. Then, put the ball in the bag again. Please, do not show me the ball nor tell me the colour because this is going to be your secret.

Next, I am going to show you a card (SHOW). If you get a RED ball, say YES. If you get a BLACK ball, say NO. If you get a GREEN ball, please reply truthfully to the question in the card. I don't know which ball you will get and your answer should always be YES or NO, so I have no way of knowing what you mean.

During the last 12 months, has anyone in your household been hunting?

- YES

- NO



(YES/ NO)

Sample questionnaire (English version)

Interviewer: ____

Date: ________________

Village: _______________________________ **Sub-village:** ___________________________

<u>**INSTRUCTIONS FOR ENUMERATOR:**</u>

Before starting the questionnaire, you must "play a game" to know which cards should be used for this household. Here are the rules:

<u>throw the die</u> I gave you, <u>count the number of points</u> and, if you get:

1, 2 or 3 points, please use cards **C**;

4, 5 or 6 points, please use cards **T**.

How many points did you get?___________________

Which cards will you use? ______________________

Please, always follow these rules! Thank you!

PLEASE READ OUT:

"My name is [name of enumerator]. I am here on behalf of Ana Nuno who is collecting information for her studies in England. We are conducting a short questionnaire about local communities in the Serengeti and this will only take a few minutes.

If you choose to take part in the questionnaire, your name will not be recorded and your answers will not be shared with other members of the community or the authorities. Would you like to continue with the questions?"

[If **NO**, write gender and approximate age of respondent and FINISH HERE]

Gender: Male _____ **Age:** 18-25 _____

Female _____ 26-45 _____

46-65 _____

66+ _____

[If **YES**, write down time interview started] **Start time:** ______________

Section A: Individual socio-demographic information (about respondent only)

1. Gender: Male ______ Female _______

2. Age: ____________

3. Are you the head of household? Yes ______ No _______

4. Ethnic group [Circle one]

a) Ikoma

b) Nata

c) Sukuma

d) Kurya

e) other: __________________________

5. Level of education [Circle one]

a) primary school

b) secondary/college education

c) no formal education

Section B: Household socio-demographic information (<u>about household</u>)

6. In this household:

a) how many adult males (15 years old or older) are there? _______________

b) how many adult females (15 years old or older) are there? _____________

c) how many children (younger than 15 years old) are there? _____________

7. During the last year, how many people in your household had:

a) full-time employment? _______________

b) seasonal employment? _______________

8. How many years has your household lived in this village? _______________

Section C: Household occupations

<u>INSTRUCTIONS FOR ENUMERATOR:</u>

To ask these questions, <u>please follow these rules</u>:

Please remember how many points you got when playing the initial game.

If you got **1, 2 or 3** points, please ask section **C1**;

If you got **4, 5 or 6** points, please ask section **C2**.

How many points did you get?___________________

Which cards will you use? ______________________

Which section will you ask? ______________________

Section C1: Household occupations (<u>ASK ONLY IF YOU GOT **1, 2 OR 3 POINTS**</u>)

[Read out] *I am going to show you a card with animals. I am going to read their names and then I want you to tell me <u>how many</u> of these animals cause problems in this area.*
Please, <u>don't tell me which ones, just tell me HOW MANY.</u>

[Show card **C with animals**, read names and ask:]

9. How many of these types of animals have caused problems in your village in the <u>last dry season (May-October)</u>? [Circle answer]

1 2 3 4

[Read out] *Now I am going to show you a card about occupations. I want you to tell me <u>how many</u> of these occupations are done by people at your household.*
Please, <u>don't tell me which ones, just tell me HOW MANY.</u>

[Show card **C with occupations**, read names and ask:]

10. During the <u>last dry season (May-October)</u>, how many of these occupations were done by people from your household? [Circle answer]

1 2 3 4

11. And how many of these occupations were done by people from your household during the <u>last wet season (November-April)</u>? [Circle answer]

1 2 3 4

12. "During the <u>last dry season (May-October)</u>, how many of these occupations were done by people at your household to <u>get cash</u>?" [Circle answer]

1 2 3 4

13. "And how many of these occupations were done by people at your household during the <u>last wet season (November-April)</u> to <u>get cash</u>?"[Circle answer]

1 2 3 4

[Go to section D]

Section C2: Household occupations (ASK ONLY IF YOU GOT **4, 5 OR 6 POINTS**)

[Read out] *I am going to show you a card with animals. I am going to read their names and then I want you to tell me* *how many* *of these animals cause problems in this area.*
Please, *don't tell me which ones, just tell me HOW MANY.*

[Show card **T with animals**, read names and ask:]

9. "How many of these types of animals have caused problems in your village in the last dry season (May-October)?" [Circle answer]

1 2 3 4 5

[Read out] *Now I am going to show you a card about occupations. I want you to tell me* *how many* *of these occupations are done by people at your household.*
Please, *don't tell me which ones, just tell me HOW MANY.*

[Show card **T with occupations**, read names and ask:]

10. "During the last dry season (May-October), how many of these occupations were done by people from your household?" [Circle answer]

1 2 3 4 5

11. "And how many of these occupations were done by people from your household during the last wet season (November-April)?" [Circle answer]

1 2 3 4 5

12. "During the last dry season (May-October), how many of these occupations were done by people from your household to get cash?" [Circle answer]

1 2 3 4 5

13. "And how many of these occupations were done by people from your household during the last wet season (November-April) to get cash?" [Circle answer]

1 2 3 4 5

[Go to section D]

Section D: Opinion about cards (FOR ALL RESPONDENTS)

[Read out] *Finally, we would like to know your opinion about the cards I showed you and the questions I asked you using these cards. For each of the topics in the table below, you should choose your answer:*

1. *Very much*
2. *Moderately*
3. *A little*
4. *Not at all*
5. *Don't know*

	14. Was this easy to understand?	15. Do you feel your answer to this was anonymous?	16. Did you feel uncomfortable answering this?
UCT cards			

[Read out] *Thank you for giving your time to complete this questionnaire. Your answers will help us understand how people live in the Serengeti and how can we improve our techniques when collecting information from local communities.*

[Write down time of completion] **End time: _______________**

QUESTIONS FOR ENUMERATOR:

Was this respondent willing to answer your questions? [Circle one]

Very much Moderately A little Not at all

How well did this person understand the questions? [Circle one]

Very well Moderately A little Not at all

Do you think this person was honest when replying? [Circle one]

Very much Moderately A little Not at all

Other comments? ____

____

____

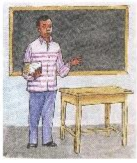
____

Kadi C

Ufugaji 

Kilimo 

Bishara ndogo ndogo 

Ualimu 

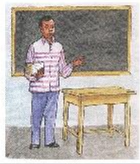
Kadi T

Ufugaji 

Kilimo 

Bishara ndogo ndogo 

Uwindaji 

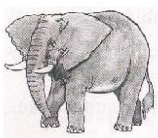
Ualimu 

Kadi C

Simba 

Chui 

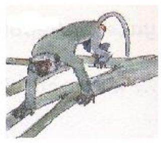
Nyani 

Tembo 

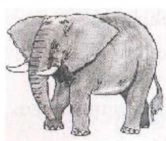
Kadi T

Simba 

Chui 

Nyani 

Fisi 

Tembo 

Descriptive summaries and model selection tables

Table B1. Set of models selected based on AICc for: a) willingness to collaborate in survey; b) easiness in understanding question. Models were generalised linear models (GLM) with a binomial error structure and logit link function. The number of parameters in the model (k), the log-likelihood (log(L)), the information criterion value (AICc), the AICc difference (ΔAICc) and AICc weight are given for each model.

Model	**k**	**log(L)**	**AICc**	**ΔAICc**	**AICc weight**
a) Model for willingness to collaborate in survey					
Age	2	-20.291	44.8	0.00	0.546
Age+Sex	3	-19.919	46.3	1.47	0.261
Age+Technique	5	-18.416	47.9	3.15	0.113
Age+Sex+Technique	6	-17.531	48.6	3.85	0.080
b) Model for easiness in understanding question					
Age+Sex+Technique	6	-27.125	67.8	0.00	0.506
Age+Technique	5	-29.052	69.2	1.38	0.254
Sex+Technique	5	-29.650	70.4	2.58	0.140
Technique	4	-31.167	71.1	3.23	0.101

Table B2. Parameter logit estimates from the averaged generalised linear models for: a) willingness to collaborate in survey; b) easiness in understanding question. The unmatched-count technique (UCT) is included in the intercept term. The relative importance of predictor variables is expressed as the sum of the Akaike weights for the variables included in the averaged models (Burnham & Anderson 2002).

Parameter	**Estimate (standardized)**	**S.E.**	**Lower CI**	**Upper CI**	**Relative variable importance**
a) Model for willingness to collaborate in survey					
Intercept	2.57	0.87	0.82	4.32	1
Age	1.81	1.01	-0.21	3.84	1
Sex: male	0.87	0.95	-1.04	2.78	0.34
Technique					0.19
2 card	-1.26	1.09	-3.45	0.93	
Ballot box	-0.28	1.46	-3.21	2.65	
RRT	1.02	1.34	-1.67	3.72	
b) Model for easiness in understanding question					
Intercept	2.67	1.15	0.37	4.97	1
Technique					1
2 card	-2.00	1.30	-4.61	0.61	
Ballot box	-2.13	1.22	-4.58	0.31	
RRT	-4.39	1.41	-7.20	-1.57	
Age	-0.85	0.41	-1.68	-0.02	0.76
Sex: male	1.30	0.71	-0.12	2.73	0.64

Table B3. Summary of the explanatory variables for the main study. Missing data is reported as a percentage out of 1163 survey respondents.

Continuous variables	Median	S.D.	Min	Max	Missing data (%)
Age	39.0	14.2	18	93	1.1
Distance to national park (km)	9.0	5.5	2.1	19.9	0
Distance to urban areas (km)	14.6	21.6	1.6	72.9	0
Distance to lake Victoria (km)	65.9	45.5	1.4	111.5	0
Population size	2164	892	1379	4587	0

Categorical variables	Level	Count	Missing data (%)
Sex	Male	693	0.6
	Female	400	
Level of education	Primary school	818	0.3
	Secondary school	133	
	No formal education	142	
Head of household?	Yes	825	0.6
	No	268	
Ethnic group	Kurya	484	0.3
	Sukuma	214	
	Ikoma	148	
	Ikizu	97	

	Other	150	
Household size	Below median (<8)	545	0.6
	Equal or above median (≥8)	548	
Household seasonal employment?	Yes	652	0.3
	No	441	
Household full-time employment?	Yes	125	1.5
	No	968	
Household years in the village	Below median (<17)	536	1.5
	Equal or above median (≥ 17)	557	
District	Serengeti	651	0
	Bunda	442	

Table B4. Parameter logit estimates from the full generalised linear model with a binomial error structure and logit link function for allocated cards (control or treatment).

Parameter	Estimate	SE	z-value	Pr(>|z|)
Intercept	0.044	0.389	0.114	0.91
Sex: male	-0.128	0.162	-0.787	0.43
Age	-0.006	0.007	-0.866	0.39
Education				
Primary	-0.001	0.215	-0.008	0.99
Secondary	-0.270	0.306	-0.883	0.38
Household size: ≥ 8 ppl	0.088	0.065	1.348	0.18
Household full-time employment	0.064	0.241	0.269	0.79
Household seasonal employment	0.147	0.143	1.020	0.31
Household years in the village: ≥ 17 years	0.003	0.069	0.047	0.96
Head of household	0.480	0.400	-1.120	0.26
Ethnic group				
Ikoma	-0.140	0.283	-0.493	0.62
Kurya	-0.274	0.233	-1.177	0.23
Other	-0.385	0.811	-0.475	0.63
Sukuma	0.941	0.838	1.122	0.26

Table B5. Effects of socio-demographic variables on estimated prevalence of bushmeat hunting. Only averaged estimates from interactions between socio-demographic variables and treatment status in the linear mixed models fitted to UCT answers are presented, indicating differences between the reported number of behaviours in the two conditions for each predictor variable. Variance explained by village was 21.9% and by individual was 34.3%. [a] Reference level is "dry season for cash". [b] Reference level is "no formal education".

Parameter	Estimate	S.E.	t-value	Relative variable importance
Household seasonal employment	0.172	0.083	2.049	1
Question [a]				1
Dry season	0.006	0.042	0.137	
Wet season	-0.031	0.042	0.749	
Wet season for cash	-0.066	0.042	1.589	
Household full-time employment	0.098	0.110	0.891	1
Household size: ≥8	-0.160	0.066	2.429	1
Education level [b]				0.64
Primary	0.130	0.093	1.389	
Secondary	0.239	0.134	1.785	
Household years in the village: ≥17	0.098	0.066	1.479	0.64
Age	0.001	0.003	0.043	0.23
Head of household	0.043	0.082	0.519	0.15
Sex: Male	-0.007	0.068	0.101	0.13

Table B6. Set of models selected based on AICc for bushmeat hunting. The number of parameters in the model (k), the log-likelihood (log(L)), the information criterion value (AICc), the AICc difference (ΔAICc) and AICc weight are given for each model.

Model	*k*	log(L)	AICc	ΔAICc	AICc weight
Education+ Full-time employment +Years in the village + Household size + Question topic + Seasonal employment	26	-3833.15	7718.62	0	0.22
Full-time employment + Years in the village + Household size + Question topic + Seasonal employment	22	-3837.64	7719.52	0.90	0.14
Full-time employment + Household size + Question topic + Seasonal employment	20	-3839.88	7719.95	1.33	0.11
Education + Full-time employment + Household size + Question topic + Seasonal employment	24	-3836.07	7720.42	1.80	0.09
Age+ Education + Full-time employment + Years in the village + Household size + Question topic + Seasonal employment	28	-3832.12	7720.62	2.00	0.08
Age+ Education + Full-time employment + Household size + Question topic + Seasonal employment	26	-3834.15	7720.62	2.00	0.08
Education + Full-time employment + Sex + Years in the village + Household size + Question topic + Seasonal employment	28	-3832.61	7721.59	2.97	0.05
Education + Full-time employment + Head of household + Years in the village + Household size + Question topic + Seasonal employment	28	-3832.76	7721.89	3.27	0.04
Education + Sex + Years in the village + Household size + Question topic + Seasonal employment	24	-3836.87	7722.02	3.40	0.04
Age+ Education + Full-time employment + Head of household	28	-3832.87	7722.12	3.50	0.04

+ Household size + Question topic + Seasonal employment					
Full-time employment + Sex + Household size + Question topic + Seasonal employment	22	-3839.00	7722.23	3.61	0.04
Age+ Education + Full-time employment + Head of household + Years in the village + Household size + Question topic + Seasonal employment	30	-3830.97	7722.38	3.76	0.03
Full-time employment + Head of household + Years in the village + Household size + Question topic + Seasonal employment	24	-3837.15	7722.57	3.95	0.03

Table B7. Set of models selected based on AICc for the best linear unbiased predictors (BLUPs) of the random effect of "village". Models were generalised linear models (GLM) with a Gaussian error structure and identity link function. The number of parameters in the model (k), the log-likelihood (log(L)), the information criterion value (AICc), the AICc difference (ΔAICc) and AICc weight are given for each model.

Model	k	logLik	AICc	ΔAIC	Weight
log(distance to NP)+ log(distance to NP)^2 + log(distance to urban areas)	5	18.822	-21.0	0	0.452
log(distance to NP)+ log(distance to NP)^2	4	16.208	-20.4	0.56	0.342
log(distance to NP)+ log(distance to NP)^2 + log(population size) + log(distance to urban areas)	6	19.848	-17.2	3.78	0.068

Table B8. Parameter estimates from the averaged generalised linear models for the best linear unbiased predictors (BLUPs) of the random effect of "village". The relative importance of predictor variables is expressed as the sum of the Akaike weights for the variables included in the averaged models (Burnham & Anderson 2002).

Parameter	Estimate	S.E.	z-value	Relative variable importance
Intercept	0.346	0.292	1.090	1
log(distance to NP)	-0.603	0.211	2.572	1
log(distance to NP)^2	0.186	0.053	3.142	1
log(distance to urban area)	0.042	0.020	1.928	0.60
log(population size)	-0.079	0.065	1.065	0.08

Table B9. Distribution and percentage of respondents' answers for each category (N=1093).

	Very much	Moderately	A little	Not at all	"Don't know"
UCT: easy	710 (65.0%)	200 (18.3%)	83 (7.6%)	95 (8.7%)	5 (0.4%)
UCT: anonymous	94 (8.6%)	114 (10.4%)	113 (10.3%)	769 (70.4%)	3 (0.3%)
UCT: uncomfortable	101 (9.2%	80 (7.4%)	63 (5.8%)	843 (77.1%)	6 (0.5%)

Table B10. Set of models selected based on AICc for respondents' self-reported: a) survey easiness; b) discomfort; c) perceived survey anonymity. Models were cumulative logit models for ordinal responses with village as random effects. The number of parameters in the model (k), the log-likelihood (log(L)), the information criterion value (AICc), the AICc difference (ΔAICc) and AICc weight are given for each model.

Model	*K*	log(L)	AICc	ΔAICc	AICc weight
Model for survey easiness					
Null model (only random effect)	4	-752.780	1514.80	0	0.287
Sex	5	-752.374	1516.01	1.21	0.157
Age	5	-752.696	1516.65	1.85	0.114
head of hh	5	-752.774	1516.81	2.01	0.105
Sex + Age	6	-752.221	1517.72	2.92	0.067
Sex + head of hh	6	-752.227	1517.73	2.93	0.066
Education	6	-752.629	1518.54	3.74	0.044
Age + head of hh	6	-752.692	1518.66	3.86	0.042
Model for survey discomfort					
head of hh + Sample*UCT	8	-645.338	1306.81	0	0.137
Sample*UCT	7	-646.605	1307.31	0.503	0.106
Age + head of hh + Sample*UCT	9	-645.310	1308.79	1.98	0.051
Sex + head of hh + Sample*UCT	9	-645.331	1308.83	2.02	0.05
Sex + Sample*UCT	8	-646.406	1308.95	2.13	0.047
Age + Sample*UCT	8	-646.459	1309.05	2.24	0.045
Education + head of hh + Sample*UCT	10	-644.440	1309.09	2.28	0.044
Head	5	-649.550	1309.16	2.35	0.042
Education + Sample*UCT	9	-645.600	1309.37	2.56	0.038
Null model (only random effect)	4	-650.767	1309.53	2.76	0.034
head of hh + Sample	6	-648.801	1309.68	2.89	0.032
Sample	5	-650.032	1310.12	3.31	0.026
Sex + Age + Sample*UCT	9	-646.308	1310.78	3.97	0.019
Model for survey anonymity					
Age + Sample	6	-664.247	1340.57	0	0.108
Age	5	-665.346	1340.75	0.18	0.099
Sample	5	-665.771	1341.60	1.02	0.064
Null model (only random effect)	4	-666.825	1341.69	1.11	0.062
Age + Sample*UCT	8	-663.057	1342.25	1.68	0.046
Sex + age + Sample	7	-664.242	1342.59	2.02	0.039

Age + head of hh + sample	7	-664.244	1342.59	2.02	0.039
Sex + Age	6	-665.331	1342.74	2.17	0.036
Age + head of hh	6	-665.346	1342.77	2.20	0.036
Age + Education + Sample	8	-663.403	1342.94	2.37	0.033
Head of hh + Sample	6	-665.540	1343.16	2.59	0.030
head of hh	5	-666.552	1343.16	2.59	0.030
Age + Education	7	-664.592	1343.29	2.72	0.028
Sample*UCT	7	-664.624	1343.35	2.78	0.027
Sex + Sample	6	-665.686	1343.45	2.88	0.026
Sex	5	-666.711	1343.48	2.91	0.025
Sex + Age + Sample*UCT	9	-663.028	1344.22	3.65	0.017
Age + head of hh + Sample*UCT	9	-663.056	1344.28	3.71	0.017
Age + Education + Sample*UCT	10	-662.133	1344.47	3.90	0.015

Table B11. Maximum likelihood estimates from the averaged cumulative logit mixed models (village as random effects) fitted to self-reported levels of: a) understanding, b) anonymity and c) discomfort. The first rows for each model represent intercepts (cut-points between categories) and the rest predictor coefficients. [a] Relative variable importance. [b] Reference level is "no formal education".

	Understanding		Anonymity		Discomfort	
	Estimate (S.E.)	Imp[a]	Estimate (S.E.)	Imp[a]	Estimate (S.E.)	Imp[a]
Intercepts		1		1		1
Not at all| A little	-4.355 (0.651)		2.321 (0.854)		2.752 (0.391)	
A little | Moderately	-2.526 (0.628)		3.571 (0.860)		3.312 (0.392)	
Moderately | Very much	-0.617 (0.619)		5.020 (0.869)		4.151 (0.394)	
Sex: Male	0.150 (0.157)	0.33	0.018 (0.177)	0.184	-0.061(0.134)	0.173
Age	-0.003 (0.006)	0.25	-0.011(0.007)	0.660	-0.001(0.006)	0.171
Head of household	-0.123(0.177)	0.24	0.052(0.202)	0.196	-0.328(0.142)	0.531
Education [b]		0.05		0.098		0.122
Primary	0.035(0.21)		-0.029(0.260)		-0.264(0.247)	
Secondary	-0.089(0.29)		0.323 (0.355)		0.087(0.249)	
Sample: Treatment			-0.153(0.248)	0.593	0.226(0.287)	0.887
UCT			-0.002(0.062)	0.157	0.085 (0.10)	0.800
Sample*UCT			-0.164(0.136)	0.157	-0.015 (0.14)	0.800

Appendix C – Supplementary information for Chapter 5

Modelling ungulate population dynamics

We used a post-breeding census, age-structured two-sex matrix model with variable size according to ungulate species to represent population dynamics (Caswell 2001):

$$M = \begin{pmatrix} 0 & \eta S_{y,f}F_{y,f} & \eta S_{a,f}F_{a,f} & \cdots & \eta S_{s,f}F_{s,f} & 0 & 0 & \eta S_{a,m}F_{a,m} & \cdots & 0 \\ S_{j,f} & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & \cdots & 0 \\ 0 & S_{y,f} & 0 & \cdots & 0 & 0 & 0 & 0 & \cdots & 0 \\ 0 & 0 & S_{a,f} & 0 & 0 & 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & 0 & S_{a,f} & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & S_{a,f} & S_{s,f} & 0 & 0 & 0 & \cdots & 0 \\ 0 & \eta S_{y,f}F_{y,f} & \eta S_{a,f}F_{a,f} & \cdots & \eta S_{s,f}F_{s,f} & 0 & 0 & \eta S_{a,m}F_{a,m} & \cdots & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{j,m} & 0 & 0 & \cdots & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{y,m} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{a,m} & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & 0 & S_{a,m} & \vdots \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{a,m} & S_{s,m} \end{pmatrix} \qquad \text{Eqn C1}$$

where S_j, S_y, S_a, S_s are survival rates of juveniles, yearlings, adults and senescent adults respectively; sex-specific survival rates were used only for impala, for which these sex-differences have been described (Jarman & Jarman 1973). Births are allocated to females and males according to a sex ratio at birth η=0.5. $F_{y,f}$ and $F_{a,f}$ are the fecundity of yearling and adult females respectively, and $F_{a,m}$ is the fecundity for adult males.

Given the population vector N with the number of females and males in each age class up to senescence s:

$$N = \begin{pmatrix} F_1 \\ \cdots \\ F_s \\ M_1 \\ \cdots \\ M_s \end{pmatrix} \qquad \text{Eqn C2}$$

the transition between one year and the next is calculated by multiplying the matrix M with the population vector N

$$N_{t+1} = MN_t \qquad \text{Eqn C3}$$

to get next year's population.

The model includes juveniles (< 1 year old), yearlings (2nd year), adults (> 2 years old), and senescent adults (impala: ≥ 8 years; wildebeest: ≥ 14 years). The matrix model is parameterised using vital rates presented in Table C1 from studies on wildebeest (Mduma, Hilborn, & Sinclair 1998; Mduma, Sinclair, & Hilborn 1999; Owen-Smith 2006), impala (Jarman & Jarman 1973; Fairall 1983; Owen-Smith, Mason, & Ogutu 2005) and general ungulate life-history (Gaillard *et al.* 2000). Due to limited information on wildebeest survival, we followed the assumption that annual adult survival concerns wildebeest older than one year of age (Mduma, Sinclair, & Hilborn 1999) and we used Gaillard *et al.'s* (2000) general estimate to account for senescence and expected lower survival. Moreover, in the absence of information on temporal variation in impala survival rates, we used relative variability obtained from multiple studies on bovids (Gaillard *et al.* 2000). If the original papers only reported standard errors (SE) or coefficient of variation (CV), these were converted into standard deviation (SD). Stochasticity was added to the vital rates by varying them by the standard deviation multiplied by standard normal deviates with mean 0 and standard deviation 1 (z-values).

Table C1. Parameters used in the operating model for ungulate population dynamics.

Parameter	Symbol	Wildebeest		Impala	
		Mean (SD)	Reference	Mean (SD)	Reference
Fecundity: yearlings	F_y	0.271 (0.281)	(Mduma, Sinclair, & Hilborn 1999)	0.693 (0.155)	(Fairall 1983)
Fecundity: adults	F_a	0.903 (0.075)	(Mduma, Sinclair, & Hilborn 1999)	0.906 (0.076)	(Fairall 1983)
Survival: juveniles	S_j	0.431 (0.151)	(Mduma, Hilborn, & Sinclair 1998)	Density-dependent	Assumed
Juvenile mortality: slope	Mb_j	---	---	0.0014	Assumed
Juvenile mortality: intercept	Ma_j	---	---	0.3	(Owen-Smith, Mason, & Ogutu 2005)
Survival: yearlings	S_y	Density-dependent	(Mduma, Sinclair, & Hilborn 1999; Owen-Smith 2006)	♂: 0.650 (0.093) ♀: 0.813 (0.116)	(Jarman & Jarman 1973; Gaillard *et al.* 2000)
Survival: adults	S_a	Density-dependent	(Mduma, Sinclair, & Hilborn 1999; Owen-Smith 2006)	♂: 0.992 (0.072) ♀: 0.889 (0.065)	(Jarman & Jarman 1973; Gaillard *et al.* 2000)
Yearling + adult mortality: slope	Mb_{older}	1.65×10^{-5}	Table C2	---	---
Yearling + adult mortality: intercept	Ma_{older}	-0.023	Table C2	---	---
Survival: senescent adults	S_a	0.825 (0.147)	(Gaillard *et al.* 2000)	♂: 0.594 (0.106) ♀: 0.685	(Jarman & Jarman 1973;

				(0.122)	Gaillard *et al.* 2000)
Adult weight (kg)	*W*	♂: 210 ♀: 163	(Sachs 1967)	♂: 57 ♀: 42	(Sachs 1967)
"Harem" size	*h*	25	(Talbot & Talbot 1963)	15	(Murray 1982)

a) Survival, rainfall and density-dependence

Seasonal rainfall in African savannahs is a key driver of population dynamics (Boone, Thirgood, & Hopcraft 2006) and this relationship may be modified by the prevailing population density (Gaidet & Gaillard 2008; Hopcraft, Olff, & Sinclair 2010). In the Serengeti, the greatest variation in rainfall between regions occurs during the dry season, when grass growth is linearly related to rainfall (Sinclair 1975); thus, we used per capita rainfall as an index of per capita grass production (Hilborn & Mangel 1997; Pascual, Kareiva, & Hilborn 1997). The effects of dry-season rainfall and density-dependence were assumed to act upon juvenile survival for the less well studied impala population, as is the case for other similar-sized ungulate species (Gaillard, Festa-Bianchet, & Yoccoz 1998; Gaillard *et al.* 2000). Adult survival has been suggested to be the main regulating factor in the wildebeest population (Mduma, Sinclair, & Hilborn 1999) and annual juvenile survival has been suggested to be unrelated to density (Owen-Smith 2006), therefore only rainfall- and density-dependent adult survival were considered for the wildebeest population.

Following Mduma, Hilborn, & Sinclair (1998), we created a truncated (non-negative) normal distribution to simulate dry-season rainfall in the study. Averaged dry-season rainfall from five rain gauges with relatively long-term records (1961-2007) in the Northern Serengeti was used to check normality assumptions through normality plots and a Shapiro-Wilks normality test ($W = 0.97$, p-value = 0.35). Stochasticity was added to the rainfall values by varying them by the standard deviation multiplied by standard normal deviates with mean 0 and standard deviation 1 (z-values).

Population density was indexed using the biomass of the total population, calculated from the stage structure of the population and the mean mass of animals in each sex- and age-class. For each sex, juvenile and yearling weights in the dry season were assumed to be 50% and 75% of the adult weight, respectively (Fairall 1983). To model survival as a function of ungulate biomass density and rainfall, we followed Owen-Smith (2006) and used a linear transformation of the inverse hyperbolic function of resource gains:

$$S_t = 1 - Ma + Mb\left(\frac{B_t}{R_t}\right) \qquad \text{Eqn C4}$$

where S_t is survival in year t, B_t is ungulate biomass density (estimated for each species separately), R_t is the logarithmic transformation of dry-season rainfall, *Ma* is a constant that represents minimum mortality rate, and *Mb* is a constant that represents how steeply the mortality rate increases. For wildebeest, the slope and intercept were estimated from rainfall and age-structured abundance data described in Mduma, Hilborn, & Sinclair (1998) and Mduma, Sinclair, & Hilborn (1999). For impala, similar data were not available and reasonable values for the intercept and slopes were assumed (Table C1).

b) Fecundity and harem size

To incorporate multiple reproductive age classes, accounting for polygynous mating behaviour and possible differences between sexes in harvest offtake, the fecundity functions included the contributions of all possible combinations of male and female stages. Following Caswell (2001), the births *B* were considered as a sum of the contributions of mating classified by male and female age:

$$\mathrm{B} = \sum_{\mathrm{i}} \sum_{\mathrm{j}} \mathrm{B}_{\mathrm{ij}} \qquad \text{Eqn C5}$$

where *i* is the age-class of the father and *j* the age-class of the mother. Senescent male adults are often not able to hold their harems and adults account for the vast majority of matings in ungulates (McElligott, Altwegg, & Hayden 2002; Yoccoz *et al.* 2002) so we only considered adult male fecundity. The per-capita fecundity of an adult male is given by:

$$F_{m,a} = \sum_j \frac{k_j N_{f,j}}{N_m + N_f h^{-1}} \qquad \text{Eqn C6}$$

and that of a female of age *j* by

$$F_{f,y} = \frac{k_j N_m}{N_m + N_f h^{-1}} \qquad \text{Eqn C7}$$

where F_m and F_f is the fecundity for males and females respectively, depending on the age-specific number of calves borne by female *k*, the number of females N_f and males N_m and the number of harems, which is $N_f h^{-1}$with harem size *h*.

Parameter determination for wildebeest rainfall- and density-dependence

We adapted Owen-Smith (2006)'s methodology to determine the intercept and slope defining rainfall and density-dependence of the annual mortality for wildebeest. Data for dry-season rainfall and wildebeest abundance in the Serengeti were obtained or converted from Mduma, Sinclair, & Hilborn (1999) and Mduma, Hilborn, & Sinclair (1998). Data were used only for years when the calf:adult ratio and number of yearlings were available (N=14).

Annual adult survival was calculated by relating the projected number of adults and yearlings in January (Mduma, Sinclair, & Hilborn (1999): column 2 of Table 5) to the projected number later in December of the same year (Mduma, Sinclair, & Hilborn (1999): column 4 of Table 5). We followed the assumption made by (Mduma, Sinclair, & Hilborn 1999) that annual adult survival concerns wildebeest older than one year of age.

The proportion of yearlings in the population was estimated by relating the projected number of 10-11 months calves in December (Mduma, Sinclair, & Hilborn (1999): column 12 of Table 5) to the projected number of adults and yearlings in January of the following year (Mduma, Sinclair, & Hilborn (1999): column 2 of Table 5). Calf:adult ratios (Mduma, Sinclair, & Hilborn (1999): Table 2) were used to calculate abundance of calves.

Biomass density was estimated by calculating the biomass of each age-group (calves, yearlings and adults) and sex-class (assuming an even sex ratio) and dividing by the approximate area occupied by wildebeest during the dry-season (5000km^2; Mduma (1996)).

A generalised linear model with Gaussian error distribution was fitted to the annual adult mortality with the ratio between biomass density and logarithmic rainfall as explanatory variable (Owen-Smith 2006).

Table C2. Parameter estimates from the generalised linear model fitted to annual adult mortality in the wildebeest population (N=14)

Parameter	Estimate	S.E.	t value
Intercept	-0.023	0.020	-1.145
Biomass density/ ln(rainfall)	$1.65\text{x}10^{-5}$	$0.27\text{x}10^{-05}$	6.125

Appendix D – Supplementary information for Chapter 6

Topic guide for semi-structured interviews

This is an outline of key issues and areas of questioning used to structure the discussion with each participant, with its use (flow and wording) guided by the experiences of the respondent:

1. In your opinion, what are the top 5 threats to the system? (If bushmeat hunting is not mentioned, ask where it fits)
2. Looking at the MSE framework (show Figure 6.1), is there anything you would add to this framework? (do you think all main processes and actors in the system are represented?)
3. What are the main benefits of working with other organizations operating in this system? (Ask specific examples). What about challenges? (Ask specific examples)
4. Where do you think the main information gaps in this system are? Is that currently being addressed? How or why not?
5. What prevents the exchange of information and knowledge between organizations?
6. What constrains applying information/knowledge when implementing management? (Ask specifically about monitoring wildlife and translating this into management changes)
7. Do you think the current management strategies have been effective at controlling bushmeat hunting? (Ask specific examples of strategies, outcomes and why they think that's the case)
8. Do you think the current management strategies have been implemented as planned? Why? (Ask examples of discrepancies between decisions and their realization)
9. Do you think it would be possible to test different management strategies? How? Any expected challenges? (mention modelling if they don't)
10. Do you feel the local communities are being engaged and considered in the current management strategies? (Assess perceptions of what local communities need and should be entitled to)
11. Thank you for your time. Is there anything else you'd like to add or comment?

Questionnaire

Name: ____

Organization(s): _______________________________________

Main place of work: ____________________________________

Nationality: ____

Age: ________ **Sex:** ________

How long have you been working in the Serengeti?

- ☐ <1 year
- ☐ 2-5 years
- ☐ 6-10 years
- ☐ >10 years

Could you please briefly describe your <u>academic and disciplinary background</u>?

What type of work best describes your work within your organization?

- ☐ Administration/Management
- ☐ Program coordination/Project management
- ☐ Analysis
- ☐ Field work
- ☐ Research
- ☐ Other: ____

Area of work (<u>please choose as many as apply</u>):

- ☐ Academic
- ☐ Anti-poaching
- ☐ Wildlife monitoring
- ☐ Livelihood alternatives & engagement with local communities
- ☐ Tourism
- ☐ Other: ____

<u>Scenario-building exercise:</u> Now, I'm going to ask you to briefly describe what you think it's going to happen, and what you'd like to happen, in the Serengeti in the future. What are the constraints to going from expected to ideal situation?

	Expected short-term **(5 years)**	**Desired short-term** **(5 years)**	**Expected long-term** **(20 years)**	**Desired long-term** **(20 years)**
How do you think the Serengeti ecosystem will be/ how would you like the Serengeti ecosystem to be in <u>5/20</u> years?				
How do you think **bushmeat hunting** in Serengeti ecosystem will be/ how would you like bushmeat hunting the Serengeti ecosystem to be in <u>5/20</u> years?				
How do you think **ecological value** in Serengeti ecosystem will be/ how would you like ecological value in the Serengeti ecosystem to be in <u>5/20</u> years?				
How do you think **poverty** in Serengeti ecosystem will be/ how would you like poverty in the Serengeti ecosystem to be in <u>5/20</u> years?				

<u>Institutional analysis exercise:</u> Please list institutions operating in the bushmeat hunting system in the Serengeti, where do you think they play a role in our MSE framework and their importance for decision-making and intervention implementation.

Institution	Wildlife monitoring	Social monitoring	Management (decision-making)	Management (implementation)	Other (which?)	Importance for decision-making 1- Weak 2- Medium 3- Strong	Importance for intervention implementation 1- Weak 2- Medium 3- Strong

<u>Social network exercise</u>: Please list up to 10 individuals with whom you have collaborated on Serengeti projects or issues <u>during the past year</u>, along with the name of their organization, and frequency and nature of collaboration.

Name (First name + surname)	Organization	How often do you communicate with this person about Serengeti projects or issues?			What are your main reasons for collaborating with this person?				
		Less than monthly	Monthly or every 2 weeks	Daily or weekly	Advice or technical support	Influencing policy decision-making	Project management	Project implementation	Other (which?)

Is there anyone else you would like to add to this list?

Table D1. Categories of top threats to the Serengeti ecosystem mentioned by the study participants and the number of respondents (out of 19) reporting each specific threat.

Threats	Frequency
Human population growth	12
Land-use conflicts and encroachment (e.g. overstocking of livestock, grazing inside protected areas)	10
Poaching (bushmeat and ivory)	10
Climate change and environmental stress	8
Development, infrastructures and tourism (e.g. roads, railways)	6
Poor management and governance (e.g. dependence on unstable funding; institutional complexity; instability in policies)	6
Poverty and lack of opportunities	3
Diseases (human/wildlife/livestock)	3
Habitat degradation and water scarcity (e.g. Mara river)	3
Invasive species	3
Human-wildlife conflict (e.g. crop-raiding and retaliatory killing)	2
Mining	1

Table D2. Example quotes illustrating the main types of issues affecting conservation implementation in the Serengeti, as described by the study participants.

Type of issue	Challenges described	Quotes from the interviews
Multiple goals and lack of integrated approaches	trade-offs between tourism, development and conservation	*"Tourists in the Serengeti come for wildlife… in their natural habitat. If we put up infrastructures, we're obviously jeopardising the resources that we accrue from tourism"* *"if we don't get money, we can't put up anti-poaching activities. Tourism is the main source of revenue"* *"the spiritual and traditional ideas of having them* [wildlife] *as their heritage is much better than one based on making money from tourism because that can go up and down"*
	coordination between actors	*"The management of the system itself…should sit together…because we have just a common overall goal but each one taking a different route"*
	balance of objectives	*"we are concentrating so much inside the park… and we are forgetting about the surrounding communities"*
Adaptive responses to change under uncertainty	unexpected threats and outcomes	*"this road issue came out of the blue…we have to be prepared that things like this might happen"*
Poor governance	participation	*"local people should be central…not just being told what to do"*
	performance	*"levels of bureaucracy that are completely unnecessary"*
	transparency	*"there should be more transparency… revenues increasing but also being spent … more invested back into conservation"*
	equity	*"the way people are benefiting from conservation… is not really evenly distributed"*
	rule of law	*"livestock in protected areas… that is prohibited by law but the enforcers are getting blockages"*
Institutional barriers	lack of a common and long-term vision in the regulations and interventions	*"this ecosystem is too big and managed by different guidelines…one regulation might affect the others"*
	difficulty in data access	*"Accessing data not easy… all seems confidential to an organization"*
	difficulty in bringing together and reaching	*"by the time you gathered everyone together and agreed on something, the*

	consensus with many stakeholders	*budget is gone"*
	mistrust between institutional actors	*"during a presentation, there's sometimes doubt of the things they're presenting"*
Individual characteristics	diverse personalities	*"conflicts between different types of personality…this can be disastrous if we fail to understand each other"*
	commitment	*"People usually come for 2-3 years, they get sick of it, they get disillusioned, they leave"*
	reluctance to learn and adapt	*"even if they don't have the knowledge to do it, they prefer to do it alone instead of integrating with others that know"*
Perceived value and use of scientific information	researchers not sharing their findings widely	*"we failed in sharing information with other audiences and so impact has been minimal"*
	researchers not addressing questions of management interest	*"not many researchers go into management-oriented kind of research"*
	data quality not being adequate for management decisions	*"estimates with wide confidence limits… they are not a very good thing to set your hunting quotas"*
	information not being perceived as valuable or trustworthy	*"monitoring…it's just an academic exercise"*
Lack of proper incentives	economic drivers in quota-setting	*"they were just halved because people wanted to make more money"*
	commitment to actual implementation	*"if you have a plan but it's just a piece of paper and no one is holding it to it, there's absolutely no incentive to follow it"*
	time scale	*" the interventions are frequently short-term and very dependent on grants and specific people… and this lack of continuity results in loss of trust in these interventions"*
Relationships with local communities	perceptions of conservation by local communities	*"strategies should focus on showing benefits of conservation to local communities…we have failed to show them these benefits"*
	expectations about the interventions	*"local communities have high expectations most of the time … that affects the intervention. They expect instant money"*
	effectiveness	*"community-based conservation is simply not working! And one of the reasons why it doesn't work is because it's naive."*
	insufficient participation	*"maybe there's a better way… if people*

	of local communities	*sit together with the villagers and talk about it and how to go about it*"
	engagement of "elites"	"*if we engage, it's only the political figures from the local communities*"
	scale of the decisions	"*we should keep them* [local communities] *out of making a local decision on a national issue*"
	lack of organizational and intellectual skills	"*they have not participated in the decisions because they were not able to understand*"

Table D3. Main institutions operating in the bushmeat hunting system and their perceived proportional importance for decision-making and intervention implementation when controlling bushmeat hunting, according to the study participants.

Institution	Importance for decision-making	Importance for implementation
Tanzania National Parks (TANAPA)	21.8 (1st)	20.8 (1st)
Frankfurt Zoological Society (FZS)	17.9 (2nd)	20.2 (2nd)
Tanzania Wildlife Research Institute (TAWIRI)	13.5 (3rd)	12.5 (3rd)
Wildlife Division (WD)	11.5 (4th)	10.1 (5th)
Grumeti Fund	8.3 (5th)	10.7 (4th)
Wildlife Management Areas (WMAs; Ikona and Makao)	5.1 (6th)	5.4 (6th)
District Council (e.g. District Game Office)	4.5 (7th)	4.8 (8th)
Ngorongoro Conservation Area Authority (NCAA)	4.5 (7th)	3.6 (9th)
Other NGOs (e.g. WWF, Friedkin Conservation Fund, AWF, Jane Goodall Institute)	3.8 (9th)	2.4 (10th)
Villages + local governments	3.2 (10th)	5.4 (6th)
Game Reserves (Ikorongo-Grumeti and Maswa)	3.2 (10th)	1.2 (12th)
Hunting company (TGT)	1.3 (12th)	1.8 (11th)
Universities	1.3 (12th)	1.2(12th)

Table D4. Characteristics of social networks in Serengeti projects of study respondents.

Measures	Network-type			
	General (73 ppl)	**Advice and support** (44 ppl)	**Policy** (36 ppl)	**Implementation** (56 ppl)
Number of links	110	52	35	85
Proportion of intra-institutional links	18%	23%	6%	20%
Edge connectivity	1	0	0	1
Density	0.04	0.05	0.06	0.06
Mean geodesic distance	3.2	16.4	16.1	3.1
Actors with highest degree	14[FZS], 4[FZS], 12[FZS]	14[FZS], 10[FZS], 11[Univ.], 4[FZS]	14[FZS], 10[FZS], 4[FZS]	14[FZS], 12[FZS], 4[FZS]
Actors with highest eigenvector centrality	14[FZS], 13[FZS], 4[FZS]	14[FZS], 13[FZS], 11[Univ.]	9[NGOs], 10[FZS], 14[FZS], 27[WMAs]	14[FZS], 13[FZS], 12[FZS]
Actors with highest betweenness centrality	14[FZS], 2[FZS], 12[FZS]	14[FZS], 11[Univ.], 10[FZS]	14[FZS], 4[FZS], 32[Gov.], 10[FZS]	14[FZS], 2[FZS], 12[FZS]