

**Bushmeat Catch per Unit Effort in space and time: a
monitoring tool for bushmeat hunting**

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Abstract

This study evaluates the potential of using Catch per Unit Effort (CPUE) as an index of abundance with which to monitor exploited tropical forest species, and so aid the sustainable management of bushmeat hunting. Both the theoretical validity and practical feasibility of the CPUE model are investigated using data collected from a 15 month study based in the hunting community of Midyobo Anvom, Equatorial Guinea. Economic measures of hunting effort were found to be as good at explaining variation in catch as biologically-relevant measures, and hunter skill is likely to be an important factor in reducing unexplained variation in hunter catch. Hunters were found to be quantitatively and spatially accurate in the reporting of their hunting activities and locally-based methods of data collection were able to reliably detect useful levels of change in community-level CPUE. The existence of a proportional relationship between CPUE and density was found for some of the principle bushmeat prey species. This study concludes that a bushmeat CPUE index has the potential to be both theoretically valid and practically feasible, and as part of a wider management strategy involving food and livelihood alternatives could make a valuable contribution to the achievement of sustainable levels of bushmeat hunting.

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Declaration

All the work presented in this thesis is my own

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Introduction

Problem statement

Unsustainable levels of hunting currently threaten many wildlife species in tropical forest areas, and therefore the food and livelihood security of people who depend on this resource. Solutions for both people and wildlife will involve sustainable use. Achieving sustainable use, in biological terms, requires the design of sustainable harvesting strategies, for which an understanding of the impacts of hunting is required, and hence information on prey species abundance. In tropical forest systems estimating abundance is particularly difficult, and the resources available for biological monitoring are extremely limited. Simple tools that allow the impacts of hunting on prey species abundance to be assessed indirectly could make a key contribution to management. To this end the use of a Catch per Unit Effort (CPUE) index derived from hunting data has been suggested. The use of CPUE is based on the assumption that CPUE is proportional to population size, but this assumption is not always valid. The nature of the relationship between CPUE and abundance therefore needs to be validated, using un-biased data on CPUE and independent abundance estimates. If validated, CPUE could act as a low cost alternative to assessing the status of tropical forest species, and be used to inform decisions that could improve the management of hunting in tropical forests, while facilitating the involvement of local communities in management of their natural resources

Aim and research objectives

The aim of this thesis is to investigate the potential of CPUE as an index of abundance, with which to monitor prey populations, and so aid the sustainable management of bushmeat hunting. This aim will be addressed through the following two research objectives:

1. Determine the theoretical validity of using CPUE as an index of abundance
2. Determine the practical feasibility of using CPUE as a monitoring tool

Thesis Outline

This study uses a combination of field work, and modelling approaches to build successively through each chapter, a greater understanding of both the possibilities and problems that the use of CPUE might present as a tool for the monitoring and management of bushmeat hunting.

Chapter 1 - Research background

This chapter provides the background to the study. It briefly explains the concept of sustainable use, and the barriers that exist to its achievement. It describes a specific case of use, the bushmeat trade, including its causes, effects and possible solutions. It describes the increasing need for monitoring, covering some of the techniques available, both traditional and novel. Lastly it presents a detailed summary of CPUE as an index to abundance, including its history, theory, problems and strengths.

Chapter 2 - Predictors of abundance in species exposed to bushmeat hunting

This chapter separates the independent effects of hunting and habitat on prey species abundance, providing a critical assessment of which species are affected by hunting, and demonstrating that habitat heterogeneity and its relative importance to different prey species should be considered when managing hunting systems.

Chapter 3 - How should hunting effort be measured to reflect its biological impacts on prey species?

This chapter investigates how hunting effort should be measured so that it best reflects the biological impact of hunting on prey species, illustrating the potential sources of bias that can result from the use of economic measures of hunter effort.

Chapter 4 - The importance of effort, hunter characteristics and seasonal effects in determining catch

This chapter builds on the last to determine which of the effort measures identified explains the most variation in catch, how is this influenced by the scale of measurement, and what other factors need to be considered if CPUE indices are going to accurately reflect prey abundance.

Chapter 5 - Hunter reporting of Catch per Unit Effort as a monitoring tool: an evaluation of professional versus locally-based methods

This chapter investigates the quantitative and spatial accuracy of hunter reporting, the ability of locally-based methods for CPUE trend detection, and compares the sampling efficiency of locally-based and professional CPUE data collection methods.

Chapter 6 - The relationship between hunter Catch per Unit Effort and bushmeat prey species density

This chapter builds on the findings of all other Chapters in order to investigate the relationship between CPUE and prey species density

Chapter 7 - Discussion

This last chapter presents a synthesis of the study findings and discusses their implications for the use of CPUE as a monitoring tool, while considering the wider context in which bushmeat hunting occurs. It then makes some recommendations for future research and for the practical application of this method.

Study site

Geography

This study was carried out in the village of Midyobo Anvom, Rio Muni, mainland Equatorial Guinea. Equatorial Guinea is a small Spanish speaking country in Western-Central Africa (2°00 N, 10°00 E). It lies just north of the equator, between Gabon to the South and Cameroon to the North. It is comprised of five islands and the mainland region, Rio Muni, which makes up a total area of 28,051km² (CIA 2007). The islands include Bioko (2000km²) which is off the coast of Cameroon in the Gulf of Guinea, and contains the countries capital Malabo, Annobon, Corisco, Elobey Grande and Elobey Chico.

History

The first inhabitants of Equatorial Guinea were pygmies, of whom small populations remain only in northern Río Muni. They were largely displaced by Bantu migrations between the 17th and 19th centuries, by coastal tribes and later the Fang (Liniger-Goumaz 1989). Bioko was formerly known as Fernando Po after the Portuguese explorer who discovered it in 1472. The island of Bioko was ceded to the Spanish in 1777 by its original Portuguese colonisers. Spain then went on to settle the mainland province of Rio Muni in 1844. In 1904 the two territories were united as the Western African Territories and later renamed Spanish Guinea. Spanish Guinea achieved independence from Spain in March 1968 and became the Republic of Equatorial Guinea (FCO 2007). Equatorial Guinea's first president Francisco Macías Nguema, was overthrown in 1979 in a military coup d'état, President Teodoro Obiang Nguema Mbasogo Obiang has been in power ever since.

Population

The majority of the country's population of 551,201 (CIA 2007) or 1,157,000 (Ministério de Planificación y Desarrollo Económico 2002), live on the mainland region Rio Muni, which is 26,017km². The city of Bata (population approximately 55,000) is the main urban centre in the region. The main town within the landscape is Evinayong, with a population of approximately 6,000. However, most of the rural population live in settlements along the roads. The majority practice subsistence agriculture, using slash and-and-burn techniques. Most of the population in the landscape belong to the ethnic Fang Okak group, other groups include the Bubi, the majority group on Bioko, and the coastal Ndowe.

Economy

After a period of unrest and economic decline following the independence from Spain in 1968 (Sabater-Pi 1981), Equatorial Guinea is experiencing an oil boom after the discovery of large oil reserves in the 1980's (CIA 2007). Equatorial Guinea is now one of the largest oil producers in Sub-Saharan Africa and current production is estimated in over 4200,000 barrels per day (CIA 2007). Due to the discovery of oil, Equatorial Guinea was one of the fastest growing economies in the world; real GDP growth in 2004 was 34.2% but this has since settled down to about 6% in 2006. But this impressive GDP from oil revenue masks stagnation in the rest of the economy, with timber and agriculture only minor sources of exports (FCO 2007). Equatorial Guinea's human development index ranking has deteriorated in recent years, it currently ranks 109th out of 177 countries on the Human Development Index (UNDP 2007).

Biodiversity and climate

Equatorial Guinea is extremely biodiverse, it straddles the Guinean Forests of West Africa Hotspot and the Congo Basin High Biodiversity Wilderness Area (Conservation International 2006), and is one of the highest priority conservation landscapes in the Congo Basin (CARPE 2006). The forest cover of Equatorial Guinea is estimated at 78% (Forests Monitor 2006) and is home to a large number (104) of globally threatened species, including 18 mammals, 5 reptiles, 10 fish, 5 birds, 3 amphibians and 63 plants, with 41 of these species listed as critically endangered, endangered or vulnerable (IUCN 2007).

The country has the fourth highest primate diversity in Africa (Chapman 1999) and 11 endangered primate species or subspecies. Bioko Island is home to several endemic sub-species, including the Drill, Africa's most endangered primate (IUCN 2007). Monte Alen national park alone contains 265 recorded bird species (Birdlife International 2006) and at least 109 mammal, 65 reptile, 57 amphibian, and 62 fish species (Lasso Alcala 1995). Sixteen primate species are found within Monte Alen National Park, including the Western lowland gorilla (*Gorilla gorilla gorilla*), chimpanzee (*Pan troglodytes*), and black colobus monkey (*Colobus satanus*) (Garcia & Mba 1997), as well as other species of conservation concern including the forest elephant (*Loxodonta africana*), leopard (*Panthera pardus*), buffalo (*Syncerus caffer*), giant pangolin (*Smutsia gigantea*) and the grey necked picathartes (*Picathartes oreas*).

Equatorial Guineas flora has been better studied (Wilks & Issembe 2000). The regions' vegetation forms part of the Guineo-Congolian forest (Sayer et al 1992), characterised by moist tropical lowland and upland forest. The habitat and topography vary with distance from the coast. The western littoral zone extends in to 20-30km from the coast, separated from the flatter interior by Rio Uolo and the Niefang mountains (Wilks & Issembe 2000). Monte Alen and Monte Mitra are the highest peaks on Rio Muni

and estimated at around 1300m, and form part of the Monte Alen-Mont de Cristal Inselberg Forest Landscape (Bonilla 2003).

Average annual rainfall is about 2,500mm, with the main rainy season between September and November and a smaller one between March and May. The climate is equatorial, with an average humidity of 90% and an average minimum temperature of 25°C throughout the year (Wilks & Issembe 2000).

Threats

Despite this high biodiversity, conservation in the country is lacking and biodiversity threats and their impacts are not well known. Logging is largely unregulated, and has increased since 1980 from below 50,000m³ per year to about 790,000m³ in 1999. Logging concessions to about 60 companies now cover close to 70% of the landmass of the country (approx. 1,720,000 ha). Logging is selective and these companies export mainly Okoume (*Aucoumea klaineana*, 70% of exports). About 85% of the production is exported in whole logs to Asian markets (Bonilla 2003). Despite this the majority (78%) of the country is still covered in forest (Forests Monitor 2006) and the discovery of large oil reserves in the 1990's has caused a shift in attention away from logging. Therefore while forest fragmentation due to logging affects wildlife, the increasing trade in bushmeat particularly in endangered species, such as primates, is a more immediate threat to Equatorial Guinea's biodiversity.

Bushmeat consumption has increased in past years, fuelled by oil wealth (East et al. 2005). The national road network is being refurbished and expanded, and new roads are being cut into the forest by logging concessions and there are also many more cars on the roads. Hunters can get deeper into the forest, and bring their catch to the city market more quickly (Bonilla 2003). In comparison with neighbouring countries the bushmeat trade in Equatorial Guinea has been little studied. Most work to date has focused on Bioko Island and market surveys (Fa 2000; Fa et al. 2002), with less attention on the mainland (except see Fa (2001), Keylock (2002), Kumpel (2006)). Bushmeat hunting is widely prevalent, practised openly, and likely to be occurring at unsustainable levels (Fa & Yuste 2001; Fa et al. 1995). A better understanding of the wider impacts of hunting and the likely degree of sustainability of the bushmeat trade is particularly important given the currently limited alternative protein sources in Equatorial Guinea and apparent dependence on bushmeat for food and livelihood security.

Conservation

Equatorial Guinea has a relatively new network of protected areas which were established under Spanish colonial rule (Appendix 8.1). From 1986 to 1990 the Spanish Technical Co-operation developed a conservation and research programme (Castroviejo et al. 1994), as a result of which a network of protected areas for Equatorial Guinea was

proposed by the Ecuato-Guinean government in the 1988. Ley 8/1988 outlined the protection of nine main zones as protected areas, covering a total area of 3400km² (8.2% of the country's total land surface) (Garcia & Mba 1997).

Since 1992 the EU programme 'Conservation and Rational Utilization of Tropical forest ecosystems in Central Africa' (ECOFAC) has been responsible for overseeing the management of the park. This network has been substantially modified in recent years by the EU-funded Proyecto Conservación y Utilización Racional de los Ecosistemas Forestales (CUREF) based in Bata, through the designation of different levels of protection for each area (Sunderland & Tanyi Tako 1999). In 1997 the incorporation of the Monte Mitra area into the Monte Alen National Park, produced a combined area of 160,000 hectares, and the national park now covers approximately 10% of Rio Muni (Gautier-Hion et al 1999). After the 1998 Yaounde meeting of the Congo Basin Forest Partnership (CBFP) the national protected areas system was expanded and now contains 13 protected areas.

In reality however, this protected area system exists only on paper, with little to no enforcement or biodiversity monitoring occurring. While existing legislation protects several species and prohibits hunting within protected areas, enforcement is minimal. The national agencies that should enforce the laws to control and prevent logging and hunting do not have the staff, expertise, equipment or financial resources needed to carry out their mandate, and are isolated from the international conservation community (Bonilla 2003).

Recently, in response to the second CBFP meeting in Brazzaville (June 2004), the president of Equatorial Guinea called for a new 600,000 hectare national forest to be created that would double the area of the country under conservation management, bringing the total to 37% of Equatorial Guineas territory. This is more than any other member of the Commission for the Forests of Central Africa (COMIFAC), and one of the highest percentages in the world. This new national forest corridor would integrate 600,000 hectares of forestry concessions and connect six national parks, including one in Gabon, into a wilderness corridor (Conservation International, pers. com.), however three years on these plans are still not a reality.

Chapter 1

Research background

1. Research background

1.1 Sustainable use of wild living resources

The need for sustainable use

Human beings have exploited wildlife throughout their history (Bahuchet 1993), however today's levels of exploitation are massively more severe (Regan et al. 2001). The human population now exceeds 6.7 billion people and is projected to continue to increase for hundreds of years into the future (United Nations 2007). These large population sizes combined with our technological advances have allowed us to exploit natural resources at rapidly growing scales, and with increasing levels of efficiency (Mace & Reynolds 2001a). Consequently, our use of natural resources is such that it represents a major threat to many plant and animals species (IUCN 2007). Various forms of use have been implicated in species declines, including commercial fishing (Pauly et al. 2005), subsistence hunting (Oates et al. 2000), extraction (Laporte et al. 2007), collecting (Peres et al. 2003; Siebert 2004; Soehartono & Newton 2002) and trade (Baum & Vincent 2005; Blake et al. 2007).

If people are to continue to use or derive benefit from wild living resources then the goal must be one of sustainable use (Mangel et al. 1996). Indeed, it has been argued that sustainable use can act as a strategy to achieve conservation (Hutton & Leader-Williams 2003). By promoting use, or allowing use to continue, wild resources are valued by people, and these incentives for conservation discourage the destruction of species and their habitats (IUCN 2000). As such, the strategy of sustainable use has been formally adopted by many within the conservation community, and beyond, as part of a framework for sustainable development (United Nations 1992b).

There has been much debate surrounding the meaning of sustainable use (Hutton & Leader-Williams 2003), and the meaning of the term may vary depending on the context in which it is used (Robinson 1993; Sutherland 2001). It can be useful to think about sustainable use as having biological and social components. The biological component refers to the resource itself and the ecosystem of which it is a part, and the social component, to the people who gain benefit from the resource (Sample & Sedjo 1996). These ideas are encompassed by the definition of sustainable use given in article two of the Convention on Biological Diversity, as the "use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations" (United Nations 1992a).

Barriers to sustainable use

Put most simply, there are two main obstacles to the sustainable use of wild living resources: a lack of knowledge and limits on control (Mace & Reynolds 2001b).

Effective conservation of a resource requires an understanding of how that resource responds to exploitation (Milner-Gulland 1998). As such, the limits to our knowledge of the state of harvested populations represents an obstacle to achieving sustainable use. There are still many biological difficulties in estimating key life history parameters (Bielby et al. 2007), and in many cases accurate census of the population under threat may be difficult or impossible (Karanth et al. 2006). Time series of observations may be short or confined to small segments of the population, there may be a lack of replicates or scientific controls, and data may be biased by confounding effects of equipment or census techniques (Ludwig 2001a). In addition, natural populations often go through large fluctuations due to interactions with other species, changes in food supply, or unknown causes (Beddington & May 1977; Holling 1973). This makes it difficult to determine if exploitation is implicated in a population decline, or whether the decline is due to other factors (Ludwig 2001a).

Limits to control relate to the social and political context in which use occurs. For many people living in developing countries, the use of wild living resources is an imperative (Hutton & Leader-Williams 2003; Pimentel et al. 1997), and they depend heavily on fishing, hunting and gathering to meet their basic needs (de Merode et al. 2004; Wilkie & Godoy 2001). Without alternatives and with continued population growth, levels of use are only likely to continue to rise. Even if controls on use were ethically acceptable, while there is such a strong imperative for use, they would be extremely difficult to enforce (Rowcliffe et al. 2004). The tragedy of the commons (Hardin 1968) features in many discussions about the problems involved with controlling use. The metaphor illustrates how free access and unrestricted demand for a finite resource ultimately dooms the resource through over-exploitation. This occurs because the benefits of exploitation accrue to individuals or groups, each of whom is motivated to maximize use of the resource, while the costs of the exploitation are distributed among all those to whom the resource is available. Natural controls to over-exploitation, such as the uneconomic harvesting of depleted populations, are often removed by economic subsidies, which are a common problem across terrestrial, freshwater, and marine ecosystems (Myers 1998). Such governmental policies artificially alter market dynamics so that the true costs of production and benefits of the resources are not represented (Milner-Gulland 1998). For example, it is only the huge economic subsidies that make unsustainable western fishing practices possible (Branch et al. 2006; Hilborn et al. 2005; Pimm et al. 2001).

Clearly, in spite of a long history of management of renewable resources, conservation professionals and natural resource managers are still far from being able to ensure the sustainable use of wild populations (Ludwig et al. 1993). It is evident that even if we can get the biology right, biological questions are only part of the problem, and that economic, political and social issues pose the biggest barriers to sustainable use (Rosenberg et al. 1993), as well as our failure to synthesize and act upon what we already know (Johannes 1998; Ludwig 2001a; Pimm et al. 2001). The conservation of exploited species therefore represents a considerable biological and social challenge (Mace & Reynolds 2001a).

1.2 The bushmeat trade as a specific case of use

Scale and statistics

Throughout the developing world, rural people meet many of their food and livelihood needs by harvesting wildlife (Pimentel et al. 1997). Bushmeat is the term commonly used to describe wild animals that are hunted for food (Bennett et al. 2007), and it represents a highly valuable non-timber forest product across the whole of tropical Africa, Asia and the Neotropics (Robinson & Bennett 2004). In recent years there has been an important transition from subsistence to commercial hunting (Wilkie & Carpenter 1999), and the trade in this commodity is considered to be one of the most important threats to biodiversity in these regions (Bakarr et al. 2001; Milner-Gulland & Bennett 2003; Redford 1992; Robinson & Bennett 2002). Estimates of the volume of bushmeat extracted range from between one and five million tonnes per year for the Congo Basin (Wilkie & Carpenter 1999), and conservative estimates of single-species offtake have been made: 28 million bay duikers, 16 million blue duikers (Wilkie & Carpenter 1999), and more than seven million red colobus are being taken from the forests of central Africa every year (Fa & Peres 2001).

Tropical forests typically have a low productivity in comparison to other ecological zones, with limited potential to produce meat from either wild or domestic herbivores (Barnes 2002a; Barnes & Lahm 1997). It has been estimated that tropical forests are capable of sustainably providing for the protein needs of approximately one person per km² (Robinson & Bennett 2000), however on average there are 99 people per km² of remaining forest in West and Central Africa (Naughton-Treves et al. 2003). In central Africa about 645kg of wild meat are extracted from each square kilometre of forest every year (Wilkie & Carpenter 1999), with the estimate for maximum sustainable production being under 102kg/km²/yr, wildlife is therefore being extracted from the forest at six times the sustainable rate (Robinson & Bennett 2000). Analyses suggest that in the Congo

basin 60% of the mammal species are being harvested unsustainably (Fa et al. 2002), hence the commonly used term 'The bushmeat crisis' (BCTF 2004).

Due to figures such as these the term bushmeat has become synonymous with overexploitation (Cowlshaw et al. 2005b). On a broad scale it is undoubtedly true that levels of hunting to supply the bushmeat trade are widely unsustainable over much of west and central Africa Asia (Bennett et al. 2002). However, at the local scale this may not always be the case (Cowlshaw et al. 2005b), and perhaps defining the trade as either sustainable or unsustainable is not particularly helpful. Instead it is more informative to ask under what conditions might bushmeat hunting be sustainable (Ohi-Schacherer et al. 2007; Peres, 2006; Robinson, 2004).

Causes

The current bushmeat crisis has arisen due to a number of interacting factors. There is rapid human population growth in the forest zone from both reproduction and immigration. The human population of sub-Saharan Africa grew to about 612 million in 2000 (UN 2000). In addition, between 1980 and 1990 Africa lost 18% of its forest area (WRI 2005). In combination these figures show that the pressure on the remaining habitat is likely to be even greater than population statistics alone would suggest (Bennett 2002). Changes in hunting technology, for example the use of more efficient methods such as firearms and cable traps (Cannon 2001; Lahm et al. 1998), the conversion of forests for alternative land uses (Bennett et al. 2006; Metzger 2003), increased access and road development in previously remote areas provided by logging operations (Bakarr et al. 2001; Wilkie et al. 2000) are all additional contributing factors. The scale of this problem is only amplified by the increasing aspirations and need for cash among rural people, the low fixed and opportunity costs of hunting (Wilkie & Godoy 2001), weak governance (Laurance 2004; Smith et al. 2003), inefficient natural resource management (Hayes 2006), and growing urban prosperity stimulating demand for bushmeat and commercialisation of markets (Fa et al. 1995; Fa et al. 2000).

Biological effects

A wide range of species are affected by the bushmeat trade, including birds, reptiles and mammals (Bowen-Jones et al. 2002). Species vary in their vulnerability to threatening processes, and responses to anthropogenic threats such as hunting vary markedly across taxa; depending on a species intrinsic traits, but also on extrinsic factors (Isaac & Cowlshaw 2004; Price & Gittleman 2007). Large bodied animals with low reproductive rates are most susceptible to over-exploitation (Bodmer et al. 1997), particularly primates (Cowlshaw & Dunbar 2000) compared with smaller more productive species, such as the

larger rodents and some of the smaller antelopes, that apparently tolerate relatively intensive hunting (Mangel et al. 1996; Wilkie & Carpenter 1999).

Hunting leads to reductions in density (Fa et al. 1995), and may lead to local extinctions (Behra 1987; Fay 1989) or in extremes cases the possibility of global species extinctions (Oates 1986). In addition to direct mortality acting on population size, population structure can also be affected, and hunting can act indirectly on individual behaviour within the exploited populations (Cowlshaw & Dunbar 2000; Gadsby 1990; Muchaal & Ngandjui 1999; Watanabe 1981; Zuberbuhler et al. 1997). Furthermore, the implications of hunting may be far wider than the direct impacts on the prey populations themselves (Bennett et al. 2002). Many bushmeat prey species are important components of tropical forest ecosystems, for example primates account for the bulk of medium-sized mammalian biomass in many tropical forests (Oates et al. 1990), and have significant roles in ecosystem functioning such as seed dispersal and germination (Cullen et al. 2001; Maisels et al. 2001; Moore 2001). A collection of recent studies have identified considerable indirect effects of hunting on tropical forest plant communities, emphasising the wider consequences of hunting for ecosystem dynamics (Nunez-Iturri & Howe 2007; Peres & Palacios 2007; Stoner et al. 2007; Wright et al. 2007a; Wright et al. 2007b).

A need for integrated solutions

Awareness of the bushmeat issue has increased enormously in recent years, and as well as being a conservation concern, it has also been of interest to development agencies (Brown & Williams 2003). Forest products such as bushmeat are of vital importance in the diets and economies of many people in the tropics (Pimentel et al. 1997). In Liberia, for example, 75% of the meat consumed in the country originates from wild animals (Anstey 1991). The cost of wildlife loss is likely to fall most heavily on rural populations, reducing the amount of protein available to them, and eroding one of the few commodities they can sell, thus having important implications for rural livelihoods and food security in these areas (Bennett 2002; Davies 2002b; de Merode et al. 2004; Mendelson et al. 2003).

From both conservation and development perspectives, this poor management of wildlife resources is a critical problem (Bennett et al. 2007), and a solution for both wildlife-dependent human populations and exploited species is urgently needed (Rosser & Mainka 2002). The problem faced is how to protect exploited species from continued declines and possible extinction, while at the same time ensuring the food security and the livelihoods of the people who depend most on this resource (Rao & McGowan 2002). In the long term, site-specific integrated solutions that regulate sustained offtake of certain species with protection of other more vulnerable species, that provide alternative sources of protein and income for the rural poor, that curtail the commercial trade, and

that secure wildlife in protected areas, will be needed (Davies 2002b; Hackel 1999; Robinson & Bennett 2002; Wilkie & Carpenter 1999). This issue needs to be tackled from development and conservation perspectives, requiring an interdisciplinary approach that incorporates biological, economic, social, and political components (Bennett et al. 2007; Rowcliffe 2002; Wilkie et al. 1998).

Bushmeat research to date and future directions

The first bushmeat studies were largely anecdotal, aimed at focusing the world's attention on the issue (Ammann 1999; Pearce & Ammann 1995). Others provided more quantitative assessments, documenting the species diversity and quantity of bushmeat harvest, trade, or consumption (Anstey 1991; Auzel 1996; Chardonnet et al. 1995). However, these first studies provided little information with which to address sustainability, tending not to report the catchment areas from which animals were taken.

It was recognised that there was a need to move away from descriptions of harvest patterns towards assessing the sustainability of harvest. The response was the development of sustainability indices, such as the Robinson and Redford method (Robinson & Redford 1991; Robinson & Bodmer 1999). These indices are based on highly simplified population models, with which the effects of removing individuals through hunting can be predicted. Offtake rates are compared with the expected maximum production rate of the population in question, the inference being that if offtake exceeds the maximum production rate, then the harvest must be unsustainable. These indices have become the standard used in the field (Ohi-Schacherer et al. 2007), but despite being relatively cheap and easy to perform, they suffer from a number of limitations, for which they have been criticised (Milner-Gulland & Akcakaya 2001).

The incorporation of factors such as spatial structure (McCullough 1996; Salas & Kim 2002), source-sink dynamics and dispersal (Naranjo & Bodmer 2007; Novaro et al. 2000) sociality and species interactions (Rowcliffe et al. 2003), would enable more biologically accurate assessments of sustainability. Also recognised has been the need to allow the incorporation of the uncertainty surrounding model parameters, and to produce assessments that are accompanied by a measure of the degree of certainty (Milner-Gulland & Akcakaya 2001; Milner-Gulland et al. 2001). This has led to interest in how alternatives could be developed that would allow the incorporation of greater biological realism into sustainability assessments (Milner-Gulland & Akcakaya 2001).

Current bushmeat research focuses on many of these issues. For example, the use of dynamic bio-economic models to assess the sustainability of bushmeat hunting (Ling & Milner-Gulland 2006), the modelling of hunting impacts in multi-species communities to produce prey profiles with which to assess the sustainability of hunting at the community level (Rowcliffe et al. 2003), evaluating the potential of different habitat types to support

sustainable hunting (Gavin 2007), and an increasing recognition of the importance of spatial structure in determining the sustainability of hunting (Ling & Milner-Gulland 2007; Naranjo & Bodmer 2007; Ohl-Schacherer et al. 2007).

1.3 Monitoring of wild living resources

The need for monitoring

Our increasing use of wild living resources, in combination with other threats such as climate change (May 2007; Thuiller 2007), habitat loss (Laurance 1999), and invasive species (McGeoch et al. 2006), means that there is an urgent need to increase the effectiveness of conservation efforts (Achard et al. 2002; Dirzo & Raven 2003; Laurance 1999; Pimm et al. 1995). This is especially so in the tropics where biodiversity is greatest and where threats are felt most keenly (Myers et al. 2000). With these growing threats to biodiversity, the need for, and science behind, monitoring is becoming a dominant theme in conservation biology (Balmford et al. 2003; Bawa & Menon 1997; Nichols & Williams 2006). This is so for those working to address single threat processes, such as that of overexploitation (Bennett et al. 2007), right up to those working at a global level on our international commitments to reducing biodiversity loss (UNEP 2002). Therefore robust and repeatable systems for monitoring the changing state of nature are required (Balmford et al. 2003; Jenkins et al. 2003). As well as providing information on system state and trends, monitoring can also provide information on the drivers of change, for example, interactions with other species, or the effects of human activities (Yoccoz et al. 2001). Monitoring should also be integrated with management (Nichols & Williams 2006), allowing the effects of management interventions to be determined, and adapted when necessary (Kremen et al. 1994; Royal Society 2003; Walters 1986).

The estimation of abundance

Population change is detected using repeated measures of abundance over time (Thomas 1996). The estimation of abundance is therefore crucial to conservation monitoring, as well as forming an essential part of much research in the fields of ecology and population biology (Caughley 1977; Sutherland 1996). There is a wealth of literature relating to the estimation of animal abundance (Caughley 1977; Schwarz & Seber 1999; Seber 1982; Wilson et al. 1994) and new developments and additions to the field are continually being made, both in the statistical underpinning (Thomas 1996), and in the practical implementation of techniques (Plumptre & Cox 2006).

There are many methods available to quantify abundance, ranging from relatively simple to sophisticated techniques. Since it is rarely feasible to census an entire

population, estimates of abundance are most often made using these techniques to survey a sample of the population. The simplest methods are based on counting individuals or their signs on a random sample of plots or strips (Schwarz & Seber 1999). The resulting sample estimate of the number of individuals or units such as groups, per unit area can then be converted into a population total by multiplying by the population area (Davies 2002a). Where sign, such as ape nests (Morgan et al. 2006), tracks (Payne 1992), or dung (Barnes 2001; Wilkie & Finn 1990) is counted, then a relative measure, or index of population density is produced, and if reliable correction factors can be calculated then the index can be converted into population density (Barnes et al. 1997; Barnes & Barnes 1992).

Other frequently used sampling units are lines and points. In line transect sampling, the observer travels by foot, plane or boat along a randomly placed line or transect (Schwarz & Seber 1999). Perpendicular distances from the line to sighted animals are measured, and by modelling the probability of detection as a function of distance from the line, these distances can be converted into an estimate population density (Buckland et al. 2001; Thomas 2006). This is the technique most frequently used in tropical forest environments to survey mammal species (Plumptre 2000; White & Edwards 2000; Whitesides et al. 1988). Point sampling is similar in principle and frequently used to survey birds (Buckland 2006), with distances of sightings from the point being measured, and with survey effort being measured in units of time.

Catch-effort methods are based on the ratio of the catching effort invested to the number of animals removed from the population, and it is this principle which forms the basis for the sophisticated stock assessments that are conducted in many commercial fisheries (Gulland 1983; Hilborn 1992; Quinn 1999). Capture-recapture methods are another widely used method, in which a sample of animals are collected, tagged or marked and released back into the population, the second sample of animals are caught and the procedure repeated. Capture histories are then used to estimate population size (White & Burnham 1999).

All of these methods of estimating abundance have underlying assumptions, such as random sampling, the absence of observer bias, no loss of tags or marks, or no differences in capture or sighting probability between animals and observers. Therefore much research has been directed at identifying and examining the effects of departures from these assumptions and modifying the underlying models to allow for, or incorporate such information (Schwarz & Seber 1999).

New techniques for estimating abundance

In recent years there has been considerable research attention directed at identifying simple and inexpensive alternative methods for estimating abundance and hence for

monitoring wildlife populations. For example, the use of volunteer based surveys (Gregory et al. 2005; Toms & Newson 2006), or species lists (Roberts et al. 2007). At the same time a number of conceptual shifts in ecology have occurred (Berkes 2004), towards including humans as an integral part of the ecosystem (Bradshaw & Bekoff 2001), and away from expert-based approaches towards more participatory and inclusive conservation and management (Ludwig 2001b).

These changes are particularly relevant to the estimation of abundance for the monitoring of many wildlife species in developing countries. In these countries, where many people depend upon natural resources to meet many of their needs (Pimentel et al. 1997), attempts are being made to integrate this use with conservation (Kremen et al. 1994), by involving rural people as an integral part of wildlife conservation policy (Hackel 1999). This approach is seen as an alternative to the more exclusionary protectionist policies of the past, which often alienated rural people from conservation efforts, or put the needs of wildlife above those of people (Owen-Smith 1993). One of the key elements of such programmes is that local communities participate in resource monitoring and management (Hackel 1999). There are a suite of methods that attempt to involve local communities in monitoring, such as a collection of techniques termed locally-based methods (Danielsen et al. 2005), the use of expert local opinion (van der Hoeven 2004) or Traditional Ecological Knowledge (TEK) (Davis & Wagner 2003; Drew 2005; Neis et al. 1999).

One case of TEK, involves the use of traditional management systems (Moller et al. 2004). The harvesting of wildlife or other natural resources is a way of life for many societies throughout the world and in the past there have been traditional systems in place in order to manage these resources (Donovan & Puri 2004; Preece 2007; Stave et al. 2007). However, mounting economic pressures in many cases mean that these systems are being degraded or are no longer used. Such traditional management systems may prove complementary to scientific monitoring, and the differences between the two are often more theoretical than real (Moller et al. 2004). Involving harvesters by using their own monitoring methods is much more likely to lead to the application of the recommendations resulting from monitoring, and altered harvest practices where needed for sustainability (Danielsen et al. 2005). The concept of hunting returns or Catch per Unit Effort (CPUE), forms part of many traditional ecological management systems, indeed it is the currency on which many hunters and fishermen are likely to base their decisions (Lyver 2002), and has been successfully used by local communities as a tool for population monitoring (Kitson 2004). Complementing scientific or professional monitoring with traditional ecological knowledge is therefore a potentially workable and cost effective technique (Johannes 1998).

1.4 Catch per Unit Effort

The Catch per Unit Effort model

In marine environments, determining abundance, and therefore monitoring the effects of harvesting is particularly problematic, and the approach adopted has been the use of catch-effort data (Hilborn 1992; Quinn 1999). This is based on the observation that the size of the catch from an animal population typically increases when either population density or effort increases (Seber 1992). So in principle CPUE can act as an index of abundance, and be used to detect declines in the same way as abundance itself. The use of CPUE as an index of abundance is based on a fundamental relationship that relates catch to abundance and effort:

$$C_t = qE_tN_t$$

Where C_t is catch at time t , E_t is the effort expended at time t , N_t is abundance at time t , and q is the portion of the stock captured by one unit of effort (often called the catchability coefficient). This equation can be rearranged to form the relationship between CPUE and abundance:

$$C_t / E_t = qN_t$$

Making CPUE proportional to abundance,

$$CPUE \propto N_t$$

Provided that q is constant over time.

This assumption that CPUE is directly proportional to abundance is one that is widely made in quantitative fisheries analysis, with CPUE forming the basis of stock assessments for many commercially important species (Hilborn 1992; Quinn 1999).

Hyperstability and Hyperdepletion

The CPUE model, despite extensive use in the fisheries has a number of shortcomings. Strict proportionality between CPUE and abundance is frequently assumed (Harley et al. 2001), but it has long been recognised that the assumption that catch is directly proportional to effort may not always be true, and that CPUE may not accurately reflect changes in abundance (Beverton & Holt 1957). A linear relationship might oversimplify

the link between CPUE and abundance, and in reality CPUE may change either more or less steeply than abundance (Figure 1.1). The first two curves show Hyperstability ($\beta < 1$), when abundance declines faster than CPUE. For natural resource managers this means that a population is declining without any change in CPUE to arouse concerns, and is considered to be one of the biggest problems for fisheries managers (Hilborn 1992). Hyperstability appears to be the most common relationship, being well documented in many fish species. Some of the most well known fisheries collapses in the world have been ascribed to Hyperstability, such as the Northern Cod (Rose & Kulka 1999; Shelton 2005).

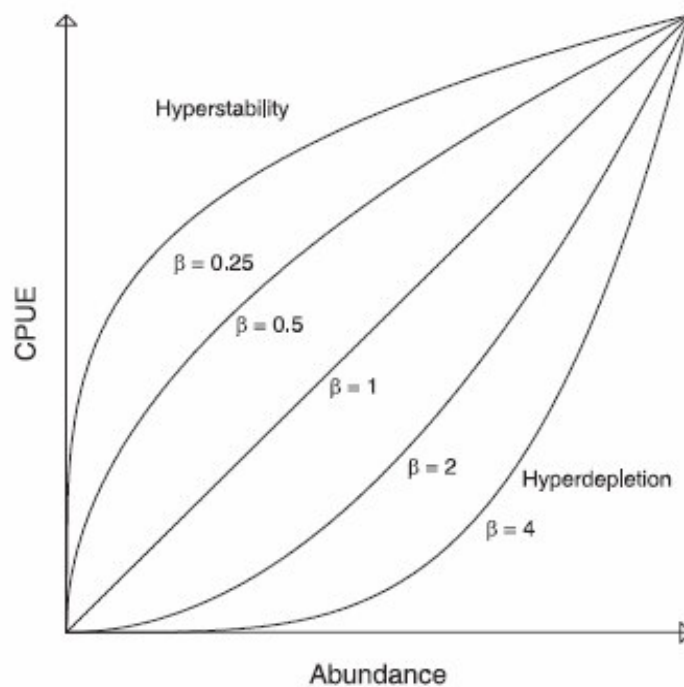


Figure 1.1 Relationship between CPUE and abundance based on different values of the shape parameter (β), taken from Harley (2001)

The middle curve shows a proportional relationship between CPUE and abundance, as is frequently assumed, and the last two curves show Hyperdepletion ($\beta > 1$), when CPUE drops faster than abundance. With Hyperdepletion, the population appears to be depleted, yet abundance has not greatly declined, this rarely occurs, but there are some examples, such as the south Australian rock lobster (Hilborn 1992).

Causes of non-proportionality: exploiter behaviour

There are many aspects of an exploiter's behaviour that may result in a non-linear relationship between CPUE and abundance.

Efficiency of search

In order for CPUE to be proportional to abundance in an area, harvesting effort should be distributed at random within that area with respect to the prey. However, it is almost impossible for this to be true, since exploiters will go where they believe their prey to be. If exploiters have knowledge about where prey can be found, then effort will not be randomly distributed, but instead will be concentrated on those sites of highest abundance. Such efficiency of search can lead to problems when CPUE data are aggregated over large areas, since catch may reflect abundance in a small number of high density locations rather than that of the whole area. In this way efficient search can lead to Hyperstability (Salthaug & Aanes 2003), and the more skilful the exploiter, the poorer the CPUE index will be as a measure of population abundance (Moller et al. 2004).

Spatial allocation of effort

If the costs of exploitation and the desirability of areas vary in space, then both Hyperstability and Hyperdepletion can result. For example, consider that two areas initially at the same level of prey abundance, one area is close to home and the other is far away, dangerous, expensive to exploit, or for some other reason undesirable. Effort will first be spent in the close area, until at some point exploiters are willing to trade off the undesirable aspects of the other area for its higher CPUE. If we assume that CPUE in the less desirable area must be twice as high as CPUE in the close desirable area before effort will switch, then all effort will concentrate on the close area until it is driven down to half of its unexploited size. At this point total biomass will be 75% of the unexploited size but CPUE will be 50% of its original level, and Hyperdepletion will result. Effort will then start to shift to the undesirable area and the CPUE will increase even though total abundance may still be declining, resulting in Hyperstability (Hilborn 1992; Quinn 1999). This demonstrates how CPUE can remain stable or even increase due to increases in, or shifts in, the area exploited, as the overall abundance in the new or expanded area declines, leading to Hyperstability. For these reasons, it can be useful to spatially disaggregate CPUE data and patterns of effort, to reveal localised declines as each new area is fished or hunted out (Fonteneau 1999).

Handling time and variable catchability

In order for CPUE to be proportional to abundance there should be no significant proportion of the exploiter's time budget allocated to handling (Hilborn 1992). Searching and handling time are mutually exclusive activities (Stephens & Krebs 1986). For this reason, encounter rates per unit 'time searched' rather than a cruder measure of effort such as overall time should sometimes be used (Holling 1959). If there are significant components of handling time in harvesting, and if catchability is variable, then in periods of higher catchability more time will be spent handling, and the gear will effectively under sample the periods of high catchability, and over sample periods of low catchability. The net effect will be that CPUE will not be an average of periods of low and high catchability, but weighted more towards periods of low catchability. This will cause a bias in the relationship between CPUE and abundance towards Hyperdepletion (Hilborn 1992). Another important consideration is that of changes in an exploiters' efficiency can occur over time. For example, gear saturation can occur in fisheries if all hooks are taken up or if a net is full. Similarly a hunter becomes saturated when he can no longer carry any more prey (Charnov 1976), or when his traps are all full, preventing the capture of further prey. These saturation effects on exploiter efficiency would lead to CPUE being independent of prey density, so not reflecting prey density when it is high and hence the production of Hyperdepletion in the relationship between CPUE and abundance.

Exploiter interactions and interference competition

Exploiters rarely work independently of one another. A study by Gaertner (2004) simulated the impact of information exchange amongst fishing vessels on the shape of the relationship between CPUE and abundance, and concluded that Hyperstability is mainly attributable to information exchange among vessels, because the sharing of information leads to non-random search. Competition among exploiters, as well as collaboration can occur; interference competition is characterised by a reversible reduction in foraging success due to interactions among foragers or between forager activities and prey behaviour (Begon et al. 1996). When interference is great enough, even if abundance is high it will not be reflected in the CPUE obtained, and the assumed relationship between CPUE and local abundance will break down (Gillis & Peterman 1998), resulting in Hyperdepletion.

Prey selection

Catch is a function of encounter rates which are function of density, so catch rates should be directly proportional to density. For the preferred species which the exploiter always kills on encounter this likely to be true, but there may be an effect of species preference by the exploiter (Alvard 1993; Alvard 1995) so that for the less preferred species only presence in the area is indicated and catch provides an under representation of

population size. In the field of optimal foraging theory (Stephens & Krebs 1986), the occurrence of such selection between simultaneously encountered prey types is termed partial preferences (Waddington 1982). In some cases this may not pose a great problem since it may be that it is often the most preferred and therefore most exploited species, for which we require information (Puertas & Bodmer 2005).

Causes of non-proportionality: Prey distribution, biology and behaviour

Prey spatial distribution

The distribution of prey in space has implications for harvesting success (Jonzen et al. 2001), and the relationship between abundance and CPUE. The abundance of sedentary or highly territorial species depends only on conditions within the local area, rather than what goes on in neighbouring areas, therefore each local area can be thought of as an independent population (Hilborn & Mangel 1997). In an unexploited state the distribution of abundance would depend upon the distribution of carrying capacities among the locations. If they are all similar then we would expect prey distribution to be uniform. If some places are better, then densities would be higher in these areas (Fretwell 1972). If high density areas are less desirable than others to exploiters on some basis other than CPUE, there will be a tendency for Hyperdepletion, the less desirable areas will become a reserve of underutilised areas of abundance (Hilborn 1992).

For diffusive species, abundance at any one location will depend on the abundance elsewhere. CPUE in an area may be directly related to the initial abundance, but then is changed as successive fishing effort is applied to the same area, and these local area effects may produce Hyperstability (Battaille & Quinn 2006). To allow CPUE to remain constant, density must remain constant. This can occur in schooling fish as they redistribute themselves over a smaller area to provide the same density (Rose & Kulka 1999). Similarly, this could occur in highly social species such as primates if they aggregate to maintain minimum group sizes (Cowlshaw & Dunbar 2000). The importance of considering the exploited area can be illustrated as follows: if CPUE in a site increases by factor of 1.5 from one year to the next, but the area occupied by the population is halved (contracts at the lower density), then population abundance decreases to 0.75 of that in the first year. If the population contraction is unobserved then the inference of increasing abundance from the increased CPUE is completely wrong, and Hyperstability will occur undetected. This is the exact mechanism that was behind the collapse of the Northern Cod (Rose & Kulka 1999; Shelton 2005).

Prey behaviour and variable catchability

If the behaviour of the prey species is predictable then targeting by the exploiter will be possible, for example, primates aggregating at fruiting trees (Peres 1994). This may

mean that at low population sizes the costs of harvesting will not decrease linearly with population size, resulting in Hyperstability. The population may then decline dramatically while catches appear to be healthy giving no indication that harvesting is occurring at an unsustainable level (Milner-Gulland 1998), and this has been shown to occur in fish due to habitat selection (Freon et al. 1993). Conversely, Hyperdepletion could result from variable catchability if individuals of the prey species respond differentially to the gear, such that there is a small but highly vulnerable subset of the prey population which is depleted, leaving behind a much less vulnerable but still abundant subset of the population. In this way prey populations would appear to be depleted, but abundance would not have declined greatly (Hilborn 1992).

Summary of causes of non-proportionality

The relationship between CPUE and abundance can be influenced by both prey and exploiter. Information on prey biology and exploiter behaviour will therefore provide an idea of whether the assumption of proportionality is likely to be violated and hence how closely CPUE will be related to abundance. The contributions of prey biology and exploiter behaviour to Hyperstability and Hyperdepletion are summarised in the table below (Table 1.1)

Table 1.1 Summary of the key reasons why the assumption of proportionality between Catch per Unit Effort and abundance might be violated. Adapted from Hilborn (1992) and Milner-Gulland (2007)

Violation	Cause	Specific detail
Hyperstability	Prey	Prey behaviour is predictable and individuals or groups remain easy to find despite reduced abundance
	Prey	Individuals aggregate as depletion proceeds due to habitat selection or con-specific attraction
	Exploiter	Cooperation and information exchange among exploiters
	Exploiter	Increasing efficiency of harvest method over time
	Exploiter	Increase in area exploited
Hyperdepletion	Prey	Individuals learn to avoid capture
	Prey	Heterogeneous capture probabilities so that vulnerable individuals are caught first, leaving a less vulnerable subset
	Exploiter	Interference competition between exploiters
	Exploiter	Prey species selection against non-preferred species
	Exploiter	If undesirable areas remain unexploited

The use of catch-effort data

Trends in catch, effort and CPUE

Total catch is an important signal for a harvesting system, and is often used as an approximate indicator of the system state, for example, time series of catches have been used in the fisheries in this way (Grainger & Garcia 1996). When total harvesting effort is also available, CPUE can be calculated as an index of abundance. Trends in catch, effort and CPUE can then be used in relatively simple ways to provide information on the status of the harvested population (FAO 2006). If for example, both catch and effort are increasing (or both are decreasing), so that CPUE is fairly constant then it may be that harvesting is having little effect on the population being exploited (assuming the exploited area is constant). If fishing effort is fairly constant, but catches have gone up or down then it can be assumed that the population size has also gone up or down, for example due to environmental factors (Vickers 1991). If on the other hand, effort is increasing but catches have remained fairly constant, CPUE is therefore decreasing, which then

suggests that the population is declining in size. In the worst case, if effort has increased but catches have declined, CPUE will be decreasing rapidly, and this may imply that the population is declining even faster than the catches (FAO 2006).

Equilibrium methods

One of the fundamental concepts of fisheries theory is that there is a repeatable relationship between effort and average catch (Gulland 1983; Hilborn 1992). Yield increases as effort increases up to a certain point, the Maximum Sustainable Yield (MSY), at which point yield begins to decline with further increases in effort (Fig. 1.2). Many fish stock assessments have been based on trying to estimate the optimum effort and the MSY (Beddington & Kirkwood 2005).

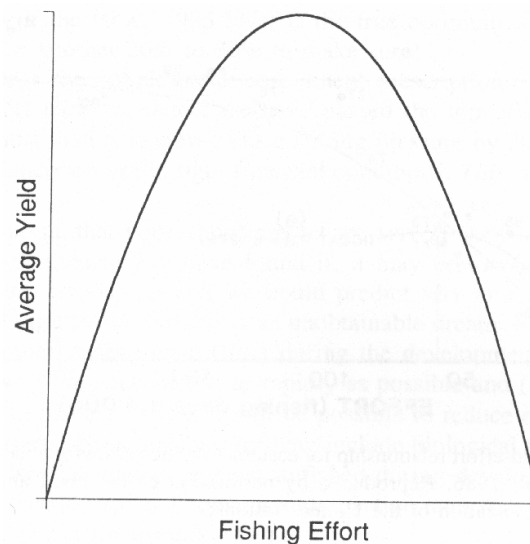


Figure.1.2 The assumed relationship between fishing effort and average fishing yield, taken from Hilborn (1992)

Because of this predicted relationship between equilibrium catch and effort, in theory if we have catch-effort data for widely varying levels of effort, then plotting the catch-effort curve may enable us to define a domed response that can be used to determine whether a population is being overexploited or not (Milner-Gulland & Rowcliffe 2007). If current effort and catch are on the right-hand side of the peak, the population is overexploited as it has gone below the size at which it is maximally productive (MSY).

This is extremely misleading however, because it assumes equilibrium, i.e. that population size is constant, as offtake equals the population growth (Kingsland 1985). In reality, data will always be from dynamic systems, with varying levels of effort and a time

lag occurring in the response of populations to changing harvest levels (Maxwell & Jennings 2005). If catch and effort from a time series of data from a single location are plotted against one another in order to define a maximum, MSY will almost always be overestimated (FAO 2006; Milner-Gulland & Rowcliffe 2007). One type of equilibrium analysis that has been useful on occasion involves spatial contrast in effort, which has been applied in artisanal fisheries (Munro & Thompson 1983). Using data from several spatially separated populations, that have been harvested at contrasting rates, could allow this method to work in principle, but only if each population is close to its equilibrium state, having been harvested at more or less constant rates for a considerable period of time (Milner-Gulland & Rowcliffe 2007). It would also require considerable contrast in order to define the full shape of the catch-effort relationship, with data from both heavily exploited and unexploited sites, in practice such data are very hard to find.

Dynamic models

Dynamic models do not assume that the population is at equilibrium and so provide a way around these problems. They use catch-effort time series to model the underlying changes in population size by fitting a dynamic population model to the data (FAO 2006). This approach requires historical catch data and an index of abundance. One of the central problems in stock assessment is to obtain an abundance index that is proportional to stock size and will hence reflect trends and responses to changing management regimes, CPUE is often used, but may not always be adequate (FAO 2006).

The catch-effort time series is used to model the underlying changes in population size from one point in time to the next by adding the population growth and subtracting the catch. The basic idea is to take an initial estimate of the population size at the beginning of the data series available, then use the model to predict the whole time series. The parameter values are then adjusted to provide the best fit of the predicted-to-observed time-series of abundance (CPUE) or catch data. There are a number of accessible tools for fitting such dynamic models, such as the Catch Effort Data Analysis package (Kirkwood et al. 2001). However, this approach is data hungry, and in order to estimate population parameters, good contrast between CPUE and effort is required, with considerable historical variation in population size and exploitation pressure (FAO 2006).

Depletion estimates of population size

The principle of depletion estimators is to examine how measured removals of prey influence the relative abundance (CPUE), of prey remaining in the total population or in a designated depletion study area. The fundamental idea behind depletion analyses is very simple, if you remove (catch) animals from a population, the population size will fall, and this will be reflected by a fall in the abundance index, for example, in CPUE.

The following hypothetical example from Kirkwood (2001) illustrates the principle: suppose there is a population that when harvested gives an original CPUE of 8.73 fish/hour. In a short space of time (so that no natural mortality or recruitment takes place), 1000 fish are caught, and afterwards the CPUE has dropped to 6.16. If the CPUE is an accurate indicator of relative population size, what was the initial population size? Catching 1000 fish caused the CPUE to drop by $(8.73 - 6.16) / 8.73 = 29.4\%$, so to reduce the CPUE by 100% (reducing the population size to zero), $1000 \times 100 / 29.4 = 3396$ fish would have to have been caught. If a catch of 3396 would cause the population size to fall zero, then there must have been 3396 fish there originally. When it is possible to intensively harvest over a short period of time, depletion methods can be a powerful technique to assess initial abundance, and have been said to be one of the most valuable but underused techniques available (Hilborn 1992).

Technical issues with the use of catch-effort data

There are a number of issues that need to be considered when collecting and analysing catch-effort data, many of these are related to the causes of non-proportionality previously discussed

Catch-effort standardisation

The catchability coefficient (q) is the fraction of abundance captured by one unit of effort (Maunder & Punt 2004). It is assumed to be a constant, independent of time, space and exploiter (Gulland 1983). However, the catchability coefficient may be influenced by a number of factors, such as the effects of species targeting, environmental factors, changes in catchability of a population, and differences in the efficiency of individual exploiters (Maunder et al. 2006).

Changes in species targeting by exploiters generally leads to catchability increases for the new target species and decreases for the previous target species, for example due to a change in depth of fishing gear (Ward & Myers 2005). The catchability of a population can increase over time as the efficiency of a fleet or group of hunters' increases, due to learning more about the location and behaviour of prey, or how best to operate the gear (Hilborn 1992). This has been very important in fisheries where many technological advances have been made causing the overcapacity of fishing fleets (Beddington et al. 2007).

Differences in the skill or ability of individual exploiters can be considerable, and they may show large variation in their CPUE for a given unit of effort when exploiting the same density of prey at the same time and place (Beverton & Holt 1959). The efficiency of a hunter or fishing vessel is defined as its 'power' relative to that of a standard hunter or vessel (Salthaug & Godo 2001). As well as causing CPUE data to be highly variable,

differences in power are an important consideration when comparing CPUE over time or space. Problems can arise if differences in hunter catching power are mistaken for differences in abundance. For this reason standardisation of effort to correct for changes in hunter or fishing fleet composition among areas, or over time might be required, so that changes in CPUE are due to abundance and not exploiter composition.

Environmental factors can have a large influence on catchability over time, for example el Niño events led to greatly reduced catchability in many fisheries (Maunder et al. 2006). Temporal variation in terrestrial harvesting patterns is also strongly linked to seasonality, for example, due to the timing of tree fruiting events, and varying suitability of different weather conditions for hunting (Cowlshaw & Dunbar 2000; Juste et al. 1995; King 1994; Oates 1988).

The main goal of standardizing catch effort data is to explain the variation in catch rate that is not a consequence of changes in population size, by identifying explanatory variables that reduce the unexplained variability in the response variable. The ability to use CPUE as an index of abundance depends on being able to adjust for the impact on catch rates of changes over time in factors other than abundance (Maunder & Punt 2004).

Spatial and temporal stratification of catch-effort data

The analysis and comparison of catch rates and CPUE are always based upon a time and area stratification. Preferably these strata should be small in area, and short in duration, in order to minimise any changes in abundance and hence CPUE that might occur over time and in space (Fonteneau 1999). If abundance is to be calculated over large heterogeneous areas, then CPUE should be calculated as the mean of local values, weighted by area if necessary, and not as total catch over total effort (Walters 2003). In addition there may be strata of the study area for which data are missing, for these unsampled strata no inference can be drawn about what their catch might have been, but these un-fished strata should not be ignored and there are techniques involving extrapolation of data from neighbouring strata that are available for dealing with such situations (Walters 2003).

Furthermore, exploiter behaviour determines the total effort expended by exploiters and has important consequences for the spatial and temporal stratification of catch-effort data. Total effort is often related to CPUE; if exploiters cannot meet their costs, they will not do much exploiting. So if there is any spatial or temporal aggregation in the CPUE, the time or space data with good CPUE will be overrepresented and strata with poor CPUE will be underrepresented when catch-effort data is summed across strata (Hilborn 1992).

Changes in the exploited zone

The size of the area exploited is a key factor in the potential catch of exploiters; a larger area meaning a higher potential catch than a smaller one. Undetected increases in the exploited zone may lead to false impressions of sustainable levels of offtake (Milner-Gulland & Mace 1998). Therefore any changes in area exploited during the time period for which looking at abundance and CPUE need to be taken into account (FAO 2006; Fonteneau 1999).

Species aggregated CPUE

Many harvesting systems are of a multi-species nature, with any given gear type exploiting a number of species. Species-aggregated relationships between effort and catch or CPUE can provide important information for management, since aggregated catch and CPUE relates directly to the socioeconomic benefits derived from exploitation, as well as providing insights into ecosystem level responses to exploitation (Lorenzen et al. 2006).

However, the ecological interpretation of observed patterns in aggregate CPUE is therefore far from straightforward. Species aggregated catch and CPUE have been used in a number of studies on the impacts of fishing, the most influential to date being that of Myers (2003) on the rapid worldwide depletion of predatory fish communities. This study came under considerable criticism due to its use of species-aggregated CPUE as an index of community biomass (Hampton et al. 2005). One of the problems with the use of CPUE data to assess communities is that it assumes that the catchability coefficient, or vulnerability to capture, for all species is equal. The combination of CPUE across species to monitor community abundance means that trends in CPUE can be misleading, reflecting changes in abundance of one or a few dominant species. These dominant species are often those with the highest catchability, and so also those which are most depleted. In general unless catchability is similar for all species being combined, CPUE will not be proportional to community abundance (Maunder et al. 2006). Lorenzen (2006) looked at species-aggregated yield-effort relationships in inland fisheries, and found that even at highest effort levels observed, no decline in aggregated yield was observed, possibly due to maintenance of community biomass through successive replacement of large, slow-growing predatory fish with smaller faster growing fish as effort increases (Pauly et al. 1998; Pauly & Palomares 2005). This suggests that extreme caution is required when interpreting aggregated CPUE as an indicator of the impacts of exploited on biological communities (Lorenzen et al. 2006), and leads to questions about whether there is a general relationship between species-aggregated catch or CPUE and effort that applies to a wide range of species (Lorenzen et al. 2006).

Validation of Catch per Unit Effort in fisheries

Considering this widespread use of CPUE there has been relatively little research conducted to assess whether it is in fact an accurate index of abundance. In many cases this is because it represents the only method available for abundance estimation (Connell et al. 1998; Haggarty & King 2006). Serious errors in estimates of safe levels of catch and of abundance, based on CPUE information, have been found for some fisheries, and a plea has been made for validation of CPUE measurements as indices of abundance (Westerheim 1990).

A number of studies have focused on the relationship between CPUE and abundance for a single species (Connell et al. 1998; Crecco & Overholtz 1990; Peterman & Steer 1981; Swain & Sinclair 1994), but the most comprehensive investigation so far in the fisheries literature is that by Harley (2001) who made the first large-scale attempt to test the assumption of proportionality. They conducted a meta-analysis of 297 time series of CPUE and independent abundance data, taken from research trawl surveys from ICES (International Council for the Exploration of the Sea) stock assessment reports, in order to test the hypothesis that CPUE is proportional to true abundance. They found widespread and strong evidence for Hyperstability, caused by habitat selection and aggregative behaviour in fish, and due to the ability of fishermen to locate these concentrations.

However, some studies have found evidence to support the existence of a proportional relationship between CPUE and abundance. For example, Haggarty (2006) used density measurements derived by SCUBA diving, to verify research angling CPUE as a useful measurement of the relative abundance of near-shore reef species. Similarly, Richards (1986) compared visual estimates of reef-fish density with CPUE estimates obtained by research angling at the same sites, and found that for the dominant reef species the relationship was one of strict proportionality, but that CPUE was a poor abundance index when data were combined across species.

The evidence is therefore mixed, and while the assumption of proportionality may be valid in some cases, there is much evidence to suggest that Hyperstability frequently occurs in the relationship between CPUE and abundance. The experience of fisheries researchers shows that the relationship between abundance and CPUE is not a simple one, it can vary between species, habitats and with gear type, and can be affected by both prey and exploiter behaviour. The existence of a proportional relationship between CPUE and abundance should not be assumed.

The use of Catch per Unit Effort for the management of terrestrial harvesting systems

In comparison to its extensive use in the fisheries, CPUE has been little used for the management of harvesting in terrestrial systems. According to Seber (1982) CPUE was first used in a terrestrial system in 1914 to estimate bear populations in Norway. Since then a number of authors have used hunting based statistics like CPUE to model population sizes of harvested ungulates such as white-tailed deer (*Odocoileus virginianus*) (Dupont 1983) and elk (*Cervus elaphis*) (Laake 1992). Despite this use of hunting based statistics to guide wildlife management, there have been relatively few demonstrations of their precision as relative population indices, or of calibration of CPUE against prey density (Moller et al. 2004). Without the incorporation of independent estimates of abundance, the use of CPUE may lead to inaccurate estimates of population size, on which management actions will be then based (Bowyer et al. 1999b; Hatter 2001; Schmidt et al. 2005)

There are a small number of studies which have compared CPUE data to independent estimates of population size, with mixed results. Lewis (1968) compared CPUE and mark-recapture estimates for a fenced population of white-tailed deer and concluded that CPUE estimates were not realistic. Lancia (1996) also used CPUE methods to estimate the size of a population of white-tailed deer, and found CPUE estimates to be negatively biased, but to correctly reveal major increasing or decreasing trends, and so concluded that CPUE estimates are probably sufficiently accurate. More recently, Pettorelli (2007) compared white-tailed deer density estimates from aerial surveys and hunting statistics, finding a correlation between the number of deer seen per hunter-day and the density of deer from aerial surveys, but no correlation between deer density from aerial surveys and the number deer actually harvested. Some rare examples of the validation of CPUE for other species include: Choate (2006) who simultaneously compared multiple techniques to estimate population of cougar (*Puma concolor*) in North America, finding hunter CPUE to be a poor predictor of population size as estimated from radio tagging, and Kitson (2004) who looked at the use of harvest rates as a population monitoring tool for Sooty shearwaters (*Puffinus griseus*) in New Zealand, finding it to be an inexpensive and feasible way to measure population trends.

The use of Catch per Unit Effort in bushmeat research to date

Tracking the relationship between hunter catch and effort in different locations or over time was first used primarily by anthropologists working in tropical forest regions (Hames & Vickers 1982; Saffirio & Scaglione 1982; Stearman 1990; Vickers 1991), and only more recently by biologists. Currently, information on CPUE or hunting return rates are

frequently reported in many bushmeat studies (Fa & Yuste 2001; Franzen 2006; Nielsen 2006; Noss 1998b; Peres & Nascimento 2006). In many cases such information has also been used to infer levels of abundance or the presence of hunting impact (Auzel 1996; Blake 1994; Fa & Yuste 2001; Hill et al. 2003; Noss et al. 2005; Puertas 1999; Siren 2004). The possibility of using CPUE for hunter self-monitoring has been investigated by Noss (2005) in the Bolivian Chaco, where non-declining trends in species-level CPUE over a number of years were used to infer the sustainability of hunting. CPUE is therefore frequently used in the bushmeat literature, to infer the abundance of prey species, the impacts of hunting, and in some cases to make assessments of the sustainability of harvest, without yet being properly validated.

The only study to date in the bushmeat literature that has attempted to test if CPUE is indeed an index of prey abundance, is that of Puertas (2005) in an evaluation of CPUE as a tool for community based management in the Peruvian Amazon. CPUE from hunting registers recorded over a number of years were compared with relative abundance data from line transect surveys. No difference in abundance or CPUE was found between seasons in either dataset and this was used as support for CPUE as an index of abundance. While this study represents a step forward in the use of CPUE in bushmeat research, it does not offer a validation of CPUE as an index of abundance. In this study the CPUE and abundance data were taken from different years, a time period over which both abundance and CPUE can change considerably. Furthermore, the absence of a seasonality effect is not evidence of a relationship between CPUE and abundance, since variation in both is essential to demonstrate a relationship. As such the validity of the current use of CPUE, and its future potential as an index of abundance with which to monitor bushmeat hunting remains to be tested.

Chapter 2
Predictors of abundance in species exposed to
bushmeat hunting

2. Predictors of abundance in species exposed to bushmeat hunting

2.1 Abstract

Understanding the impact of bushmeat hunting on wildlife populations is crucial to achieving sustainability, and requires knowledge of how prey abundance responds to different levels of hunting. Whilst the abundance of primates has been shown to respond independently to both hunting and habitat, habitat is rarely considered simultaneously when evaluating the impacts of hunting. Furthermore, the importance of these two factors in determining the abundance of other species has not been well investigated. I evaluate the independent effects of hunting and habitat in determining the abundance of a diverse assemblage of species, using a series of predictions and field data from a study in Equatorial Guinea. Line transect surveys were conducted in six sites of varying hunting intensity and habitat. Interviews with hunters were conducted weekly to quantify current hunting effort in each site. I also consider the role of past hunting, investigate the influence of distance from human settlement, and discuss the interrelationships that exist between hunting and habitat variables. I show that for primates, hunting is important in determining abundance, while for rodent species, duikers and elephants, habitat is more important. Distance from human settlement predicts abundance for a number of species, including primates, but is not correlated with current hunting effort. My findings show that the effects of hunting and habitat on abundance can vary greatly between species, and that these factors are often confounded, requiring an approach that isolates their independent effects in order to determine the true impact of hunting. Conservation managers need to consider and incorporate habitat heterogeneity when managing hunting systems, taking into account the way in which the relative importance of these factors can vary between species.

2.2 Introduction

Hunting to supply the bushmeat trade is currently one of the greatest threats facing mammal communities in Central and Western Africa, in many cases being more important than deforestation (Redford 1992). People have hunted wildlife in tropical forested regions for millennia, but current levels of harvest are thought to be occurring at well above sustainable rates (Bennett et al. 2002; Wilkie & Carpenter 1999), due to a complex suite of socioeconomic, demographic and technological changes (Milner-Gulland & Bennett 2003). Unsustainable levels of harvest are threatening not only the survival of tropical forest species, but also the food and livelihood security of many people living throughout the tropics (Pimentel et al. 1997; Robinson & Bennett 2004). There is therefore an increasing pressure to find effective solutions to the bushmeat trade that involve sustainable use (Bennett et al. 2007; Rowcliffe 2002).

The multi-species nature of bushmeat hunting makes it difficult to define sustainability (Rowcliffe et al. 2003). An understanding of species-level responses to exploitation, in addition to other threats, is required. Species vary in their vulnerability to threatening processes, such as habitat disturbance and hunting, depending upon their intrinsic biology and on the particular threat process involved (Isaac & Cowlishaw 2004). Large-bodied species with low rates of reproduction and long generation times, such as primates, are thought to be most vulnerable to hunting (Bodmer et al. 1997; Cowlishaw & Dunbar 2000). Conversely, species with shorter life cycles and reasonably high rates of reproduction, such as the rodents and some of the smaller antelopes, are thought to be relatively robust to hunting (Naughton-Treves et al. 2003; Wilkie & Carpenter 1999). However, even once differential patterns of species vulnerability have been accounted for there are still other complicating factors. The impact of historical hunting on contemporary patterns of abundance is likely to be important (Jerozolinski & Peres 2003), but is rarely considered. Habitat type can affect levels of productivity, and so influence the impact of hunting (Cowlishaw et al. 2005a; Wilkie 1989).

A species' abundance can differ greatly between habitat types and in response to habitat disturbance independent of hunting (Haugaasen & Peres 2005; Peres 1997a). Habitat disturbance in tropical forests can arise through several mechanisms, including agriculture and selective logging. Logging can alter forest structure, composition and food availability (Johns & Skorupa 1987; Plumptre & Reynolds 1994), and lead to increased hunting (Wilkie et al. 1992) that can all affect abundance. In the case of agricultural habitat disturbance, several species of rainforest mammal are known to be drawn to agricultural land to forage on crops, fruit trees and regenerating vegetation (Naughton-Treves et al. 2003), while others are adversely affected (Isaac & Cowlishaw 2004). Habitat disturbance may also be correlated with distance from human settlement, so

apparent abundance responses to distance may be due to species' habitat preferences rather than due to any effect of higher hunting pressure in close proximity to villages.

The influence on species abundance of hunting (Bodmer et al. 1997; Peres & Nascimento 2006), habitat disturbance through logging (Chapman et al. 2000; Johns & Skorupa 1987), and agriculture (Chapman & Lambert 2000; Wilkie & Finn 1990) have been investigated independently, particularly in primates, but they have rarely been considered together. Some studies have looked at the relative importance of hunting and habitat in determining the abundance of a single species or group, such as duikers (Lwanga 2006) or primates (Peres 1997a). Few studies have simultaneously investigated the independent effects of both hunting and habitat on the abundance of a diverse assemblage of species (but see Hill et al. (1997) for hunting and vegetation type, Laurance et al. (2006) for hunting, roads and a number of habitat variables, Naughton-Treves et al. (2003) for hunting and agricultural disturbance, Peres (2000) for hunting and forest type, and Peres (2001) for hunting and forest fragmentation).

In addition to the difficulty of separating hunting and habitat effects on the abundance of multiple species, there are also methodological complications. Many studies investigating the impact of hunting compare species abundance in hunted and un-hunted zones, and find the hunted areas to be depleted of wildlife. Similarly, comparisons have been made in an area over two time periods and declines in abundance attributed to hunting. However, these approaches are problematic in that they can only provide limited controls for the effects of other factors that influence abundance. Changes in local abundance may be caused by natural, asynchronous trends in population dynamics (Beddington & May 1977; Ims et al. 2004), and with the use of such designs, this natural temporal and spatial variation in abundance can potentially give the illusion of depletion where in fact none has occurred (Hill et al. 1997). The use of multiple study sites (rather than pair-wise comparisons) and of a quantified measure of hunting (rather than a qualitative presence or absence) can greatly aid in the separation of these effects, and so in determining the true impacts of hunting. However, no studies to date have been able to adopt such an approach.

This study builds on this past work by examining the independent effects of both current and past hunting, and a range of habitat variables, on the abundance of a diverse assemblage of mammal species, using multiple sites and a quantitative measure of hunting pressure. Specifically, I ask how abundance is influenced by the independent effects of hunting and habitat, interpreting differing species responses in relation to their biology, vulnerability to, and exposure to hunting. I discuss the interrelationships that exist between habitat and hunting variables, and the relevance of this study for the management of hunting in Equatorial Guinea and for the wider assessment of hunting impacts in tropical forested areas.

2.3 Methods

2.3.1 Study location

This study was carried out in the village of Midyobo Anvom in the Centro Sur Province of Rio Muni, mainland Equatorial Guinea (1°20'N, 10°10'E), from January 2005 until March 2006. The village of Midyobo Anvom is 180 kilometres by unpaved road from the mainland's capital Bata, and is one of the most remote communities in mainland Equatorial Guinea (Fig. 2.1). Its isolation provides both a large hunting catchment area in which to find variation in abundance, and also allows very accurate quantification of spatial and temporal patterns of hunting effort due to the absence of hunters from neighbouring villages. Midyobo Anvom has a population of approximately 150-200 people, who practice shifting agriculture and hunting, who have little to no access to alternative livelihoods or food sources. The construction of a logging road linking the community to Bata, and subsequent departure of the logging companies in 2003-2004, allowed a commercial trade in bushmeat to become established and Midyobo Anvom is now one of the main sources of bushmeat to Bata's markets. The region's vegetation consists of moist tropical lowland and upland forest and forms part of the Guineo-Congolian forest (Sayer 1992). The climate is characterised by two rainy seasons per year, the main rainy season between September and November and a smaller one between March and May, and an average annual rainfall of 2500 mm (Wilks & Issembe 2000). The surrounding forest was selectively logged in 2001-2002, for the hardwood Okoumé (*Aucoumea klaineana*).

Between 50 and 80 hunters operate at any one time, predominantly using cable traps, but the use of shotguns is becoming increasingly common. GPS positions of hunting camps and other landmarks, together with discussions with hunters indicate that they have access to an area of forest covering approximately 300km², mainly to the North, South and West of Midyobo Anvom. A number of hunting camps (temporary shelters constructed from forest materials) are located in the surrounding forest. About 60% of hunters operate out of these camps, returning to the village to sell their catch at the end of each week. The remaining hunters operate out of the village each day. Only a selection of camps are used by hunters at any one time. Abandoned camps fall into disrepair and are rebuilt on the hunters' return to the area, from eight months to a number of years later once prey numbers are thought to have sufficiently recovered.

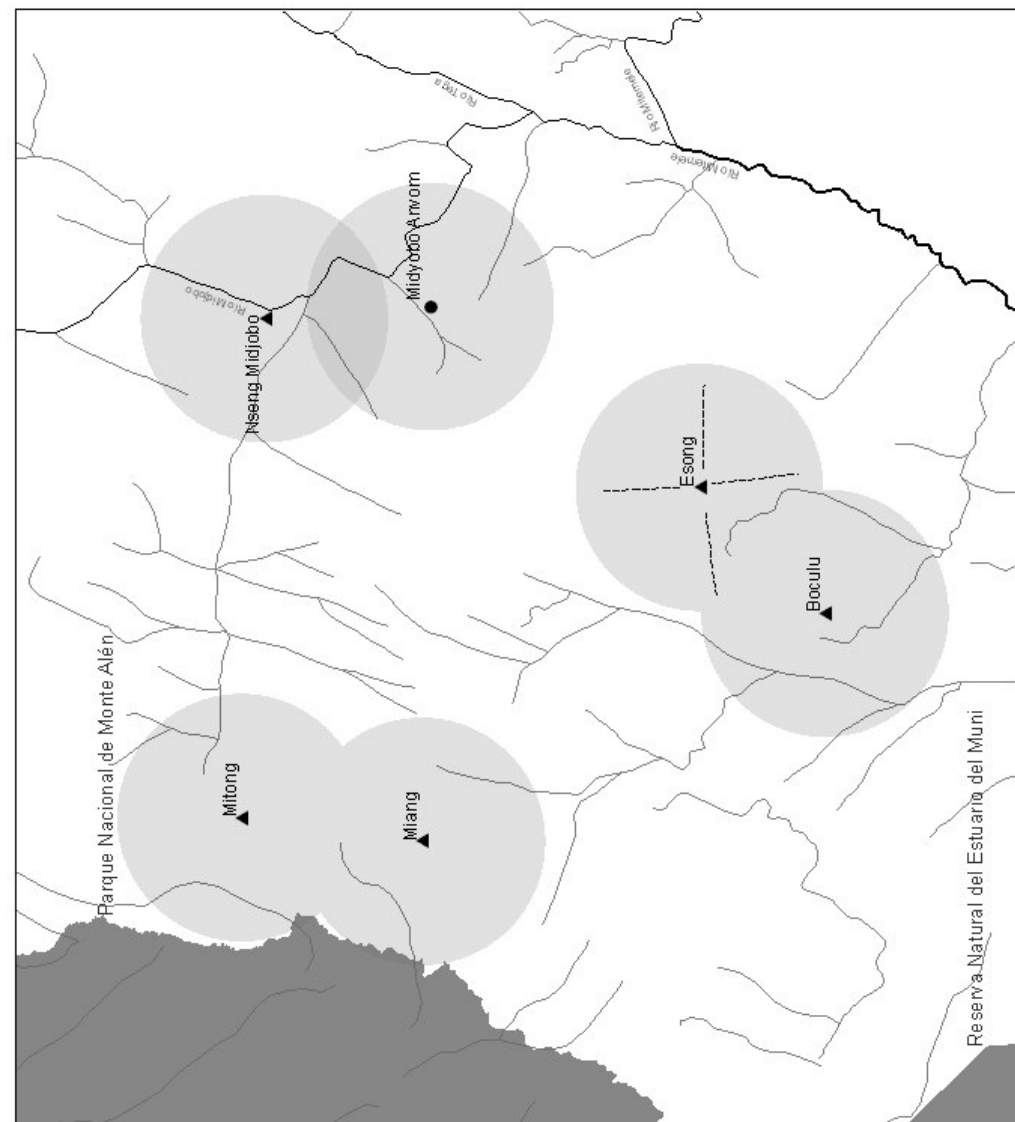
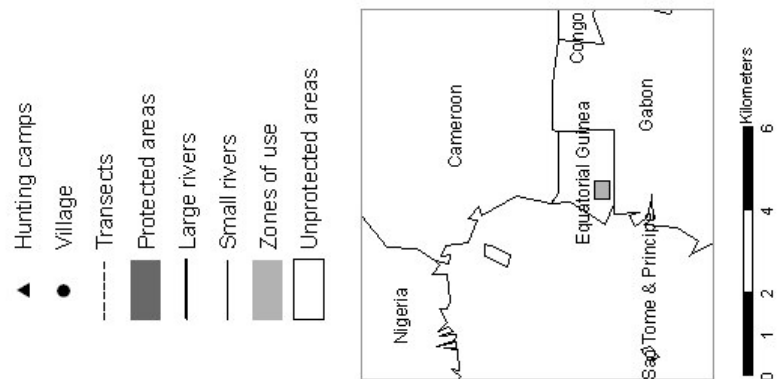


Figure 2. 1 Map of the study area and of its location within Equatorial Guinea and Central Africa. The community of Midyobo Anvorn, survey sites, zones of use and transect configuration are shown.



2.3.2 Line transect surveys

Line transect surveys were conducted to estimate the abundance of a diverse assemblage of mammal species in six sites located within the total hunting catchment area used by hunters of Midyobo Anvom (Table 2.1). These consisted of one site around the village, and five hunting camps differing in their distance from the village and in their level of current and past hunting. The zone of use around hunting camps was established from accompanying hunters on hunting trips. Hunters typically travelled 2-3km from the camp to place their traps, or with a gun in search of animals, using an area of approximately 12-30 km² around each camp. In each of the survey sites, four 2km line transects were established to estimate abundance for the zone of use around the hunting camp (Fig. 2.1). The six sites were surveyed in three pairs, each pair being surveyed for a period of 3-4 months during the year-long study period (Table 2.1). Survey periods for each pair of sites cut across a wet and dry season, and each pair was comprised of a site located near to, and a site located far from, the village. See Table 1 for a summary of survey site characteristics and survey effort.

Each transect was walked by a team of observers, comprising a research assistant skilled in mammal identification, and myself or a project volunteer skilled in survey methods, once per week during the survey period. The line transect methods used followed those of White and Edwards (2000) and Buckland et al. (2001). Observers used all visual, acoustic and olfactory cues to record encounters with animals, and searched for animal signs at ground level (e.g. duiker footprints, rodent diggings, elephant dung), eyelevel and above (e.g. ape nests). Duikers were surveyed nocturnally, which has been shown to result in higher encounter rates and therefore more accurate density estimates than with diurnal surveys (Payne 1992; Waltert et al. 2006). Nocturnal surveys were conducted using five D-cell Maglite torches to scan for eye-shine reflections, following the methods of Newing (1994).

2.3.3 Explanatory variables

The habitat description of transects followed the methods of White and Edwards (2000). A range of variables were recorded including: the number of rivers and logging roads crossing transects; percentage canopy and ground vegetation cover, canopy height, soil type, slope and altitude at 100 metre intervals along transects. All of the forest in the study area is selectively logged primary forest. I chose the two of these habitat measures for use in my analysis which I felt accurately described habitat variation and which provided the greatest multi-species relevance; the number of large rivers (defined as a width of five metres or greater) crossing each transect and the number of old logging

roads crossing each transect. These are used as measures of the amount of riverine habitat and the degree of logging disturbance, respectively. The third variable chosen was the degree of agricultural habitat disturbance, indexed by distance from the village. Although village distance has more traditionally been used as an indirect measure of hunting intensity (Hill et al. 1997), this was unnecessary in my study where a direct measure of hunting effort was available.

Many studies on the impacts of hunting use qualitative descriptions of hunting pressure (Laurance et al. 2006) or an indirect measure such as distance from human settlement (Hill et al. 1997). Here I use quantified values of actual hunting effort. All hunters in the community were interviewed about their activities at the end of each week, reporting all hunting effort and catch, interviews typically lasting 10 minutes. A detailed map of the village and the surrounding area was constructed using participatory mapping (Chambers 1994). The map was divided into zones, and used to aid hunters in the identification of hunting locations during interviews (see Appendix 8.1). Hunting effort for each mammal survey site was calculated as the average number of hours spent hunting per unit area per week ($\text{hours/km}^2/\text{week}$) across the zones around the site, for the time period in which the mammal surveys were conducted. Hunting effort was expressed as total hours spent hunting using all methods, and also for gun and trap hours separately so that effort could be matched correctly to each species. For hunts where both gun and traps were used, the total value for effort was assigned to both methods, assuming no reduction in efficiency when more than one method was used. An estimate of past hunting pressure (in the 12-18 months preceding the start of the study) at each site was also made using detailed discussion of historical hunting patterns with village hunters. Each site was assigned a value of none, low, medium or high for past overall, gun and trap hunting effort (Table 2.1).

Table 2.1 Characteristics of the six mammal survey sites, showing distance from the village, total survey effort, survey period, current hunting effort, and past hunting pressure (H=high, M=medium, L=low, N=none).

Survey site	Village distance (km)	Survey effort km (day/night)	Mean Rivers/ km	Mean logging roads/ km	Survey period	Current hunting effort (hours/km ² /week)			Past hunting history		
						All	Gun	Trap	All	Gun	Trap
Midyobo Anvom	0	98/29	0.00	2.38	Nov05- Feb06	78	10	73	H	H	H
Nseng Midyobo	4.1	160/20	0.41	0.41	Jul05-Oct05	23	3	22	H	H	H
Esong	7.8	73/17	0.25	2.75	Mar05- Jun05	121	30	106	M	M	M
Boculu	12.1	116/24	0.38	1.88	Jul05-Oct05	126	18	122	N	N	N
Miang	12.9	83/18	0.39	0.00	Mar05-Jun05	24	4	24	M	M	H
Mitong	13.2	81/25	0.26	0.65	Nov05-Feb06	29	5	27	L	L	L

2.3.4 Hunting offtake

Annual hunting offtake was calculated using the reported catch data from the interviews detailed above. This allowed me to see which species were being hunted, and to what extent, and hence aided in interpretation of abundance responses to predictor variables. Average body weights from the literature were used to calculate offtake biomass. Independent observations of hunting effort and catch were used to verify the accuracy of hunter reporting (see Appendix 2 for the information on the size and species composition of the estimated annual village hunting offtake).

2.3.5 Predictions

In order to investigate the importance of hunting and habitat in determining species abundance I first make a series of predictions for expected outcomes based on the findings of past studies in the literature (Table 2.2). Species are grouped into guilds based on their expected homogeneous responses to particular threat types. The complex nature of interactions between human hunting patterns, habitat characteristics and prey species abundance means that these predictions form a useful framework for interpretation of my model results.

Table 2.2 Predicted relationships between hunting, habitat and abundance, by species guild, with supporting references. The strengths and direction of predicted trends are indicated, zeros indicate that no relationship between abundance and the predictor is expected. SF = semifossorial, C = carnivores, SU = small ungulates, M/LU = medium/large ungulates, A = apes, M = monkeys

Abundance predictor	Species guild					Predicted relationships	Supporting references
	M	A	M/LU	SU	C	SF	
Past hunting	---	---	--	0	0	0	Jerozolimski & Peres (2003), Litvaitis et al. (2006)
	Longer lived species will be most affected by past hunting. Shorter lived species will be more resilient to hunting and more able to recover, so show little or no response. The more resilient the species, the lesser the effect past hunting will have on current abundance. Apes and monkey will be the most sensitive and show the strongest response, followed by other larger mammals like forest elephants and buffalo. Carnivores, semifossorial species and small ungulates will show no response to past hunting.						
Current hunting	---	---	--	-	-	-	Bodmer et al. (1997), Fa et al. (1995), Isaac & Cowlishaw (2004), Laurance et al. (2006), Peres (2001)
	Current hunting effort will reduce the abundance of all species. The strongest response is expected for the larger, longer-lived species. Apes and monkeys will be the most sensitive, and show the strongest response followed by other larger mammals like forest elephants and buffalo. Carnivores, semifossorial species and small ungulates will show little response to current hunting.						
Agricultural habitat disturbance	+/-	+/-	-	-	--	--	Cowlishaw & Dunbar (2000), Isaac & Cowlishaw (2004), Laurance et al. (2006), Naughton-Treves et al. (2003), Robinson & Bennett (2004), Siren (2004), Thomas (1991), Wilkie & Finn (1990),
	Independent of hunting, village distance can influence abundance mediated through its effects on the degree of agricultural habitat disturbance, which will be negatively correlated with distance. Agricultural areas act as a food source for certain species, while others are negatively affected by alteration of forest structure. Most carnivores, semifossorial species, small and some large ungulates may be attracted to agricultural areas and so show a negative relationship with village distance. Some apes and frugivorous primates (guenons) may be attracted to agricultural areas and so also show a negative relationship with distance, while folivorous primates (Colobus monkeys) may be sensitive to agricultural disturbance and show a positive relationship						
Riverine habitat	+	+	++	++	+	+	Gautier-Hion & Brugiere (2005), Peres (1997a), Kingdon (1997)
	Independent of hunting, all species will increase in abundance with increasing numbers of rivers, due to the high productivity of riverine habitat leading to increased food or prey availability. Of all the species guilds investigated, some of the small and larger ungulates will show the greatest response due to their known stronger habitat preferences for such areas.						
Selective Logging	+	+	+	+/-	+/-	+/-	Chapman et al. (2000), Davies et al. (2001), Hashimoto (1995), (Johns 1991), Laurance et al. (2006), Mathews & Matthews (2002), Ochoa & Soriano (2001), Plumptre & Reynolds (1994), Plumptre & Grieser Johns (2001), Kingdon (1997),
	Independent of hunting, selective logging may increase food availability for some species, while others will be negatively affected by alteration of forest structure. Folivorous species, such as some primates and larger ungulates, may increase in abundance in response to logging, due to increased food availability caused by the elevated leaf production during forest regeneration. Frugivorous species such as rodents and smaller ungulates may increase or decrease in response to logging. In some cases food availability has been shown to increase (elevated fruit production during regeneration) and in others decrease (if logging targets large fruit producing trees). The abundance of carnivores will follow the influence of logging on the abundance of their prey.						

2.3.6 Statistical analyses

I use abundance measured as encounter rate as my dependent variable. Small sample sizes precluded the estimation of separate detection functions and therefore robust density estimates at the transect level (Buckland et al. 2001). For some of the more common species, sighting numbers were sufficient to estimate detectability at the site level using Distance 5.0 (Thomas 2006). A comparison of global and stratified detection functions for these species showed that the Akaike information criterion (AIC) (Burnham & Anderson 1998), for the pooled detection function across sites was lower than that for the sum of the separate detection functions for each site. This indicates no significant difference in detectability between sites and thus supports the use of encounter rate as an index of abundance (Buckland et al. 2001).

To investigate the relationships between hunting and habitat abundance predictors, Pearson's product-moment correlations were used on mean values of predictor variables for each survey site. To test the significance of predictor variables on encounter rate, generalized linear mixed-effects models with Poisson error structure were used, with number of sightings per transect as the dependent variable, and total transect distance covered as an offset. Models were run within the R statistical package version 2.5.1 (R Core Development Team 2007), using the lmer function from the lme4 package (Bates & Sarkar 2007). Mixed effects model have recently become popular in ecological research because they allow both fixed (mean response to explanatory variables) and random (variation in response to explanatory variables) effects to be fitted in one analysis (Pinheiro et al. 2005). They are very useful in the analysis of spatially or temporally structured data, i.e. data with repeated measures (Crawley 2007). They were used here to take account of the spatial non-independence of transects within survey sites, by specifying site as a random effect (Crawley 2007).

Models were run for each species or species group, testing encounter rate per transect as a function of the following explanatory variables (fixed effects): current hunting effort (hours/km²/week), past hunting pressure (a two-level factor, where none or low past hunting was assigned to the first level, and medium or high was assigned to the second level), distance from village (km), logging disturbance (logging roads/km), and riverine habitat (rivers/km). Survey period was also included to control for any effects of seasonality. Both measures of hunting effort were made at the site scale, while those of habitat were at the transect scale. Only main effects and not interactions between explanatory variables were considered, due to sample size constraints. Model simplification was conducted using analysis of deviance with Chi-squared goodness of fit tests, deleting the least significant terms to obtain the minimum adequate model (Crawley 2007). Models were visually inspected using diagnostic plots for violation of model assumptions or excessive leverage.

In cases of low numbers of sightings for a species, encounters with sign were used. When sign was indistinguishable between species, they were combined into groups. All small and medium duikers were grouped into 'all duikers', while the group 'medium sized duikers' excluded the Blue duiker (*Philantomba monticola*) which is considerably smaller and often more abundant than the other species. The bushbuck (*Tragelaphus scriptus*) and sitatunga (*Tragelaphus spekeii*) were grouped into 'larger antelopes', and 'carnivores' grouped civets, mongooses and genets.

2.4 Results

2.4.1 Line transect surveys

Fifty-one mammal species were recorded in the surveys from both sign and sightings, including one critically endangered (*Gorilla gorilla*), two endangered (*Pan troglodytes*, *Potomogale velox*) and two vulnerable (*Mandrillus sphinx*, *Loxodonta africana*) species (IUCN 2007). Encounter rates varied greatly between sites for many species, other species were particularly rare or common across all sites. As expected, nocturnal surveys resulted in greater encounter rates for duikers (Table 2.3).

2.4.2 Hunting effort

Hunting effort, measured here as the average number of hours spent hunting per unit area per week (hours/km²/week), was highly variable between survey sites (Table 1). The site subject to the lowest hunting effort was the hunting camp nearest to the village, whereas the most intensely hunted site, Boculu, had a hunting effort five times greater. All sites were subject to both gun hunting and trapping. Trapping was the more frequently used method, with a mean effort across the six survey sites of 62 hours/km²/week spent trapping and 12 hours/km²/week for gun hunting effort.

2.4.3 Correlations between abundance predictors

An investigation of the strength of association between abundance predictors revealed two significant correlations. Firstly, a positive association between current gun hunting effort and the number of logging roads ($r=0.86$, $df=4$, $p=0.02$). And secondly, a negative association between past trap hunting and distance from the village ($r=-0.81$, $df=4$, $p<0.05$). Current hunting and past hunting were not found to be correlated ($r=-0.32$, $df=4$, $p=0.53$), when broken down by method, the coefficient for current and past gun hunting suggested a negative relationship but this was not significant at this sample size ($r=-0.58$, $df=4$, $p=0.23$). No association between current hunting and distance ($r=-0.18$, $df=4$,

$p=0.73$), or rivers ($r=-0.23$, $df=4$, $p=0.67$) was found, neither was a relationship between past hunting and rivers ($r=-0.41$, $df=4$, $p=0.41$) or logging ($r=-0.043$, $df=4$, $p=0.93$).

Table 2.3 Species encounter rate (encs/km survey effort) and number of encounters by survey site for each species abundance model analysis with the survey data type used in parentheses (D=day, N=nocturnal, L=live encounters, S=sign). Species proportional contribution to total annual offtake with carcass numbers in parentheses is also shown.

Species guild	Species or group (data type)	Survey site							% of total annual offtake (biomass)
		Midyobo Anvom	Nseng Midyobo	Esong	Boculu	Miang	Mitong	Tot.	
Primate	<i>C.cephus</i> (D,L)	0.09(9)	0.12(19)	0.18 (13)	0.17(20)	0.35(27)	0.18(15)	103	2.3(269)
	<i>C.nictitans</i> (D,L)	0.09(9)	0.11(18)	0.11(8)	0.14(16)	0.38(30)	0.30(25)	106	4.6(355)
	<i>C.pogonias</i> (D,L)	0.12(10)	0.15(25)	0.03(2)	0.10(11)	0.25(20)	0.14(11)	79	0.6(63)
	<i>C.satanus</i> (D,L)	0.04(4)	0.09(14)	0.11(8)	0.15(17)	0.21(17)	0.17(13)	73	12.0(546)
	<i>C.cephus</i> (D,L)	(0)	0.13(21)	0.10(7)	0.10(11)	0.14(11)	0.03(3)	53	-
	<i>C.nictitans</i> (D,S)	0.21(21)	0.43(68)	0.42(31)	0.30(35)	0.52(42)	0.32(26)	223	-
	<i>C.pogonias</i> (D,S)	0.14(14)	0.51(81)	0.15(11)	0.16(19)	0.30(24)	0.22(17)	166	-
	<i>C.satanus</i> (D,S)	0.02(2)	0.09(15)	0.19(14)	0.16(19)	0.22(18)	0.20(16)	84	-
	<i>M.sphinx</i> (D,L)	0.02(2)	0.01(1)	0.03(2)	0.02(2)	0.04(3)	0.05(4)	14	5.0(240)
	<i>M.sphinx</i> (D,S)	(0)	0.03(5)	0.03(2)	0.04(4)	0.10(8)	0.06(4)	23	-
	<i>P.troglodytes</i> (D,S)	0.06(6)	0.03(5)	0.15(11)	0.17(20)	0.12(10)	0.06(5)	57	2(23)
	<i>G.gorilla</i> (D,S)	0.01(1)	0.01(1)	(0)	(0)	0.03(2)	0.05(4)	8	(0)
Ungulate	All duikers (D,L)	(0)	0.02(4)	0.05(4)	0.02(2)	0.09(7)	0.06(5)	22	70.5(2841)
	Med.Duikers(D,L)	(0)	0.01(1)	(0)	(0)	0.05(4)	0.02(2)	7	42.9(371)
	<i>C.dorsalis</i> (D,L)	(0)	0.01(1)	(0)	(0)	0.05(4)	0.01(1)	6	14.6(362)
	<i>C.monticola</i> (D,L)	(0)	0.023	0.05(4)	0.02(2)	0.04(3)	0.04(3)	15	27.6(2470)
	All duikers (N,L)	0.23(7)	0.42(8)	0.38(9)	0.51(12)	0.35(6)	0.40(10)	42	-
	Med.Duikers(N,L)	0.10(3)	0.14(3)	0.04(1)	0.04(1)	0.13(2)	0.09(2)	12	-
	<i>C.dorsalis</i> (N,L)	(0)	0.14(3)	0.04(1)	0.04(1)	0.13(2)	0.04(1)	8	-
	<i>P.monticola</i> (N,L)	0.13(4)	0.28(5)	0.34(8)	0.46(11)	0.23(4)	0.31(8)	40	-
	All duikers (D,S)	0.53(52)	1.16(183)	0.71(53)	1.54(179)	0.31(24)	0.77(60)	551	-
	Med.Duikers(D,S)	0.31(31)	0.46(73)	0.38(28)	0.46(53)	0.07(5)	0.38(30)	220	-
	<i>P.monticola</i> (D,S)	0.22(21)	0.70(110)	0.34(25)	1.09(126)	0.24(19)	0.39(30)	331	-
	Lge.antelope(D,S)	0.04(4)	0.21(34)	0.01(1)	(0)	0.01(1)	(0)	40	0.6(7)
	<i>P.porcus</i> (D,S)	0.38(37)	0.10(17)	0.29(21)	0.15(17)	0.13(11)	0.01(1)	104	2.2(29)
	<i>S.caffer</i> (D,S)	(0)	0.01(1)	0.03(2)	0.14(16)	0.07(5)	0.09(8)	32	(0)
Semi-fossorial	<i>A.africanus</i> (D,S)	(0)	0.09(15)	0.10(7)	0.10(11)	0.05(4)	(0)	37	13.2(1741)
	<i>C.emini</i> (D,S)	(0)	0.15(23)	0.31(22)	0.10(11)	0.04(3)	0.11(9)	68	1.5(563)
	<i>C.emini</i> (N,L)	(0)	0.15(4)	0.20(3)	0.17(4)	0.24(5)	0.09(2)	18	-
	<i>P.tricuspis</i> (D,S)	0.39(39)	0.22(35)	0.08(6)	0.20(23)	0.23(18)	0.16(12)	133	3.2(710)
	All squirrels (D,L)	0.65(63)	0.50(76)	0.28(20)	0.36(41)	0.30(25)	0.34(28)	253	0.02(29)
Others	<i>S.gigantea</i> (D,S)	0.16(16)	0.19(32)	0.35(25)	0.59(69)	0.39(32)	0.49(39)	213	1.3(25)
	<i>L.africana</i> (D,S)	0.12(12)	0.27(43)	0.29(20)	0.30(35)	0.10(8)	0.34(26)	144	(1)
	Carnivores (D,S)	(0)	0.037(4)	0.04(3)	0.03(4)	(0)	0.04(3)	14	1.3(220)
	Carnivores (N,L)	0.03(1)	0.19(3)	0.09(2)	0.13(3)	0.190(4)	0.08(2)	15	-

2.4.4 Hunting, habitat and abundance

Of all explanatory variables, current hunting effort most strongly predicted overall mammal abundance, with higher effort predicting lower abundance (Table 2.4). Habitat also predicted abundance, with lower mammal abundance predicted by closer proximity to the village and with a greater number of rivers predicted lower overall abundance. No effect of survey period on abundance was found for any species. Primates as a group appear to show two main responses. Firstly, as predicted, increased abundance was associated with decreased current gun hunting effort. This was seen in two of the four monkey species: the crowned monkey (*Cercopithecus pogonias*), and the putty-nosed monkey *Cercopithecus nictitans*). Secondly, increased abundance was strongly associated with increased distance from the village, seen in three of the four monkey species: the black colobus (*Colobus satanus*), the moustached monkey (*Cercopithecus cephus*) and the putty-nosed monkey. Both trends together are seen in one species, the putty-nosed monkey. For the great apes, the chimpanzee (*P. troglodytes*) was most abundant further from the village, whereas the gorilla (*G. gorilla*) was more abundant where there was less current gun hunting. Unexpectedly, chimpanzees were also more abundant where current gun hunting effort and past gun hunting pressure were highest. No effect of either riverine habitat or logging disturbance was detected in either ape species.

Neither current nor past hunting was a significant predictor of reduced abundance for any of the three most commonly harvested semi-fossorial species, the brush-tailed porcupine (*Atherurus africanus*), the tree pangolin (*Phataginus tricuspis*) or the giant pouched rat (*Cricetomys emini*). Nevertheless, some effects of habitat were detected; rivers and logging roads increased brush-tailed porcupine abundance, while rivers increased giant pouched rat abundance. No significant habitat predictors were found for the tree pangolin. The giant pangolin (*Smutsia gigantea*) occurred at higher abundances closer to the village and where there were fewer logging roads. Squirrels (*Funisciurus spp.*), which unlike the other rodent species are not targeted by hunters, also showed no effect of hunting on abundance. Their response to village distance was as predicted on the basis of habitat preferences, with lower abundance found further from the village. The negative response of squirrels to rivers combined with the high number of squirrel encounters relative to other species is likely to be driving the overall negative response between mammal encounter rate and rivers, which is the opposite of that predicted.

When all duikers were considered together regardless of size, neither current nor past trapping predicted abundance. The only habitat variable found to be important was rivers, which were associated with higher abundance, as predicted. No significant

predictor of abundance was found for medium duikers. For the blue duiker, more rivers were also associated with higher abundance.

Table 2.4 Minimum adequate model results for species abundance analyses (those with at least one significant abundance predictor). For clarity of interpretation the significance and direction of trends are indicated by symbols (1 symbol = $p < 0.05$, 2 symbols = $p < 0.01$, 3 symbols = $p < 0.005$), 'zero' indicates that no significant effect of that predictor was detected. The survey data type and hunting effort measures used for analysis are shown (D = day, N = nocturnal, L = live encounters, S = sign).

Species guild	Species or species group	Hunting effort type	Abundance predictor				
			Current hunting	Past hunting	Village distance	Rivers	Logging
All	All species (D,L)	All	---	0	+	-	0
Primate	Black colobus (D,L)	Gun	0	0	+++	0	0
	Moustached monkey(D,L)	Gun	0	+	++	0	0
	Putty-nosed monkey(D,L)	Gun	--	0	+++	0	0
	Crowned monkey (D,L)	Gun	--	0	0	0	0
	Gorilla (D,S)	All	--	0	0	0	0
	Chimpanzee (D,S)	All	++	+	+++	0	0
Semi-fossorial	Brush-tailed porcupine(D,S)	Trap	0	0	0	++	++
	Giant Pouched rat (D,S)	Trap	0	0	0	+	0
	Squirrels (D,L)	Trap	0	0	--	-	0
Ungulate	Forest buffalo (D,S)	All	0	-	+	0	0
	All duiker species (N,L)	Trap	0	0	0	+	0
	Blue duiker (N,L)	Trap	0	0	0	+	0
	Red river hog	All	+++	+++	0	++	0
Other	Elephant	All	-	--	-	++	+++
	Giant pangolin	All	+	0	++	0	-

The model for the large ungulates (*T. scriptus* and *T. spekeii*) failed to converge, due to almost all of the 40 encounters being found in one site, Esong, with no encounters in two sites (Boculu and Mitong).

Elephants (*L. africana*) were less abundant where both past and current hunting efforts were high. However, elephant abundance was also strongly associated with habitat, occurring in greater numbers in those areas that were closer to the village and had more rivers and logging roads. Lower past but not current hunting was associated with higher abundance of forest buffalos (*Syncerus caffer*), together with increased distance from the village. For the red river hog (*Potamochoerus porcus*), both greater past and current hunting were associated with increased abundance, the opposite of my

predicted relationships. Neither hunting nor habitat was associated with carnivore abundance, measured by either sightings or sign.

2.5 Discussion

This study provides an analysis of the independent effects of hunting and habitat on the abundance of a wide range of species exposed to bushmeat hunting. I have shown that a combination of current hunting effort and habitat effects determine the abundance of mammal species overall, but that the importance of hunting and habitat variables varies between species and species groups. These findings are consistent with those of previous studies which have demonstrated differential susceptibility to hunting among prey species (Bodmer et al. 1994; Cowlshaw et al. 2005a) and differing species responses to hunting and habitat (Laurance et al. 2006). However, many habitat variables (human settlement, logging and rivers) are confounded with hunting and the relative importance of their hunting and habitat-mediated effects may vary between species.

My study design has allowed me to isolate the true influence of these factors, future studies may also benefit from using such an approach, so that differences in abundance due to habitat factors are not wrongly attributed to hunting. While hunting may be important in determining the abundance of primates, other large-bodied species, such as elephants, forest buffalo and the great apes have been shown not to be routinely targeted by hunters in this study site, so any negative responses to hunting are more likely to be due to an avoidance of humans in hunted areas rather than actual hunting impacts (see also Barnes et al. 1991). For taxa such as the rodents and duikers, habitat seems to be the most important determinant of abundance. This might indicate that these species are either not affected by the current levels of hunting, or that the increased habitat suitability of riverine or logged areas obscures any negative effects of hunting that they might experience. Habitat also appears to be important for elephants, with increased abundance predicted by both increased riverine habitat and most strongly by the presence of logging roads, consistent with previous studies (Barnes et al. 1991; Struhsaker et al. 1996).

For other species or species groups the effects of hunting and habitat on abundance are less clear. Mandrills (*M. sphinx*), despite being quite heavily hunted, showed no patterns in abundance, perhaps because their wide ranging behaviour makes it difficult to attribute an observed abundance at any one locality to measures of hunting or habitat. Other species such as the red-river hog, chimpanzee and giant pangolin showed responses to hunting which are the opposite of those which might at first be expected based on predictions from the literature. One possibility is that, despite being hunted, the numbers actually taken are relatively low (Table 2.3), so they may be able to benefit from a combination of density-dependent population growth and inter-specific competitive

release, increasing in abundance in heavily hunted areas due to the reduced abundance of frugivorous competitors such as monkeys, that are more intensively targeted by hunters.

2.5.1 Logging, hunting and abundance

The influence of logging roads in leading to increased levels of hunting has been frequently demonstrated (Laurance et al. 2006; Wilkie et al. 1992) and I have found this to also be the case in my study. Current gun hunting effort is associated with the number of logging roads. However, when controlling for this elevated hunting effort, logging roads are not themselves found to be associated with reduced abundance for any species. In this study, the independent effects of hunting and logging have been separated so any effect of this variable in my models is related to the effects of logging on habitat. In some species such as the brush-tailed porcupine and elephant, more logging roads predict higher levels of abundance. The effects of logging on abundance mediated through changes in forest structure and food availability have also been shown in other studies (Chapman & Chapman 1997; Davies et al. 2001; Struhsaker et al. 1996).

2.5.2 Past hunting

Although historical hunting is rarely considered in studies of hunting impacts, it is thought that current abundance can be affected by past levels of hunting, particularly in larger bodied species (Jerozolinski & Peres 2003). Whereas, the abundance of those species most resilient to hunting might be expected to recover relatively quickly, making past hunting less important. Current and past hunting appeared to be negatively correlated, but this was not significant, possibly due to small sample size. The presence of an effect of past hunting but not current hunting effort might suggest that a species used to be targeted, but is not currently, and is slow to recover. This could be the case for the forest buffalo; however this seems unlikely given the recent onset of commercial hunting. Based on my predictions, I might have expected the arboreal primates to show a response to past hunting, yet this was not the case. This may be because my measure of past hunting, over the 12-18 months previous to my study, was not a sufficiently long time period with which to detect an effect in these species, or alternatively because the intensity of current hunting is such that it obscures any effect of past hunting.

2.5.3 Village distance

In this study I used village distance as an index of agricultural habitat disturbance. The increased abundance of squirrels and elephants closer to the village is likely to be due to

a habitat preference for agriculturally disturbed areas and a tendency to raid crops. In contrast, some primates (*Colobus satanus*, *Cercopithecus nictitans* and *Cercopithecus pogonias*) increased in abundance with increased distance which might reflect a negative response to agricultural habitat disturbance or an avoidance of areas of human activity by these species.

A key determinant of spatial variation in hunting intensity is accessibility. Hunting is limited by travel costs and so hunting intensity is often greatest along roadsides and closest to settlements (Cowlshaw & Dunbar 2000). The abundance of large-bodied species in particular has been shown to increase with distance from the nearest point of access to the forest, such as rivers or roads (Blom et al. 2005; Muchaal & Ngandjui 1999; Wilkie & Finn 1990). Distance from human settlement has therefore been used as an indirect measure of hunting pressure (Hill et al. 1997; Peres & Laake 2003; Siren 2004).

However, the presence of temporary hunter camps, rivers and logging roads may all affect the travel costs of hunting and so influence the spatial distribution of hunting effort. In this study distance from the village was not correlated with current hunting effort, due to the use of a camp rotation system. Thus hunting effort did not simply show a continuous decline with distance from the village, but was rather distributed in a series of hotspots. Furthermore these hotspots moved in space and time as hunters responded to changes in their hunting success. Given the association between high levels of abundance and distance from the village but not current hunting effort, distance from the village may more accurately reflect the cumulative impact of hunting over a multi-year period rather than the current level of hunting effort, indeed past trapping effort was found to be negatively correlated with distance. Such a cumulative hunting effect might explain the strong abundance responses shown by some primates to village distance, but not to current hunting.

2.5.4 Conclusion

I have shown that mammal abundance can be determined by a combination of both hunting and habitat, but that many habitat variables, such as distance from human settlement, logging and rivers, can be confounded with hunting, and the relative importance of their hunting and habitat-mediated effects may vary between species. This necessitates an approach that isolates their independent effects, so that differences in abundance due to habitat factors are not wrongly attributed to hunting. Conservation managers need to consider and incorporate habitat heterogeneity when managing hunting systems, and ideally take into account the way in which the relative importance of these factors can vary between species. The use of core hunting zones and no take areas has been suggested for improving the sustainability of hunting in tropical forests,

but habitat heterogeneity as well as hunter access should be taken into account when undertaking spatial zonation for management.

Chapter 3

**How should hunting effort be measured to reflect
its biological impact on prey species?**

3. How should hunting effort be measured to reflect its biological impact on prey species?

3.1 Abstract

The negative impacts of bushmeat hunting on prey species have been frequently demonstrated, but to date, little thought has been given to how hunting should most appropriately be measured. Current methods range from qualitative descriptions such as the presence or absence of hunting, to quantified measures of the time spent hunting, numbers of hunters operating, units of equipment used, or distances traveled. In many cases these are used as measures of the biological impact of hunting, when they are in fact economic measures of the effort invested by a hunter. The choice of effort measure used has important implications not only for correctly attributing observed levels of prey abundance to a particular level of hunting, but also for the use of hunting statistics such as Catch per Unit Effort, as indices of abundance. I use information from hunter follows and hunting camp diaries taken from a 15 month study in Equatorial Guinea, to investigate how hunting effort can be most appropriately measured in order to reflect its biological impacts, exploring the possible sources of bias that can exist with the use of different measures. I show that the use of time measures can lead to increasing overestimations of effort with the distance travelled to the hunting location, and that the quantification of trapping effort is particularly problematic due to variable rates of trap-checking, and variable trap group composition. This is the first study to investigate and explicitly quantify the sources of bias that exist between economic and biological measures of hunting effort, and provides a context in which to compare the ability of these effort measures to explain variation catch. If we hope to quantify hunting impacts, then quantitative measures of effort that account for these biases, and that explain variation in catch are required. My results have important implications for how future studies should measure hunting effort in order to properly assess the biological impact of bushmeat hunting; further comparative studies to investigate the existence of bias in effort measures in different hunting systems would be beneficial.

3.2 Introduction

Many studies continue to demonstrate the negative impact of bushmeat hunting on prey species abundance (Corlett 2007; Laurance et al. 2006; Naranjo & Bodmer 2007; Peres & Nascimento 2006), but few give consideration to the most appropriate way to measure hunting. Indeed, the terms 'hunting pressure' and 'hunting intensity' are frequently used without a clear definition being given, and are assumed to represent measures of the direct effect of hunting on prey species mortality, when in actual fact they are often measures of the effort invested by a hunter. Such economic effort measures may or may not reflect the true biological impact of hunting. Hunting mortality refers to the probability of an animal being captured (Bousquet et al. 2001; Rowcliffe et al. 2003), whereas hunting effort is an economic measure of the time or other resources invested by a hunter that can therefore not be used in other activities (Cuthill & Houston 1997).

Table 3.1 details a brief review of recent hunting studies which illustrates the diversity of effort measures currently being used, showing that the choice to date has been highly variable and somewhat arbitrary (Bodmer & Robinson 2005). Perhaps justifiably studies tend to concentrate on what is easiest to measure rather than what is ideal in terms of identifying a measure of effort that is correlated with prey mortality. Deciding on the appropriate measure of hunting is crucial when inferring hunting impacts on prey abundance, and especially so when using hunting statistics such as Catch per Unit Effort (CPUE) to infer species abundance. Measuring harvesting effort is not a new problem (Bordalo-Machado 2006), the CPUE concept forms the core of fisheries stock assessments, and considerable energy has therefore been applied by fisheries researchers to develop reliable measures of effort (Beverton & Holt 1957).

Many studies use qualitative descriptions of hunting to compare abundance between areas (Naranjo et al. 2005). Some use hunting offtake to infer the level of hunting effort (Bodmer et al. 1997), however offtake is a product of hunting effort and the abundance of prey. In the case of hunters in tropical forests, hunter effort may be quantified in units of time such as hours (Franzen 2006), days (Peres & Nascimento 2006), or months (Noss et al. 2005). Hunter effort can also be measured in a number of ways other than time, such as the number of hunters operating in an area (Naughton-Treves et al. 2003), in units of hunting equipment such as the number of traps set (Nielsen 2006) or nets used (Noss 1998a), or measured as the distance from human settlement (Rao et al. 2005), to the nearest point of access (Hill et al. 1997) or that travelled by a hunter during the hunt itself (Siren 2004), or even as an index based on the frequency of encounters with hunter sign (Cullen et al. 2001) (Table 3.1).

Table 3.1 Summary of recent hunting studies to illustrate the diversity of hunting measures used. The location, broad type and specific details of the hunting measure, together with whether the measure was used to calculate Catch per Unit Effort are given for each study.

Reference	Study Location	Data source	Broad type	Specific hunting measure	CPUE calculated
Blake (1994)	Congo	Unknown	Time	Hunter hours	kg/hour
Bodmer (2005)	Peru	Hunting registers	Time	Hunter days	animals/time
Franzen (2006)	Ecuador	Interviews	Time	Hunt duration	kg/hour
Noss (2005)	Bolivia	Activity records	Time	Hunter months	animals/100 hunter months
Peres (2006)	Brazil	Interviews	Time	Hunter Days	animals/day
Puertas (2005)	Peru	Hunting registers	Time	Hunter days	animals/day
Fa (2001)	Equatorial Guinea	Interviews	Time	Hunter days, number traps, trap nights	animals/day
Hill (1997)	Paraguay	Mapping	Distance	Distance from nearest point of access	-
Rao (2005)	Myanmar	Interviews	Distance	Proximity to settlement and large trading towns	kg/hunting trip
Peres (2003)	Brazil	Mapping	Distance	Distance from nearest point of access	-
Siren (2004)	Ecuador	Interviews and map	Distance	Distance walked/km ² /year	animals/km walked/km ² /year
Cullen (2001)	Brazil	Surveys	Hunting sign	Gunshots, hunting platforms, hunters, hunting dogs	-
Hill (2003)	Paraguay	Surveys	Hunting sign	Hunter sign	-
Wilkie (1992)	Congo	Surveys	Hunting sign	Spent shotgun shells	-
Muchaal (1999)	Cameroon	Surveys	Equipment	Trap density	-
Nielsen (2006)	Tanzania	Interviews	Equipment	Number of traps and trap nights	animals/trap night
Noss (1998b)	CAR	Hunter follows	Equipment	Trap nights	captures/trap night
Noss (1998a)	DRC	Hunter follows	No. hunters	Number of hunters and net casts	encounters/person net cast
Naughton-Treves (2003)	Peru	Interviews	No. hunters	Number of hunters in community	-
Fa (2005)	C/W Africa	Literature	No. hunters	Number of hunters active/100 days	-
Jerozolinski (2003)	Neotropics	Literature	Site characters	Settlement age and size	-
Bodmer (1997)	Peru	Literature	Qualitative	Persistent/infrequent based on animals harvested/km ² /year	-
de Thoisy (2005)	French Guiana	Interviews	Qualitative	None/light/heavy based on days and distance covered	-
Laurance (2006)	Gabon	Surveys	Qualitative	Hunted/un-hunted based on hunting sign encounters	-
Peres (2001)	Brazil	Interviews	Qualitative	Light/moderate/heavy based on frequency/intensity harvest	-
Naranjo (2005), (2007)	Mexico	Surveys	Qualitative	Light or persistent based on hunting signs/100km ⁻¹	-

The most frequently used quantitative measure of hunter effort is that of time spent hunting (Table 3.1), but deciding on how best to measure time spent hunting so that it accurately reflects prey mortality may not be that simple. The daily activities of hunters may not always be constant, so using a rough time measure such as the number of days spent hunting makes assumptions about the average activity of hunters during hunting trips (Bodmer & Robinson 2005). When using time measures, it can be useful to think of the total time that a hunter invests in hunting as consisting of components (Hilborn 1992), with time allocated between travelling, resting and hunting (Stephens & Krebs 1986). According to the assumptions of foraging theory, hunters are expected to maximize their short-term harvesting rate, i.e. the rate at which resources are harvested per unit time (Alvard 1993; Stephens & Krebs 1986). So from an economic perspective, the total time spent out of the village is important as this time cannot be allocated simultaneously to alternative activities (Cuthill & Houston 1997). However, from a biological perspective, the travelling and resting components of hunter time are irrelevant, only the hours for which a hunter is actively hunting, and during which an animal is exposed to a risk of capture are important. Time spent on other activities should therefore not be included in biological measures of effort (Cooke & Beddington 1984). If the proportion of total time spent actively hunting is constant, then total time may also reflect prey mortality, however if this proportion is affected by other factors, total time spent hunting will reflect only an economic measure of hunter effort and not a biologically relevant measure.

Furthermore, another component within time budgets that needs to be considered, is that of handling time (Hilborn 1992), which is defined as the time required to pursue, capture and then consume a prey item (Stephens & Krebs 1986). In this case handling time is the time from encounter to capture, before the hunter is free to recommence search for the next prey item (Cuthill & Houston 1997). Searching and handling are frequently assumed to be mutually exclusive activities and that the expected number of encounters is a linear function of the time spent searching (Holling 1959). The greater the time spent handling each prey item, the smaller the proportion of total time available for active search for the next prey animal. In order for CPUE to be proportional to abundance there can be no significant proportion of the exploiter's time budgets allocated to handling time (Hilborn 1992).

If a significant component of total time is spent handling, then the use of total time to calculate CPUE for abundance estimation can be particularly problematic. At times or in areas of higher abundance, and hence catch, more time will be spent handling, so hunter effort will effectively under sample at high abundance, effort will be overestimated and CPUE will not reflect abundance in areas of high prey density (Hilborn 1992). For these reasons, 'time searched' might be more appropriate to use than a cruder measure

of effort such as total time (Hilborn 1992). If the proportion of time spent handling is large, but varies in a predictable way then measures of hunter effort can be adjusted in order to more closely equate to the effects on prey mortality.

With trap hunting one might expect the proportion of time spent handling to be correlated with catch, since each animal caught requires a separate and similar handling time to remove it from, and reset the trap. However, with gun hunting, handling time may not be so strongly correlated with catch, because an encounter can lead to an unsuccessful pursuit, a single, or even multiple capture (Rowcliffe et al. 2003). In the case of trapping, handling time may only become important if trap groups become saturated so that the probability of an animal being captured is affected by a previously caught animal blocking a trap (Charnov 1976). This has been a problem for some long-line (Cooke & Beddington 1984), and trap fisheries (Groeneveld et al. 2003), however, it is likely in hunting systems that capture rates are so low that any trap saturation effects can be ignored (Rowcliffe et al. 2003). Even so, the relationship between time spent hunting and the probability of mortality experienced by the prey may not be clear cut. What might be more important in determining the probability of mortality is the number of traps that a hunter sets in an area, rather than the time it takes him to check them. On the other hand, if the time spent is correlated with the number of traps, either may be an adequate measure.

Quantifying trapping effort so that it reflects prey mortality is further complicated by the fact that different trap types may be used to target different species. In fisheries, gear selectivity is widely acknowledged to be a problem for effort estimation (Hampton et al. 2005), with nets being selective for body size according to their mesh size, and similarly hook and line fishing in respect to fish mouth and hook size. Fishing gear may also be selective in relation to species' habits and movement patterns (Hilborn 1992). The assumption of constant catchability across species has therefore been well studied in fisheries (Gulland 1983; Quinn 1999). For hunters in tropical forested areas, traps are thought to be indiscriminate, selective only by body size, and not by species, age or sex (Noss 1998b). If trap groups contain equal proportions of all trap types then effort quantified as total trap numbers will accurately reflect the effect on prey mortality of each trap type. However, if trap group composition is variable and biased toward certain types of traps, then total trap numbers will not accurately reflect the less commonly used trap types, and hence the probability of capture for prey targeted by such trap types. Trapping effort might therefore need to be measured in terms of those traps that actually target the species of interest rather than the total number of traps.

Problems may also exist with correctly quantifying catch; a hunter may respond to a different measure of catch than that which is biologically meaningful for the prey. Economic incentives determine the effort devoted to hunting (Damanian et al. 2005), and hunter decisions about levels of effort to invest will be dynamic and based on their

hunting returns (Ling & Milner-Gulland 2006). Returns may be measured in terms of either biomass harvested per unit effort, if they are hunting for subsistence, or alternatively in monetary return per unit effort if engaging in commercial hunting. Animals that have escaped but have been fatally injured, those that are unable to be recovered, or that are discarded from traps because they are rotten may not be included in these calculations, and can represent significant numbers (Noss 1998b; Wilkie & Carpenter 1999). In fisheries, catch is made up of what is landed and what is discarded, and accurate discard information is similarly difficult to obtain (Quinn 1999). From the perspective of prey mortality it is the total number of individuals killed which is important, therefore when quantifying catch for biological monitoring purposes, a biologically relevant measure, including these sources of 'wastage' is required, whereas management may require the use of measures that are economically relevant for hunters (Crookes & Milner-Gulland 2006).

In order to determine whether economic or effort based measures of hunting correlate well to the biological impacts or mortality of hunting, I use a series of testable hypotheses to answer the following three broad questions: (1) Is measuring total time spent out of the village sufficient, or is more detailed information needed on the time spent actively hunting? (2) Would an effort measure based on time be appropriate to quantify trapping effort, or is information on trap numbers, or even trap group composition required? (3) Should catch be measured from the hunter or prey perspective and what is the magnitude of the difference between these two measures?

3.3 Methods

3.3.1 Study location

This study was carried out in the village of Midyobo Anvom in the Centro Sur Province of Rio Muni, mainland Equatorial Guinea (1°20N, 10°10E), from January 2005 until March 2006. The village of Midyobo Anvom is 180 kilometres by unpaved road from the mainland's capital Bata, and is one of the most remote communities in mainland Equatorial Guinea (Fig. 3.1). Midyobo Anvom has a population of approximately 150-200 people, who practice shifting agriculture and hunting, who have little to no access to alternative livelihoods or food sources. For further details on habitat, climate and the development of bushmeat hunting in this area see section 2.3.1.

3.3.2 Hunting system

Between 50 and 80 hunters operate at any one time in the community, predominantly using cable traps, but the use of shotguns is becoming increasingly common. There are a number of different trap types used by hunters; the majority being small and large leg traps, which differ both in the number of strands of cable used for construction of the noose and the size of the bent-over sapling or pole used in the trigger mechanism. Neck traps are also used and are either placed on the ground, or above the ground on fallen trees, using a small frame to hold the open noose vertical above the ground. The cable used to make traps was originally that left behind by logging companies, but is now brought into the village by bushmeat traders from Bata. Traditional trap types, such as pits, have been abandoned in favour of using these more efficient traps.

The hunters of Midyobo Anvom use a camp rotational system (Fig. 3.1). A number of hunting camps are located in the surrounding forest. About 60% of hunters operate out of these camps, returning to the village to sell their catch when traders from Bata visit at the end of each week. Only a few camps are used by hunters at any one time. Camps are used until prey becomes sufficiently depleted that hunters decide to move to a new location. Abandoned camps fall into disrepair and are rebuilt on the hunters' return to the area, from as little as eight months to a number of years later once prey numbers are thought to have sufficiently recovered. The remaining hunters operate out of the village each day. This combination of central place foraging (Orians & Pearson 1979) with a patch model (Stephens & Krebs 1986), is in contrast to other sites where hunters only operate out the village (Peres & Nascimento 2006). The larger area of forest available for hunters' exclusive use, and the low human population density in this area might have resulted in the adoption of this system. In addition as prey depletion occurs

close to the village a switch might be expected from central place foraging to the use of a patch model.

3.3.3 Hunter follows

Hunter follows were conducted to obtain the most detailed possible data on true hunting catch and effort, and have been previously used for investigating hunting activity (Muchaal & Ngandjui 1999; Zeleznik & Bennett 1991). A Handspring Visor PDA was used, with Magellan GPS attachment and a customized data collection programme written in CyberTracker (Steventon 2002). Follows were conducted by myself or a local research assistant. A total of 225 hunter follows were conducted, with 55 out of the 80 hunters operating during the study period, averaging 4 ± 0.4 (1SE) follows per hunter. Follows lasted for an average of 5.85 ± 0.17 hours, totalling over 1315 data collection hours during the study.

The following data was recorded either directly or as an outcome of the spatio-temporal referencing of the CyberTracker programme: hunting trip duration, the start and end of the trap groups (for 158 follows), trap totals and composition (for 167 follows), all animals encounters, the number of animals injured, killed, collected and left behind and the handling time for each animal. Scheduling was random where possible and opportunistic when necessary. Of the 225 follows, 95 follows were conducted out of hunting camps, and 130 out of the village. 143 follows were conducted with trappers, 56 with gun hunters and 26 with hunters using a gun and traps. During follows, 501 animals were caught, 307 by traps, 157 by gun and 37 by hand.

Hunter follows have been previously used for investigating hunting activity (Muchaal & Ngandjui 1999; Zeleznik & Bennett 1991), however some might have concerns that this method of data collection could interfere with hunter behaviour, such as the possible influence of observers on the duration of hunts or on the encounter rates of prey species. I am confident that in this study this is not the case, no difference in hunt duration was found between observers (myself and ex-hunter research assistants), and although the inconvenience of answering our questions was acknowledged by way of small payments to hunters (1000 CFA, less than £1), this would have been insufficient compensation should our presence have led to reduced encounter rates and hence catch for hunters.

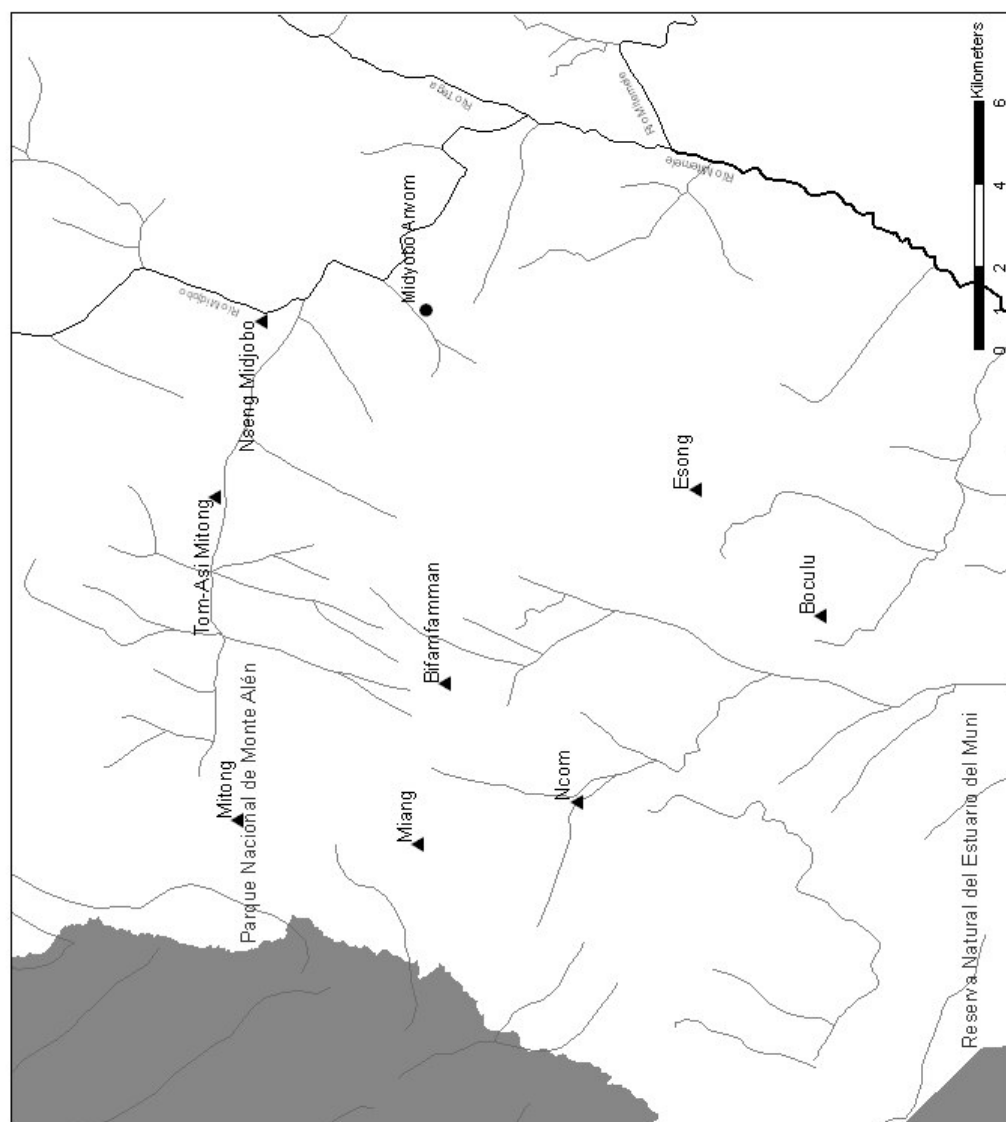
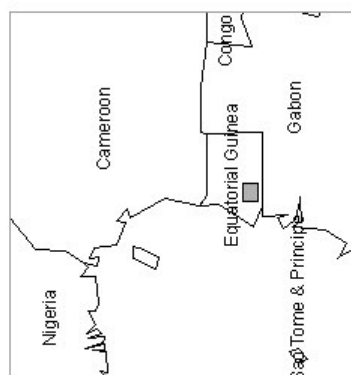


Figure 3.1 Map of the study area and of its location within Equatorial Guinea and Central Africa. The community of Midyobo Anwom and the hunting camps for which diaries were collected are shown.

- Village
- Protected areas
- Large rivers
- Small rivers
- Unprotected areas
- ▲ Hunting camps



3.3.4 Hunting camp diaries

Camp diaries were kept by a hunter in eight of the hunting camps in use during the study period (Fig. 3.1), providing detailed information on all hunting activity that occurred in the camp each week. Data were collected for an average of 20 weeks per camp. In total, information on 822 camp stays were recorded, and for 1960 individual hunts within those camp stays. A total of 3030 animals were recorded as being caught; of these, 303 were by gun, 53 by hand, 12 by lasso, 2658 by trap and four by an unknown method. The hunters responsible for the diaries registered the arrival and departure dates, and times, for each camp stay of all hunters operating from the camp. In addition for all hunts conducted during each camp stay, the date of the hunt, time of departure and return, the hunting method used, and details of the hunters' catch were recorded (Table 3.2).

Table 3.2 Camp locations and diary information

Hunting camp	No. weeks data	Travel time from village (hours)	Distance from village (km)	No. camp stays	No. hunts	No. hunters
Nseng Midyobo	22	1.25	4.00	77	149	5
Tom Asi Mitong	27	2.50	6.91	113	230	4
Esong	26	2.25	7.85	338	562	15
Bifamfamman	13	3.00	9.08	26	75	2
Boculu	26	3.50	12.10	90	339	9
Ncom	47	4.00	12.52	124	431	4
Miang	14	4.00	12.96	38	135	8
Mitong	6	5.50	13.28	16	39	4

3.3.5 Hypotheses and statistical analyses

To determine whether economic or effort based measures of hunting correlate well with the biological impacts or mortality of hunting I have devised a series of testable hypotheses (Table 3.3). In the case that these hypotheses are not supported by my data, I shall conclude that economic and biological measures are not equal, and will try to determine the influencing factors, scale and direction of bias so that it may later be corrected for. These hypotheses will form the structure for my analyses and for the remainder of this Chapter.

Table 3.3 Hypotheses to determine whether economic or effort based measures of hunting correlate well with the biological impacts or mortality of hunting. The economic and biological measures, and data used to test each hypothesis are given

Hypothesis	Economic/Effort measure	Biological/Mortality measure	Data to test
1. Time spent hunting is a constant proportion of total time spent out of the village on a hunting trip ¹	Time spent out of the village	Time spent actively hunting	Camp diaries - compare % of time out of the village with that which is spent hunting, across camps
2. The duration of individual hunts is constant across locations ²	Days spent hunting	Time spent hunting	Camp diaries - compare mean hunt duration across camps. Follows - compare mean hunt duration of village and camp follows
3. Handling time does not represent a large % of hunting time, or is proportional to catch ²	Time spent actively hunting	Time spent actively hunting minus handling	Follows - determine % of active hunting time is spent handling
4. The % of time on a hunt spent checking traps is constant ²	Time spent actively hunting	Time spent checking traps	Follows - compare mean % hunting time spent checking traps of village and camp follows
5. Trap group size is constant across locations	Number of hunting trap groups	Total number of traps	Follows – compare mean trap group size of village and camp follows
6. Trap group size determines time spent hunting	Time spent actively hunting	Total number of traps	Follows – test if rate of trap checking is constant
7. Trap group composition is even between trap types or constant across locations	Total number of traps	Number of traps of a specific type	Follows – compare mean composition of village and camp follows
8. Trap types are not species specific	Total number of traps	Number of traps of a specific type and % species caught	Follows – compare trap composition with % species caught by trap type
9. Wastage does not represent a significant % of total catch, or is constant	Number of animals taken home	Total number of animals killed/wounded/left home	Follows - compare total no. animals with those taken home

¹ A hunting trip is greater than a day in length and composed of multiple individual hunts

² An individual hunt is less than a day in length

All analyses were performed within the R statistical package version 2.5.1 (R Core Development Team 2007). If data were not normally distributed, they were transformed appropriately; log transformations were used to normalise time spent hunting, and arcsine square root transformations in the analysis of proportions of time (Crawley 2002).

I used linear, and generalized linear, mixed effects models as described by Pinheiro (2000) and Crawley (2007), using the *lme* function from the *nlme* package (Pinheiro et al. 2005) and the *lmer* function from the *lme4* package (Bates & Sarkar 2007) respectively, to investigate the effect of distance from the village on the allocation of hunter time budgets, on trap group size, and also to investigate the factors influencing the length of a hunting trip. When looking at the effect of distance on time spent away from the village and time spent hunting, hunting camp was specified as a random factor to control for spatial autocorrelation. When looking at predictors of trap group size and hunt duration, hunter ID was fitted as a random effect to control for the non-independence of repeated follows of the same hunter.

Model simplification was by backward selection of variables from the full model and model comparison with Akaike's Information Criterion (AIC) and likelihood ratio tests (Crawley 2007; Pinheiro & Bates 2000). Significance of random effects was estimated using likelihood ratio tests, while the significance of fixed effect terms was assessed by *F*-tests and *t*-tests (Pinheiro & Bates 2000). I further evaluated statistical support from the data for inclusion of fixed effects by comparing AIC weights of models including and excluding the variable of interest to obtain the minimum adequate model. In addition I report approximate R^2 values for fixed effects using the linear model without random effects, the proportion of variation explained by random effects and the unexplained variation. All models were visually inspected using diagnostic plots for violation of model assumptions.

3.4 Results

3.4.1 Hypothesis 1 - Time spent hunting is a constant proportion of total time

Total time spent away from the village on hunting trips varied significantly among hunting camps (one way anova, $F_{7,813}=75.96$, $p<0.0001$). Time spent actively hunting during these trips, also varied significantly among hunting camps ($F_{7,813}=37.67$, $p<0.0001$) (Table 3.4).

Table 3.4 Comparison of time spent away from the village and time spent actively hunting, across hunting camps. One standard error of the mean is shown.

Hunting camp	Mean time spent out of the village per trip (hours)	Mean time spent actively hunting per trip (hours)
Nseng Midyobo	41.01 \pm 4.08	12.95 \pm 1.05
Tom Asi Mitong	42.93 \pm 2.51	10.38 \pm 0.54
Esong	26.95 \pm 1.35	9.92 \pm 0.37
Bifamfamman	54.51 \pm 2.80	15.11 \pm 15.11
Boculu	83.18 \pm 8.19	21.98 \pm 1.91
Ncom	80.26 \pm 3.73	20.96 \pm 0.91
Miang	95.60 \pm 2.74	20.88 \pm 1.19
Mitong	89.61 \pm 4.92	14.95 \pm 1.38

These differences in absolute time measures among camps are explained by the cost to the hunter in terms of the distance travelled to the hunting camp; with increasing costs of travel, hunters both stayed away from the village longer on hunting trips (lme, $F_{6,813}=22.91$, $p=0.003$), and spent more time actively hunting (lme, $F_{6,813}=17.03$ $p=0.006$) (Fig. 3.2).

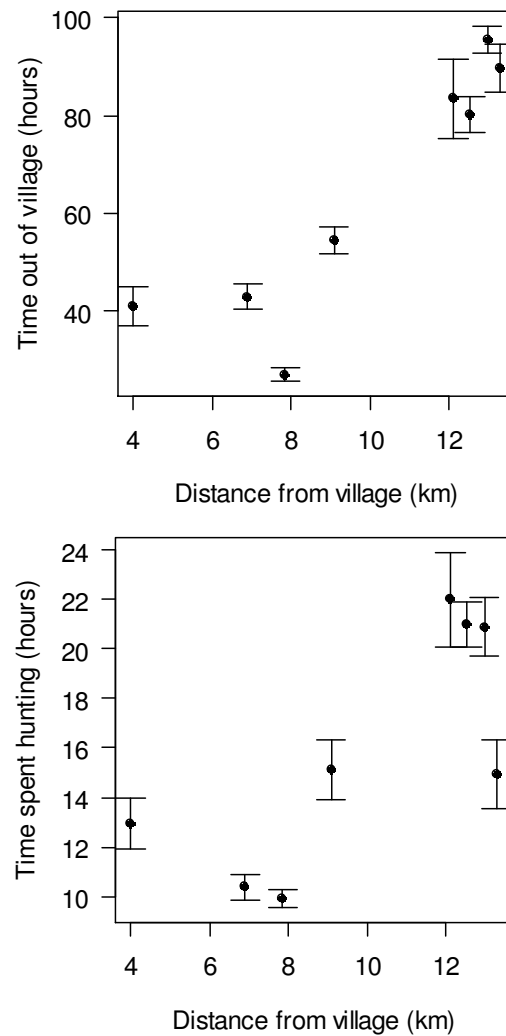


Figure 3.2 Relationship between absolute time measures and the distance travelled to the hunting camp. One standard error of the mean is shown.

In addition to the differences in absolute measures of time among hunting camps, the allocation of time to different components of hunter time budgets also varies. The proportion of time allocated to hunting is significantly different among camps (one way anova, $F_{7,813}=46.91$, $p<0.0001$). The proportion of time spent travelling is also significantly different among camps but a comparison of factor levels shows that this is due to a single hunting camp ($F_{7,813}=32.089$, $p<0.0001$; factor level for Esong: $t=5.61$, $p<0.0001$) (Fig 3.3).

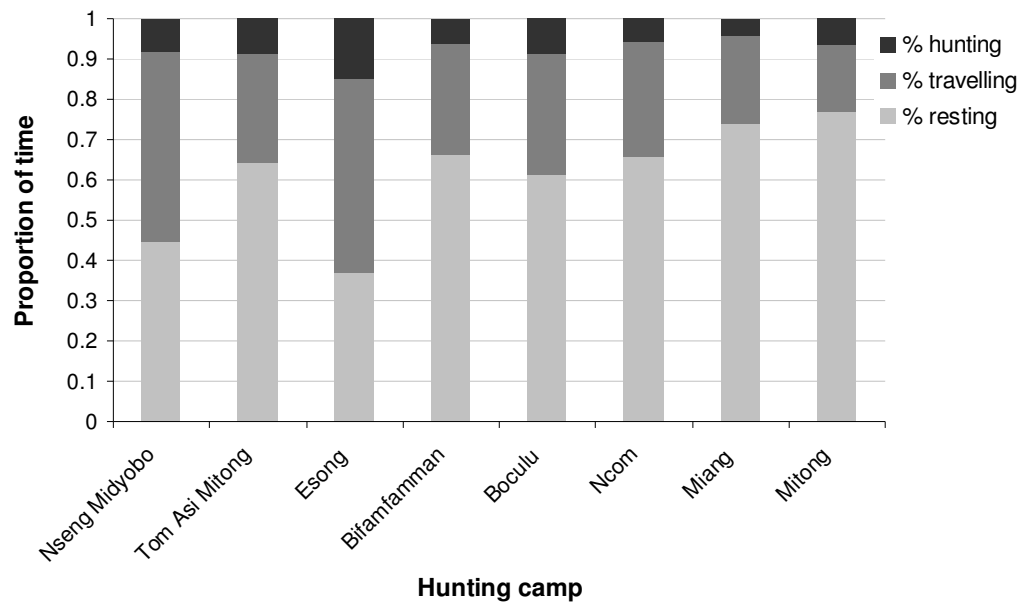


Figure 3.3 Hunter allocation of time between hunting, travelling, and resting, among hunting camps. Hunting camps are ordered from left to right by increasing distance from the village.

The variation in the proportion of time allocated to hunting is also explained by the cost to the hunter in terms of the distance travelled to the hunting camp; the proportion of time that is spent hunting decreases with increasing distance, by roughly 3% for every kilometre increase in distance (lmer, coefficient=0.03, SE=0.009, $t=-3.15$, $p=0.02$), (Fig. 3.4). However, the proportion of total time that is spent travelling to the camp is not explained by distance (lmer, $F_{6,813}=1.34$, $p=0.29$).

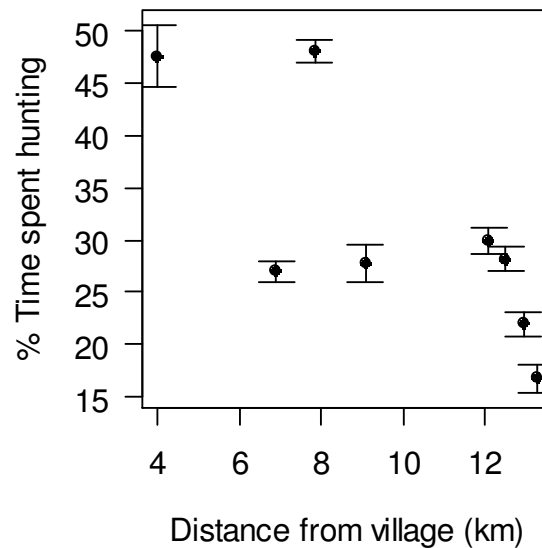


Figure 3.4 Relationship between the distance travelled to the hunting location and the proportion of total time allocated to hunting. One standard error of the mean is shown.

3.4.2 Hypothesis 2 – Hunt duration is constant across locations

The mean length of individual hunts recorded in camp diaries, across all camps was 5.8 ± 0.1 hours (1SE, $n=821$). When compared between camps, hunt duration differs significantly (one way anova, $F_{7,813}=8.25$, $p<0.0001$), however an investigation of factor levels shows that this relationship is driven by one camp, Nseng Midyobo ($t=3.62$, $p=0.0003$), (Fig. 3.5). The mean length of individual hunts recorded from hunter follows was 5.9 ± 0.2 hours ($n=225$), almost identical to that found in camp diaries. The duration of followed hunts was significantly different among hunting methods (two way anova, $F_{2,222}=8.07$, $p<0.0004$), hunts using traps (5.4 ± 0.2 hours, $n=143$) were shorter than those using a gun (6.6 ± 0.4 hours, $n=56$), or a gun and traps (7.0 ± 0.4 hours, $n=26$). Followed hunt duration was also significantly different between hunting locations, followed hunts leaving from the village (6.3 ± 0.2 hours, $n=130$) were significantly longer (Welch Two Sample t-test, $t=-3.03$, $df = 207$, $p=0.002$) than those leaving from hunting camps (5.26 ± 0.25 hours, $n=95$) (Fig. 3.5).

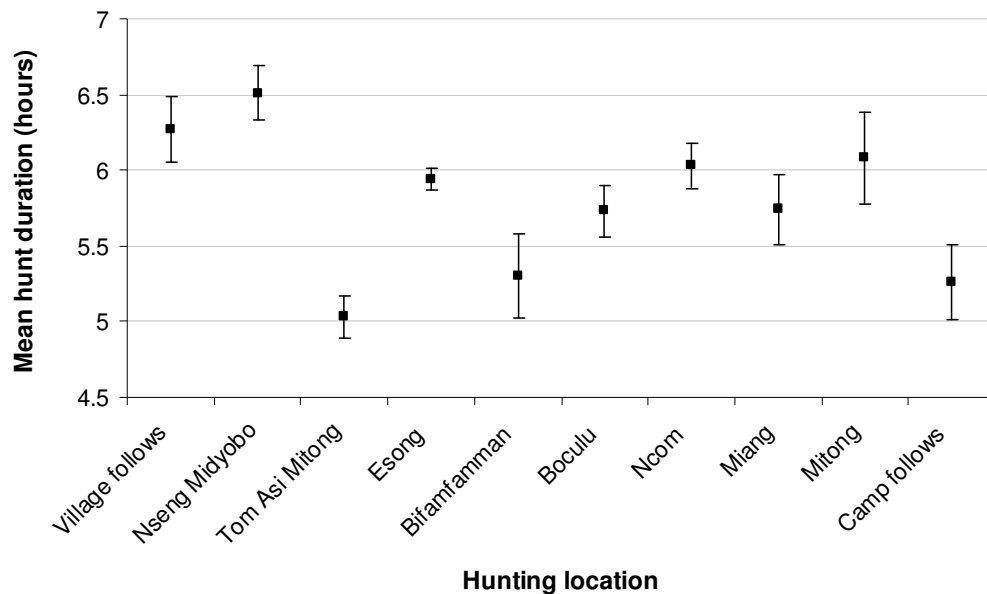


Figure 3.5 Comparison of mean hunt duration among locations. Camps are ordered from left to right by increasing distance from the village, and estimates from hunter follows for the village and for all hunting camps combined have been added for comparison. One standard error is shown

3.4.3 Hypothesis 3 – Handling time does not represent a large proportion of hunting time or is proportional to catch

Across all hunting trips recorded from follows, hunters spend on average 28.6 ± 2.2 minutes ($n = 225$), or $8.4 \pm 0.7\%$ of their time handling prey. When broken down by method the time spent handling is greater for gun hunts at $14.7 \pm 1.9\%$ of total time ($n = 56$), than for hunts using traps at $5.0 \pm 0.5\%$ of total time ($n=143$). Hunts using a gun and traps are intermediate, but closer to that for hunts with a gun alone at $13.2 \pm 1.9\%$ ($n = 26$). The average handling time per animal caught is 12.8 ± 0.4 minutes ($n=509$). When split by method it is 18.9 ± 3.6 minutes/animal for gun hunts ($n =154$), 8.1 ± 0.5 minutes/animal ($n =267$) for trap hunts, and 16.5 ± 9.1 minutes/animal ($n = 88$) for hunts with a gun and traps. The difference between methods is significant (one way anova, $F_{2,166}=20.95$, $p<0.0001$), and a comparison of factor levels shows this to be due to the lower handling time per animal for hunts using just traps ($t= -5.828$, $p<0.0001$).

The proportion of time spent handling increases with the number of animals caught during a hunt (Pearson's product-moment correlation, $r=0.31$, $df=223$, $p<0.0001$). When broken down by method this is due to a correlation between trap handling time and trap catch ($r=0.35$, $df=141$, $p<0.0001$), with no correlation between handling time and catch for gun hunts ($r=0.09$, $df=54$, $P=0.49$). However, if only successful hunts are considered then correlations increase slightly in strength; all methods ($r =0.36$), hunts with traps ($r =0.41$), and the relationship for guns becomes significant after the removal of unsuccessful pursuits ($r =0.39$, $df=30$, $p= 0.035$).

3.4.4 Hypothesis 4 - The proportion of hunting time spent checking traps is constant

The average amount of time spent checking traps recorded from hunter follows was 3.3 ± 0.1 hours ($n = 159$), representing only 55% of the total hunt duration, the rest being taken up with local travel. There was no detectable difference in the absolute amount of time spent checking traps between hunts leaving from the village and those leaving from hunting camps (two way anova, $F_{1,156}=0.76$, $p=0.39$). However, the proportion of the hunt duration spent checking traps was on average 10% lower in hunts leaving from the village than in hunts leaving from hunting camps (two way anova, $F_{1,156}=10.44$, $p=0.0013$). This suggests that more time is spent on local travel in hunts conducted close to the village, which might explain the longer mean hunt durations for the village and Nseng Midyobo (Fig. 3.5). Hunts using traps and a gun spent on average one hour longer checking traps than those just using traps ($F_{1,157}=6.04$, $p=0.015$), but there was no detectable difference in the proportion of the hunt duration spent checking traps ($F_{1,156}=0.53$, $p=0.47$).

3.4.5 Hypothesis 5 - Trap group size is constant across locations

On average hunters have 92.6 ± 4.8 traps per group ($n=167$). Trap groups checked from a camp tend to be larger on average (103.8 ± 7.9 traps, $n = 80$), compared to the village (83.0 ± 5.7 traps, $n = 87$). Trap groups that were checked with a gun tend to be smaller on average (81.8 ± 7.18 traps, $n = 26$), compared to those checked without a gun (94.8 ± 5.6 traps, $n = 132$). However, these differences in trap group size were not significant, no influence of hunting location ($F_{(1,152)} = 2.81$, $p=0.10$), hunting method ($F_{1,152} = 0.002$, $p=0.99$), hunter age (lmer, $F_{1,152} = 0.25$, $p=0.62$), or hunter age category, defined as <30, 30-60, or >60 years (lmer, $F_{1,152} = 0.16$, $p=0.85$), on trap numbers was found. Differences between hunters explained 26.43% of variation in trap numbers.

3.4.6 Hypothesis 6 - Trap group size determines time spent hunting

The mean rate of checking traps recorded during follows was 4.92 ± 0.35 traps/minute ($n=159$) but was highly variable. Three different time measures (individual hunt duration, trap-checking time and trap-checking time minus handling time) were all only very weakly explained by trap numbers. The variation in hunt duration explained by the number of traps checked is very small (Linear regression, $F_{1,156} = 6.22$, $p=0.014$, $R^2_{adjusted} = 0.032$), (Fig. 3.6), and not greatly improved by using a more accurate time measure such as trap-checking time (Linear regression, $F_{1,156}=8.38$, $p=0.0040$, $R^2_{adjusted}=0.045$) or trap-checking time minus handling time ($F_{1,156}=8.49$, $p=0.0041$, $R^2_{adjusted}=0.045$).

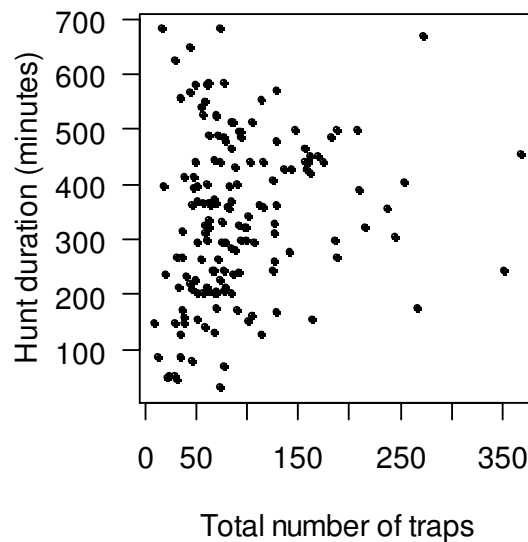


Figure 3.6 Relationship between hunt duration and the number of traps checked

Further investigation of factors other than trap numbers that might influence the duration of a hunt showed that the use of a gun, the hunting location and the number of people in the hunting party to be important. Increasing the number of people on the hunt increased the hunt duration for a given number of traps, while hunts using traps and a gun had a higher trap checking rate of 6.41 ± 0.87 traps/min ($n=26$) compared to hunts using just traps at 4.63 ± 0.38 traps/minute ($n=133$). Hunts in the village had a higher trap checking rate of 5.79 ± 0.58 traps/minute ($n=86$) than those in camps of 3.91 ± 0.30 traps/minute ($n=73$). There was no effect of hunter age, whether the hunt was conducted on a market day, nor of differences between different follow observers (Table 3.5).

Table 3.5 Minimum adequate model results for hunt duration as a function of trap numbers, hunting method, hunting location, hunting party size, hunter age, observer and market day. Explanatory variables excluded during model simplification include: hunter age ($p=0.76$), market day ($p=0.80$), and observer ($p=0.18$). This model explains 20% of total variation in hunt duration using 4 parameters ($R^2_{adjusted} = 0.1996$, $F_{4,153}=10.79$, $p<0.0001$), with 11% explained by differences between hunters.

Predictor variable	Coefficient	SE	df	<i>t</i> value	<i>p</i> value
Trap numbers	0.01	0.003	107	3.87	0.0002
Method (Trap and Gun)	1.34	0.518	107	2.62	0.01
Site (village)	1.33	0.386	107	3.44	0.0008
Hunting party size	0.85	0.229	107	3.72	0.0003

When factors influencing trap-checking time were modelled, trap numbers, hunting method, and the number of people in the hunting party all influenced the time spent checking traps. There was again no effect of hunter age, whether the hunt was conducted on a market day, or of differences between different observers, and the effect of hunting location dropped out of the minimum adequate model (Table 3.6).

Table 3.6 Minimum adequate model results for trap checking time as a function of trap numbers, hunting method, hunting location, hunting party size, hunter age, observer and market day. Explanatory variables excluded during model simplification include: hunter age ($P=0.87$), market day ($p=0.97$), observer ($p=0.74$), and hunting location ($p=0.78$). This model explains 13.30 % of the total variation in trap checking time using 3 parameters ($R^2_{adjusted} = 0.133$, $F_{3,153}=9.03$, $p<0.0001$), with 14.73% explained by differences between hunters.

Predictor variable	Value	SE	df	t value	p value
Trap numbers	0.50	33.21	108	3.63	0.0004
Method (Trap and Gun)	50.44	24.34	108	2.07	0.04
Hunting party size	28.59	10.62	108	2.69	0.0082

3.4.7 Hypothesis 7 - Trap group composition is even between trap types or constant

On average $84.50 \pm 2.05\%$ of the total number of traps in a group are leg traps and $15.50 \pm 2.05\%$ are neck traps ($n=167$). Neck traps represent $2.07 \pm 0.46\%$ ($n=80$) of trap groups located around hunting camps, and $27.86 \pm 3.42\%$ ($n=87$) for those around the village, the proportion is significantly different between hunting camps and the village (Wilcoxon rank sum test, $W=887$, $p<0.0001$). Leg traps represent $97.93 \pm 0.46\%$ of trap groups located around hunting camps, and $72.14 \pm 3.42\%$ for those around the village, the proportion is significantly different between hunting camps and the village ($W=6073$, $p<0.0001$).

3.4.8. Hypothesis 8 – Trap types are not species specific

Of the 307 animals captured in traps during the hunter follows, 25% were caught with neck traps and 75% with leg traps. Some species groups were caught exclusively by one type of trap, for example all of the duikers were caught with leg traps, whereas other species, for example small carnivores (civets, genets and mongooses), appear to be caught almost equally by neck and leg traps. Some species show further specificity within neck and leg trap types. The brush-tailed porcupine (*Atherurus africanus*) appears to be caught almost exclusively by small leg traps, and the tree pangolin (*Phataginus tricuspis*) is caught nearly 70% of the time by neck traps located off the ground (Table 3.7).

Table 3.7 Percentages of total trap catch for commonly trapped prey species, by trap type

Species	Neck trap %		Leg trap %				Total no. caught
	Off-ground	On-ground	Total	Small	Large	Total	
All semifossorial spp.	33	10	43	55	2	57	125
Brush-tailed porcupine (<i>Atherurus africanus</i>)	0	0	0	94	6	100	52
Pouched rat (<i>Cricetomys emini</i>)	35	27	62	38	0	38	26
Tree pangolin (<i>Phataginus tricuspis</i>)	69	7	76	24	0	24	45
All duikers (<i>Cephalophus spp.</i>)	0	0	0	65	35	100	102
Blue duiker (<i>Philantomba monticola</i>)	0	0	0	72	28	100	86
Bay duiker (<i>Cephalophus dorsalis</i>)	0	0	0	25	75	100	12
All small carnivore spp.	40	0	40	60	0	60	10
All species	17	8	25	59	16	75	307

Further examination shows that this is not an artefact of a species being caught in a particular trap type simply because that trap type is more common. A comparison of the relationship between the percentage of total traps in a trap group contributed by a trap type, with the percentage of the total catch of that species caught in that trap type, provides further evidence for species specificity. If traps were not specific then a proportional relationship between the two measures would be expected, as the proportional contribution of that trap type to total trap numbers increased, then so too would the proportion of total catch of the species caught in that trap type. However, if when the proportion of the trap type is low, the proportion of the species caught in it generally remains high, this suggests species targeting by certain trap types (Fig.3.7).

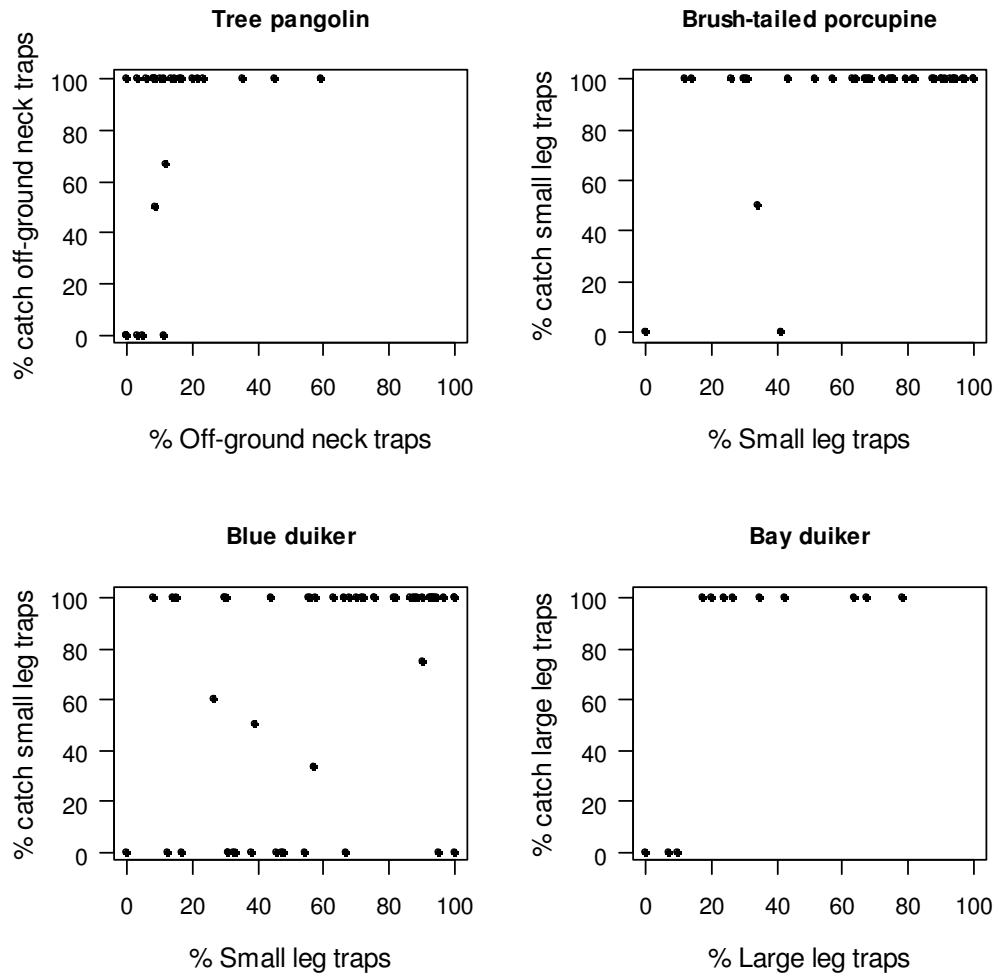


Figure 3.7 Relationship between the proportion of total catch in a specific trap type with the proportional contribution of that trap type to total trap numbers for the tree pangolin (*P. tricuspis*), brush-tailed porcupine (*A. africanus*), blue duiker (*P. monticola*) and bay duiker (*C. dorsalis*) caught.

3.4.9. Hypothesis 9 - Wastage does not represent a significant proportion of total catch, or is constant

Using complete catch data from hunter follows shows that wastage represents almost 15% of total catch; when split by method, wastage represents 11% of trap catch, and 21% of gun catch. A comparison of wastage between hunts leaving from the village and camps shows that for guns, wastage in the village is higher (22.86 ± 5.65 %, $n=30$) than in camps (16.39 ± 5.53 %, $n=14$). Whereas for traps, wastage in the village is lower (10.30 ± 2.92 %, $n=66$), than for camps (11.70 ± 3.54 %, $n=66$). A comparison by season shows higher wastage for guns in the dry season (23.55 ± 5.4 %, $n=23$), than in the rainy

season ($17.79 \pm 6.52\%$, $n=21$). Whereas for traps, wastage is higher in the rainy season (13.26 ± 3.39 , $n=67$), than the dry season ($8.24 \pm 2.87\%$, $n=57$).

3.5 Discussion

My analyses give important new insight into the sources of bias that can exist when using different measures to quantify hunting effort and catch. Many of my initial hypotheses (Table 3.3), which are frequently assumed by many hunting studies, and that predict equality between biological and economic measures of hunting, have not been accepted. I have shown that the reliability of different effort measures in representing the true effect of hunting on prey mortality can vary according to hunting method, hunting location and the species being hunted, and that the degree of bias can be considerable. These findings have important implications for measuring and attributing hunting impact, and knowledge of how these biases occur, will allow the collection of catch-effort data that more accurately represents the true biological impact of hunting effort. The implications of these findings for the measurement of hunter effort are summarised in Table 3.8.

3.5.1 Time as a measure of effort

Time spent out of the village, or similar economic time measures, are currently the most frequently used method of quantifying hunting effort (Table 3.1), however in this study I have found that the use of such measures can lead to considerably biased estimates of biologically relevant hunting effort. The proportion of total time on a hunting trip that is spent hunting decreases with increasing distance of the hunting location from the village and so absolute time measures will need to be adjusted to account for this bias. If unadjusted, hunting effort may be increasingly overestimated with increasing distance, and consequently if effort is then used to calculate CPUE, it will lead to underestimates of abundance and overestimates of the impacts of hunting. Furthermore, if distant locations are those with the highest prey abundances, then this could lead to the false prediction of Hyperstability in the relationship between CPUE and abundance.

While not directly relevant to the selection of effort measures, it is interesting to note that hunters seem to adjust the duration of their hunting trips to maintain a constant ratio between the time spent hunting and travelling, when travelling further they stay proportionally longer to compensate for the increased travel cost. The exception to this relationship was a single hunting camp, Esong, which is located directly on an abandoned logging road coming from the village, and where proportionally more time was spent travelling. The logging road reduces the cost of travel in comparison to forest trails, so hunters might be willing to spend longer travelling to this camp, in comparison to the

time they spend there hunting. This suggests that the cost of travel, rather than distance *per se* can be an important determinant of the spatial distribution of hunting effort, as has similarly been found in other studies (Belisle 2005; Bernstein et al. 1991).

Evidence for the existence of a constant hunt duration was mixed. Mean hunt duration did not differ among hunting camps, but hunts around the village were longer than those around hunting camps, so if a constant hunt duration was assumed it could lead to an underestimate for the village, and an overestimate for camps, of biologically relevant effort. Despite this, the difference between camps and the village may be sufficiently small that if effort measured as the number of hours spent hunting is too difficult or time consuming to record, then the number of days spent hunting (excluding travelling and resting days), might represent a crude but adequate measure of effort when resources for data collection are limited.

Handling time can be an important consideration for the quantification of effort if it represents a large proportion of the total time spent hunting. Handling time is unlikely to be a limiting factor on trap catch due to the lack of a trap saturation effect, and is much more likely to be a problem for gun hunting where a hunter's ability to pursue an encounter is limited by his 'handling' of the previous encounter. In this study, as expected, handling time was found to be greater for guns than for traps, but on average it represents a relatively small proportion of hunting time and so is therefore probably an unnecessary consideration when time measures are to be used to quantify hunting effort.

3.5.2 Quantifying trapping effort

Trap group size appears to be fairly constant, with no influence of hunting location, hunting method, or hunter age on trap numbers being found. The number of trap groups checked (or days spent hunting if one trap group is checked per day) might therefore be a crude but adequate measure with which to quantify trapping effort. Differences between hunters explained over a quarter of the total variation in trap group size so it is likely that characteristics other than a hunter's age influences the numbers of traps used. Traps are expensive to make, and so cost may act as a limiting factor on trap hunting effort. Trap numbers may be influenced by a hunters level of wealth and hence ability to buy cable for trap construction. Their ability to pursue other livelihood options may also affect trap group size (de Merode et al. 2004).

One might expect that hunt duration and trap numbers would be highly correlated, however only a weak correlation was found, even when time spent checking traps is used rather than total time hunting. The rate of trap checking is highly variable, and influenced by hunting method, the location of the hunt and the number of people on the hunt. Surprisingly hunter age did not explain any of the variation in trap checking rate. Differences between hunters explained only 11% of the variation, with 89% remaining

unexplained, suggesting that rates of trap checking between hunts of the same hunter can be as variable as those between hunts of different hunters. These results may have important implications for the use of time as an index of trap numbers. Furthermore, if most of the variation in trap-checking rates cannot be explained using additional information that is simple to collect, such as hunter age then calibration of time to give a more accurate measure of trapping effort will prove difficult. For those species targeted by traps, time is likely to be a relatively poor measure of hunting mortality, and trap numbers will be preferable, where possible to collect such data.

Trap group composition was found to vary greatly with hunting location, which has also been found in other studies (Wato et al. 2006), suggesting that hunters are targeting different species in different locations. Around camps, ungulates were targeted through the use of leg traps, while the importance of rodents and other semi-fossorial species increased around the village, reflected by increased use of neck traps. While total trap numbers are probably adequate for species, such as duikers, caught by commonly used trap types, they are likely to be an inaccurate indication of the hunting effort experienced by those species targeted by less commonly used trap types.

Furthermore, I found good evidence for the existence of species specificity of traps. This was not an artefact of differences in trap composition as species continued to be caught by a particular trap type even when it was present in low numbers in a trap group. This further suggests that information on trap group composition might be needed in order to accurately quantify trapping effort. The investigation of trap specificity is additionally complicated by the fact that traps are not randomly placed, but instead are set on animal runs or pathways, according to the species identified by the hunter. It is therefore possible that a particular trap type always catches a certain species because it is always placed by the hunter in order to catch that species. Trap placement may be important in determining the species caught by a given trap type (Bousquet et al. 2001), but is necessarily ignored in this study, since truly separating these effects would require detailed study involving manipulated experiments of trap placement by hunters.

3.5.3 Hunter and prey perspectives on catch

Measures of catch can differ greatly depending on whether taken from a hunter or prey perspective. Typically trapping is thought to be the more wasteful method (Noss 1998b), but here information on true catch from hunter follows shows wastage to be highest for gun hunters, representing a quarter of total catch, double that shown for traps. Previous studies have reported very high trap wastage levels, for example up to 27% of captures (Noss 1998b). In comparison the levels of trap wastage reported here are small. This might be due to the recent onset of hunting in this area meaning that hunters do not yet

travel to such great distances that regular trap checking is precluded. Furthermore, the weekly visits from market traders may act as an incentive for regular trap checking.

In addition, the degree of wastage was found to vary with location and season, being higher for guns in the village and during the dry season, but higher for traps in camps and during the wet season. An increase in trap wastage in camps in comparison to the village has been previously shown, and occurs due to less systematic trap checking with increasing distance to the trap group location (Noss 1998b). The increase in gun wastage for hunts around the village might be due to denser canopy-level vegetation preventing shot animals from falling to the ground. An increase in trap wastage during the wet season might be intuitively expected, due to faster rates of decomposition in wet conditions (Barnes et al. 1997). These findings suggest that indirect methods of recording catch data, may offer considerable opportunities for underreporting if hunters report catch from an economic and not a biological perspective. Furthermore, if hunters do not accurately report catch then wastage will prove hard to adjust for since the proportion of wastage does not appear to be consistent across methods, locations or seasons.

Table 3.8 Summary of the main findings, whether each hypothesis was rejected or accepted and the implications for measuring the biological effects of effort

	Hypothesis	Result	Interpretation
1.	Hunting time is a constant proportion of total time	Rejected - % of total time spent hunting decreases with increasing distance to hunting location	Total time would be biased and need adjustment
2.	Hunt duration is constant	Mixed evidence - hunt duration is constant across camps but differs between camps and the village	Number of hunts or days on which a hunter went hunting suitable as a coarse measure
3.	Handling time does not represent a large % of hunting time or is proportional to catch	Accepted - handling time does not represent a large % of hunting time and is weakly correlated with catch	Not necessary to account for handling time in effort calculations
4.	The % of hunting time spent checking traps is constant	Rejected - lower % in village due to increased local travel	Village effort overestimated. If trap-checking time correlates to trap numbers then hunting time will correlate to trap numbers.
5.	Trap group size is constant	Accepted - no significant differences found in trap group size due to hunting location, method or hunter age	No. of trap groups checked (or days) might be suitable as a coarse measure of trapping effort
6.	Trap group size determines hunt duration and time spent hunting	Mixed evidence - a weak relationship, not better with more specific time measure Influenced by method, no. people and location	Time going to be a poor measure of trapping effort
7.	Trap group composition is even between types or composition is constant	Rejected – composition varies with location	Trap composition required for species caught by rarer trap types
8.	Trap types are not species specific	Rejected – traps can be species specific	Trap composition required for species caught by rarer trap types
9.	Wastage is not a significant % of total catch or % wastage is constant	Rejected - wastage is large % and varies by method, location and season	Wastage hard to adjust for and accurate reporting by hunters required

3.5.4 Conclusion

I have shown that choosing an appropriate measure of hunting effort that reflects its' true biological impacts can prove difficult. Time spent hunting has been the most frequently used measure to date, but its use presents problems for quantifying both gun and trap hunting effort. I have shown that using economic measures of time spent hunting can lead to overestimates of biological hunting effort with increasing distance that may require adjustment. If hunt duration is sufficiently constant then the number of days spent hunting

may offer an adequate measure of effort when resources for data collection are limited. In the case of gun hunting, handling time is relatively small and so for the purposes of this study does not need to be considered in the quantification of effort. In the case of traps I have shown firstly that time spent hunting or even checking traps, is not well correlated with trap group size and so should not be used as a proxy for trap numbers, and that variation in trap checking rates cannot be explained by factors such as hunter age, making calibration of time to give a more accurate index of trap numbers difficult. Furthermore, trap group composition is variable and traps can be species-specific. Overall this suggests that the biological impact of trapping effort will be best measured in terms of trap numbers and composition, where possible.

This is the first study to my knowledge to investigate and explicitly quantify the sources of bias that can exist when quantifying hunting effort in various ways. While studies using qualitative descriptions of hunting intensity or pressure may be able to identify patterns of depletion, if we hope to properly assess hunting impact using catch-effort data, then quantitative measures that accurately reflect prey abundance are required. On the other hand, if we wish to target management by understanding hunter incentives, then measures related to total time allocation and economically relevant offtake, are more relevant. A better understanding of how these different measures of effort and catch relate to each other will allow future studies to collect catch-effort data that more accurately represents the true biological impact of hunting. Further information will be obtained from testing the effort measures identified in this study with catch data, to determine which effort measures best explain catch, and so best reflect the biological impacts of hunting. In addition, the relative importance and magnitude of the biases identified here may vary on a case by case basis, and so the generality of my findings to other sites may depend on the type of hunting system in place. As such the measures identified here are intended as a guide to illustrate where bias in quantifying catch and effort can occur. Further comparative studies are needed to assess the general applicability of my findings and the validity of different measures for quantifying effort and catch in different hunting systems.

Chapter 4

**The importance of effort, hunter characteristics and
seasonal effects in determining catch**

4. Chapter 4 – The importance of effort, hunter characteristics and seasonal effects in determining catch

4.1 Abstract

The use of abundance indices derived from hunting statistics such as Catch per Unit Effort (CPUE) has been suggested as a tool for monitoring the impact of bushmeat hunting, but such indices make many assumptions which frequently go untested. The CPUE index assumes a linear relationship between catch and effort, for a given abundance, when in reality many factors other than abundance may affect the relationship. I use linear mixed-effects modelling of hunting data from hunter follows, hunting camp diaries and weekly hunter interviews conducted during a study in Equatorial Guinea, to determine the nature of the relationship between hunter catch and effort. I use this approach to select measures of effort which best explain catch, to identify additional variables which reduce unexplained variation in catch, and to decompose variance in CPUE into spatial, temporal and individual hunter level components. I show that catch is related to hunting effort, but that the relationship is highly variable, and that differences in hunter skill and season may be important in determining variation in catch for a given effort. Due to this variability in the catch-effort relationship, catch-effort data aggregated across hunts frequently produced a better relationship than for individual hunts, despite the fact that more precise effort measures were available at the individual hunt level. My results suggest that the most appropriate measure of effort will depend upon the particular index of CPUE required and the resources available for data collection. For aggregate CPUE, across species and methods, effort measured as time out of the village may be adequate, but for species specific CPUE data, effort may need to be measured as individual trap numbers and trap types. Differences between hunters explained the most variation in CPUE, suggesting that individual hunter-level processes, such as individual level of skill, are at least as important in determining the catch obtained for a given level of effort as prey abundance, and that sampling a wider range of hunters as possible is going to be crucial to CPUE estimation.

4.2 Introduction

There is currently a need for simple methods which allow the impacts of hunting on prey species abundance to be assessed indirectly, such tools could make a key contribution to the development of sustainable harvesting strategies (Bodmer & Robinson 2005; Rowcliffe et al. 2003). One suggestion has been the use of hunting statistics, where hunter return rates from different areas of the forest could be used to represent differences in animal abundance (Bodmer & Robinson 2005; Wilkie & Carpenter 1999). This concept of using Catch per Unit Effort (CPUE) originated in fisheries research, where it has been used extensively (Hilborn 1992). However, the use of CPUE as an index of abundance is based on a number of assumptions, the validity of which is rarely investigated. One of these is that catch is proportional to effort; this relies on each unit of effort having a predictable effect on population size. In the fisheries literature, the fraction of abundance captured by one unit of effort is termed the catchability coefficient (Maunder & Punt 2004), and in order to use CPUE as an index of abundance, the catchability coefficient is assumed to be constant, independent of time, location and exploiter (Cooke & Beddington 1984; Gulland 1983).

In reality many factors may influence the catchability coefficient, and hence the level of catch obtained for a given effort at constant abundance (Bordalo-Machado 2006). In the fisheries literature these problems are well documented (Hilborn 1992), however in tropical forest hunting systems, the relationship between catch and effort, and the influence of factors other than effort and abundance in determining catch, such as changes in harvesting efficiency, gear saturation, differences in exploiter skill or knowledge, prey biology or behaviour, and environmental factors such as season or weather conditions, have not yet been investigated.

Undetected advances in harvesting technology have presented a major problem when quantifying effort in fisheries (Gulland 1983; Hilborn 1992; Quinn 1999). Similarly in terrestrial harvesting systems technological improvements such as the use of guns or cable traps in place of traditional hunting methods, such as bow and arrow or pit traps, can occur over time (Milner-Gulland 1998). Other factors such as the use of a dog on hunts to detect prey may greatly increase hunter efficiency (Liebenberg 2006). Conversely, under some circumstances, harvesting efficiency might decrease over time. For example, the capture efficiency of a trap might decline the longer it remains set in the forest. Similarly, gear saturation (Groeneveld et al. 2003), if it occurs, may reduce catchability by preventing further capture of prey (Rowcliffe et al. 2003). The number of hunters present on a hunting trip may also affect an individual hunter's efficiency, for gun hunters a larger group size could lead to increased chances of detection by prey species (Cowlishaw & Dunbar 2000), and for trap hunters an increase in the time spent checking traps due to the need to wait for other hunters. However, such reductions in efficiency are

likely to be much smaller in scale than gains in efficiency caused by technological advances.

As well as technological changes, differences in the knowledge and experience of exploiters can have an influence on the catch obtained for a given effort at constant abundance (Gulland 1983; Le Pape & Vigneau 2001). In terrestrial systems, hunter age has been shown to be important in determining hunting ability, with two components of hunting ability, finding prey and the probability of kill upon encounter, peaking very late in life and after the peak in physical strength (Walker et al. 2002). In fisheries, these differences in technology, skill and knowledge between individual exploiters are termed differences in 'catching power' (Salthaug & Godo 2001).

In addition to differences in the catching power of individual exploiters, environmental factors such as season and weather conditions can have a large influence on catchability over time, for example el Niño events in fisheries (Maunder et al. 2006). Temporal variation in terrestrial harvesting patterns can also be linked to seasonality (Cowlshaw & Dunbar 2000). Hunting of primates has been shown to increase during the wet season in some studies, possibly owing to the increased local abundance of frugivorous primates as they aggregate during the fruiting period (King 1994), others conversely show that primates become more detectable during the dry season, due to lower vegetation cover and improved forest access for hunters (Juste et al. 1995; Oates 1988). Seasonality may also influence detectability for trap-caught species, with animals' tracks and signs being more evident during the wet season, facilitating trap placement by hunters (Bousquet et al. 2001).

All of these factors can contribute to the lack of a good relationship between catch and effort, therefore causing high variability in CPUE data (Cooke & Beddington 1984). The utility of CPUE as an index of abundance depends upon being able to adjust for the impact of factors such as these on catch rates (Maunder & Punt 2004). In fisheries literature this is termed catch-effort standardisation, the goal of which is to explain the variation in CPUE that is not a consequence of changes in population size, by identifying explanatory variables that reduce unexplained variability in catch (Maunder & Punt 2004). This information can then be used to adjust or 'standardise' effort so that CPUE observations will more accurately reflect real differences in abundance (Beverton & Holt 1957; Gulland 1983; Hilborn 1992; Quinn 1999). In order to investigate the relative effects of such factors on the relationship between catch and effort, standardisation analyses need to be based upon a time and area stratification where abundance can be assumed to be constant. These strata should be small in area and short in duration to minimise abundance changes in time and space (Fonteneau 1999; Walters 2003).

The relationship between catch and effort is therefore influenced by many processes, operating at temporal, spatial and individual-level scales. Temporal and spatial processes are mediated through their effects on prey abundance, detectability or

prey behaviour, whereas individual-level processes reflect differences in hunter catching power. An understanding of the relative importance of each of these scales in determining the variability of CPUE will provide insight into which variables might prove useful for catch-effort standardisation. It will also provide an indication as to what is likely to be the most appropriate temporal and spatial scale at which to measure CPUE.

To my knowledge this is the first study to explicitly investigate the relationship between catch and effort for a tropical forest hunting system. I use a mixed-effects modelling approach to determine the measures of effort which best explain catch, to identify factors other than effort and abundance that influence catch and to decompose variance in CPUE estimates into spatial, temporal and individual hunter-level components. I make recommendations about the selection of effort measures, standardisation of effort for use in calculating CPUE indices, and suggestions for sampling to minimise variance in CPUE estimates.

4.3 Methods

4.3.1 Study location

This study was carried out in the village of Midyobo Anvom in the Centro Sur Province of Rio Muni, mainland Equatorial Guinea (1°20'N, 10°10'E), from January 2005 until March 2006. The village of Midyobo Anvom is 180 kilometres by unpaved road from the mainland's capital Bata, and is one of the most remote communities in mainland Equatorial Guinea (Fig. 2.1). Midyobo Anvom has a population of approximately 150-200 people, who practice shifting agriculture and hunting, who have little to no access to alternative livelihoods or food sources. For further details on habitat, climate and the development of bushmeat hunting in this area see section 2.3.1, and for further details on the hunting system see section 3.3.2.

4.3.2 Hunter follows

Hunter follows were conducted to obtain data on 'true' hunting catch and effort, using a Handspring Visor PDA with Magellan GPS attachment and a customised data collection programme written in CyberTracker (Steventon 2002). Follows were conducted by myself or a local research assistant. For further details on this method, and for information on sample sizes and scheduling see section 3.3.3.

4.3.3 Hunting camp diaries

Camp diaries were kept by a hunter for eight of the hunting camps in use during the study period (Fig. 4.1, Table 4.1), providing detailed information on all hunting activity that occurred in the hunting camp each week. For further details on this method and information on sample sizes and scheduling see section 3.3.4

4.3.4 Weekly hunter interviews

All hunters in the community were interviewed about their hunting activities at the end of each week throughout the study period, reporting for that week catch and effort information for all of their hunting trips, defined as any trip leaving and returning to the village. Interviews typically lasted 10-15 minutes and were conducted by myself or a local research assistant. A detailed map of the village and the surrounding area was constructed using participatory mapping (Chambers 1994), and divided into numbered zones to aid hunters in the identification of hunting locations during interviews (see Appendix 8.2). The following data were recorded for each hunter: whether he had been hunting that week, and if so, the method used, the dates spent hunting, the time of departure and return, the location of the hunt (by indicating the main zone out of those used during the hunt), a list of all the animals caught and the method of capture. Emphasis was placed on the need for honest reporting of both catch and effort information and that unsuccessful trips were just as important to report as successful trips.

4.3.5 Statistical analyses

All analyses were performed within the R statistical package version 2.5.1 (R Core Development Team 2007). I used linear, and generalized linear, mixed effects models as described by Pinheiro (2000) and Crawley (2007), using the *lme* function from the *nlme* package (Pinheiro et al. 2005) and the *lmer* function from the *lme4* package (Bates & Sarkar 2007) respectively, to determine the relationship between effort and catch. Similar analytical techniques are recommended for catch-effort standardisation in the fisheries literature (Maunder & Punt 2004).

This approach was applied to catch-effort data taken from three data sources: hunter follows, camp diaries and weekly hunter interviews. The simultaneous use of these three datasets allowed investigation of the catch-effort relationship at a range of different scales, from the individual hunt level (follows) to the aggregate level (camp diaries and weekly interviews), and using a range of effort measures from precise measures such as

trap numbers (follows) to cruder effort measures such as time spent out of the village (camp diaries and weekly interviews) (Table 4.2).

For each of these three catch-effort data sources, effort measures were tested against total, gun and trap catch, additionally in hunter follows some examples of species level catch were used to allow testing of the more precise trapping effort measures (rodent, duiker, brush-tailed porcupine (*Atherurus africanus*) and blue duiker (*Philantomba monticola*) catch).

In addition to effort measures, a number of other explanatory variables were also fitted in the models as covariates: hunter age (continuous) and season (two-level factor, rainy or dry) were fitted in all models. Information on the following covariates was available only for hunter follows: the use of a dog on the hunt (two-level factor, yes or no), the number of people in the hunting party (continuous), average trap age (available for 137 follows) and days since traps were last checked (available for 65 follows).

Hunting location was specified as a random factor to control for differences in the catch-effort relationship due to spatial variation in abundance. Separate models were run for each effort measure. If covariates were retained in the minimum adequate model, then the model was run without the covariates, to allow selection of the effort measure explaining the most variation in catch, and the separation of variance explained by effort from that explained by the covariates (Table 4.2). It should be noted that R^2 values cannot be interpreted as exact figures when comparing across data sets with different sample sizes, hence conclusions from such comparisons will be interpreted with this in consideration.

I used the same mixed-model approach to investigate factors influencing the variance of mean CPUE estimates, as described by Crawley (2007). This was done using two out of the three of my catch-effort datasets: camp stays and weekly interviews, due to the requirements of sufficient variation at spatial, temporal and hunter levels for analysis. Analyses used aggregated catch data (all species and hunting methods), and those effort measures identified as explaining most variation in catch from the catch-effort standardisation analysis. Hunting location, time period (monthly), and hunter ID were fitted as random effects. Time periods were nested within hunting location and hunter ID was crossed within both hunting location and time periods (Baayen et al. 2006). Likelihood ratio tests were used to determine the significance of variance components (Crawley 2007).

Model simplification was by backward selection of variables from the full model and model comparison with Akaike's Information Criterion (AIC) and likelihood ratio tests (Crawley 2007; Pinheiro & Bates 2000). Significance of random effects was estimated using likelihood ratio tests, while the significance of fixed effect terms was assessed by F -tests and t -tests (Pinheiro & Bates 2000). I further evaluated statistical support from the data for inclusion of fixed effects by comparing AIC weights of models including and

excluding the variable of interest to obtain the minimum adequate model. In addition I report approximate R^2 values for fixed effects using the linear model without random effects, and variance components for random effects. Models were visually inspected using diagnostic plots for violation of model assumptions.

Table 4.2 Summary of catch-effort standardisation model analyses showing the data source, the catch measures used, effort measures tested and the covariates fitted.

Data source	Catch measure	Effort measures tested	Covariates used
Hunter follow	Total catch	Hunt duration (hours)	Hunter age Season
Hunter follow	Gun catch	Hunt duration (hours)	Hunting party size Hunter age Season Dog used
Hunter follow	Trap catch	Hunt duration (hours) Trap-checking time (hours) Total trap numbers	Hunting party size Hunter age Season Hunting party size Average trap age Days since last checked
Hunter follow	Duiker catch ¹	Hunt duration (hours) Trap-checking time (hours) Total trap numbers Number of leg traps	Hunter age Season Hunting party size
Hunter follow	Rodent catch ¹	Hunt duration (hours) Trap-checking time (hours) Total trap numbers Number of neck traps	Hunter age Season Hunting party size
Hunter follow	Brush-tailed porcupine	Hunt duration (hours) Trap-checking time (hours) Total trap numbers Neck trap numbers Number of small leg traps (<i>Nga</i>)	Hunter age Season Hunting party size
Hunter follow	Blue duiker	Hunt duration (hours) Trap-checking time (hours) Total trap numbers Leg trap numbers Number of small leg traps (<i>Nga</i>)	Hunter age Season Hunting party size
Camp dairies	Total catch	Days spent hunting Time spent out of the village (hours) Reported total time hunting (hours)	Hunter age, Season
Camp dairies	Gun catch	Days spent hunting Time spent out of the village (hours) Reported total time hunting (hours)	Hunter age, Season
Camp dairies	Trap catch	Days spent hunting Time spent out of the village (hours) Reported total time hunting (hours)	Hunter age, Season
Weekly interviews	Total catch	Time spent out of the village (hours) Adjusted time spent out of the village ²	Hunter age, Season
Weekly interviews	Gun catch	Time spent out of the village (hours) Adjusted time spent out of the village ²	Hunter age, Season
Weekly interviews	Trap catch	Time spent out of the village (hours) Adjusted time spent out of the village ²	Hunter age, Season

¹ For information on the species included within these higher taxon groups see table 2.3² For hunting trips of more than a day in length, total time was adjusted to account for the decrease in proportion of total time spent hunting that occurs with increasing distance (figure 3.2)

4.4 Results

4.4.1 The relationship between catch and effort - hunter follows

Using catch-effort data from individual hunts recorded on hunter follows, approximately 11% of total catch (all methods and all species) was explained by effort measured as hunt duration and hunting party size. A comparison of models with and without covariates showed that hunting party size had a minimal effect (<1%) and effort is primarily responsible for explaining catch, with an increase in effort of one hour causing a mean increase in catch of 0.14 animals per hunt. The other covariates of season and hunter age had no detectable effect on total catch (Table 4.3).

When hunts are separated by method, the amount of variation in catch explained by effort varies greatly between trap and gun hunts. 23% of gun catch was explained by effort measured as hunt duration, an increase in effort of an hour caused a mean increase in catch of 0.20 animals per hunt. The use of a dog on the hunt, season, hunting party size and hunter age had no detectable effect on gun catch (Table 4.3).

For trap hunts, all three measures of effort explained variation in catch, but the amount explained was very low, and similar in all models (4%). A one hour increase in hunt duration caused a mean increase in catch of 0.08 animals per hunt, a one hour increase in trap-checking time caused a mean increase in catch of 0.9 animals per hunt, and for every extra trap set, a mean increase of 0.003 animals per hunt (meaning an increase in effort of 333 traps is required to increase catch by a single animal and 92.6 ± 4.8 traps is the average group size, see section 4.4.5). Hunter age, season, and the size of hunting party had no detectable effect on trap catch (Table 4.3). The same total trap catch model run on a subset of data for which information on trap age was available (137 of 143 hunts using traps), showed no effect of average trap age ($p=0.95$) on total trap catch. Similarly on subset of data including the number of days since the traps were last checked (65 of 143 hunts), there was no significant effect on catch detected ($p=0.86$).

The amount of variation in trap catch explained by effort increased slightly when using more precise measures of both catch and effort. For duiker catch, three measures of effort were significant in explaining catch: the number of leg traps explained the most variation in duiker catch (7%), followed by total trap numbers (5%), with hunt duration explaining very little (0.4%). An increase in leg trap numbers by one extra trap caused a mean increase in catch of 0.005 animals per hunt (meaning an increase in effort of 200 leg traps is required to increase catch by a single duiker). Effort measured as the time spent checking traps had no detectable effect on duiker catch, and neither did the covariates of hunter age, season, and hunting party size (Table 4.3).

For rodents, two measures of effort explained a comparable amount of variation in catch: neck trap numbers explained around 5%, and trap checking time 4% of the total

variation in rodent catch. For every extra hour spent checking traps, catch increased by 0.15 animals per hunt and by 0.016 animals per hunt for every extra neck trap set (requiring an increase of 62.5 neck traps to increase catch by a single rodent). There was no detectable effect of effort measured as hunt duration or total trap numbers, and no effect of season, hunting party size, or hunter age on catch (Table 4.3).

If catch and effort analyses are conducted at the species level (e.g. the blue duiker, or the brush-tailed porcupine), the variance in catch explained by the model was not greatly improved in comparison to the higher taxon level (e.g. all duikers or rodents). Variation in catch of the blue duiker was best explained by the number of leg traps numbers (6%), followed by total trap numbers (4%), then hunt duration (0.4%). No effect of effort measured as trap checking time or as the number of small leg traps was found and there was no effect of any of the covariates of hunter age, season or hunting party size. For the brush-tailed porcupine, the number of small leg traps was the effort measure which best explained catch (6%), followed by hunt duration (4%), then trap checking time (3%). No effect of effort measured as total trap numbers or leg trap numbers was found, and there was also no effect of season, hunting party size or hunter age covariates.

4.4.2 The relationship between catch and effort - hunting camp diaries

Using catch-effort data for camp stays from hunting camp diaries, variation in total catch (all species and methods) was explained by all three effort measures: the number of days spent hunting (19%), total time spent hunting during the camp stay (19%) and time spent away from the village (17%). An increase of one day spent hunting caused a mean increase in catch of 0.17 animals per camp stay, an increase of one hour in total time spent hunting during the camp stay caused a mean increase in catch of 0.02 animals per camp stay, and a one hour increase in time spent away from the village caused a mean increase in catch of 0.005 animals per camp stay. Hunter age was retained in all three models, but in all cases the effect size and the variance explained was very small. No effect of season on total catch was found (Table 4.4).

When separated by method, variation in gun catch was explained by two effort measures: the total time spent hunting during the camp stay (38%) and the number of days spent hunting (4%). An increase of an hour in total time spent hunting during the camp stay caused a mean increase in gun catch of 0.07 animals per camp stay, and an increase of one day in the number of days spent hunting caused a mean increase in gun catch of 0.13 animals per camp stay. No effect of effort measured as total time spent away from the village, hunter age or season was found (Table 4.4).

For trap catch, all three measures of effort explained variation in catch to a similar extent: the number of days spent hunting explained the most variation (20%), followed by time spent away from the village (19%) and the time spent hunting (19%). Hunter age

was retained in all three models, but in all cases the effect size and the variance explained was very small. No effect of season on trap catch was found. An increase of one day in the number of days spent hunting caused a mean increase in trap catch of 0.8 animals per camp stay, and an increase of one hour in total time spent hunting during the camp stay caused a mean increase in trap catch of 0.02 animals per camp stay (Table 4.4).

4.4.3 The relationship between catch and effort - weekly hunter interviews

Total catch on hunting trips from weekly interviews was explained by two measures of effort: total time spent out of the village and adjusted total time (Table 4.5). Adjusted total time explained more variation in catch (24%), with an increase of 24 hours resulting in an increase in catch of 0.14 animals per hunting trip. Total time explained 22% of total catch, with an increase of 24 hours resulting in an increase in catch of 0.12 animals per hunting trip. Hunter age was retained in both models but had very little effect on the variance in total catch explained. No effect of season was found on total catch (Table 4.5).

When separated by method, 8% of gun catch was explained by effort measured as total time and season, with an increase in time spent out of the village of 24 hours resulting in a mean increase in catch of 0.31 animals per hunting trip. Adjusted total time explained slightly less variation in catch (6%), with an increase in time spent out of the village of 24 hours resulting in a mean increase in catch of 0.41 animals per hunting trip. The variance explained by gun catch increased by approximately 1% with the addition of season in the models, with a mean decrease in gun catch of 0.24 animals per hunting trip in the rainy season in comparison to the dry season, in both models. No effect of hunter age on gun catch was found (Table 4.5). For trap catch, approximately 11% of trap catch was explained by effort measured as total time, an increase in time spent out of the village of 24 hours resulted in an increase in catch of 0.10 animals per hunting trip. Adjusted total time explained slightly less catch (10%), and an increase in time spent out of the village of 24 hours resulting in an increase in catch of 0.14 animals per hunting trip. Hunter age was retained in both models but had very little effect on the variance in total catch explained and no effect of season was detected in either model (Table 4.5).

Table 4.3 Minimum adequate models for individual hunt catch, from hunter follows, as a function of effort measures and covariates. Effect sizes (E) and significance levels of effort measures (p) and covariates are indicated

Catch model	Effort measure	Intercept	Hunting effort	Dog	Age	Season	Party size	Model statistics
Total	Hunt duration	E=0.28, $p=0.2$	Est=0.14, $p<0.0001$		ns	ns	E=-0.12, $p=0.07$	$R^2=0.11, F_{2,222}=15.42, p<0.0001$
Total no covar.	Hunt duration	E=0.003, $p=0.9$	E=0.14, $p<0.0001$					$R^2=0.11, F_{1,223}=29.53, p<0.0001$
Gun	Hunt duration	E=-0.69, $p=0.03$	E=0.20, $p<0.0001$	ns	ns	ns	ns	$R^2=0.23, F_{1,54}=17.6, p=0.0001$
Trap	Hunt duration	E=0.12, $p=0.5$	E=0.08, $p=0.002$		ns	ns	ns	$R^2=0.04, F_{1,141}=6.52, p=0.01$
Trap	Trap check time	E=0.27, $p=0.2$	E=0.9, $p=0.002$		ns	ns	ns	$R^2=0.04, F_{1,141}=6.21, p=0.01$
Trap	Total trap no.s	E=0.29, $p=0.008$	E=0.003, $p=0.001$		ns	ns	ns	$R^2=0.04, F_{1,141}=7.18, p=0.008$
Duiker	Hunt duration	E=-0.98, $p=0.003$	E=0.11, $p=0.01$		ns	ns	ns	$R^2=0.004, F_{1,141}=1.57, p=0.02$
Duiker	Trap check time	E=-0.37, $p=0.06$	NS		ns	ns	ns	-
Duiker	Total trap no.s	E=-0.86, $p=0.0009$	E=0.005, $p=0.002$		ns	ns	ns	$R^2=0.05, F_{1,141}=7.85, p=0.006$
Duiker	Leg trap no.s	E=-0.89, $p=0.0005$	E=0.005, $p=0.0005$		ns	ns	ns	$R^2=0.07, F_{1,141}=11.14, p=0.001$
Rodent	Hunt duration	E=-0.87, $p=0.0008$	NS		ns	ns	ns	-
Rodent	Trap check time	E=-0.93, $p<0.0001$	E=0.15, $p=0.002$		ns	ns	ns	$R^2=0.04, F_{1,141}=7.45, p=0.007$
Rodent	Total trap no.s	E=-0.75, $p=0.0002$	NS		ns	ns	ns	-
Rodent	Neck trap no.s	E=-0.60, $p<0.0001$	E=0.016, $p=0.002$		ns	ns	ns	$R^2=0.05, F_{1,141}=7.64, p=0.007$

Table 4.3 continued

Catch model	Effort measure	Intercept	Hunting effort	Dog	Age	Season	Party size	Model statistics
Blue duiker	Hunt duration	$E=-1.13, p=0.002$	$E=0.115, p=0.02$		ns	ns	ns	$R^2=0.004, F_{1,141}=1.58, p=0.021$
Blue duiker	Trap check time	$E=-0.78, p=0.007$	NS		ns	ns	ns	-
Blue duiker	Total trap no.s	$E=-1.00, p=0.0003$	$E=0.004, p=0.004$		ns	ns	ns	$R^2=0.04, F_{1,141}=7.56, p=0.007$
Blue duiker	Leg trap no.s	$E=-1.02, p=0.0002$	$E=0.005, p=0.002$		ns	ns	ns	$R^2=0.06, F_{1,141}=10.74, p=0.001$
Blue duiker	Sml leg trap no.s	$E=-0.52, p=0.01$	NS		ns	ns	ns	-
B.t. porcupine	Hunt duration	$E=-2.28, p<0.0001$	$E=0.18, p=0.01$		ns	ns	ns	$R^2=0.04, F_{1,141}=6.28, p=0.01$
B.t. porcupine	Trap check time	$E=-1.88, p<0.0001$	$E=0.18, p=0.03$		ns	ns	ns	$R^2=0.03, F_{1,141}=5.65, p=0.02$
B.t. porcupine	Total trap no.s	$E=-1.29, p<0.0001$	NS		ns	ns	ns	-
B.t. porcupine	Leg trap no.s	$E=-1.29, p<0.0001$	NS		ns	ns	ns	-
B.t. porcupine	Sml leg trap no.s	$E=-1.86, p<0.0001$	$E=0.0082, p=0.005$		ns	ns	ns	$R^2=0.06, F_{1,141}=9.78, p=0.002$

Table 4.4 Minimum adequate models for camp stay catch, from camp diaries, as a function of effort measures and covariates. Effect sizes (E) and significance levels of effort measures (p) and covariates are indicated

Catch model	Effort	Intercept	Effort	Hunter age	Season	Model statistics
Total	Total Time	E=0.90, $p<0.0001$	E=0.0052, $p<0.0001$	E=0.0045, $p=0.010$	ns	$R^2=0.17$, $F_{2,819}=87.48$, $p<0.0001$
Total no covariates	Total Time	E=1.09, $p<0.0001$	E=0.0052, $p<0.0001$			$R^2=0.17$, $F_{1,820}=175$, $p<0.0001$
Total	No. days	E=0.738, $p<0.0001$	E=0.176, $p<0.0001$	E=0.0045, $p=0.011$	ns	$R^2=0.19$, $F_{2,819}=99.05$, $p<0.0001$
Total no covariates	No. days	E=0.937, $p<0.0001$	E=0.177, $p<0.0001$			$R^2=0.19$, $F_{1,820}=198.3$, $p<0.0001$
Total covariates	Hunting time	E=0.865, $p<0.0001$	E=0.024, $p<0.0001$	E=0.0039, $p=0.026$	ns	$R^2=0.19$, $F_{2,819}=94.55$, $p<0.0001$
Total no covariates	Hunting time	E=1.04, $p<0.0001$	E=0.024, $p<0.0001$			$R^2=0.19$, $F_{1,820}=189$, $p<0.0001$
Gun covariates	Total Time	E=1.37, $p<0.0001$	ns	ns	ns	-
Gun covariates	No. days	E=1.076, $p<0.0001$	E=0.13, $p=0.043$	ns	ns	$R^2=0.04$, $F_{1,36}=2.391$, $p=0.013$
Gun covariates	Hunting time	E=0.52, $p=0.0097$	E=0.067, $p=0.0097$	ns	ns	$R^2=0.38$, $F_{1,36}=23.38$, $p<0.0001$
Trap covariates	Total Time	E=0.47, $p<0.0001$	E=0.0052, $p<0.0001$	E=0.01, $p<0.0001$	ns	$R^2=0.19$, $F_{2,737}=86.71$, $p<0.0001$
Trap no covariates	Total Time	E=0.95, $p<0.0001$	E=0.0053, $p<0.0001$			$R^2=0.18$, $F_{1,738}=168.3$, $p<0.0001$
Trap covariates	No. days	E=0.33, $p=0.0069$	E=0.17, $p<0.0001$	E=0.01, $p<0.0001$		$R^2=0.20$, $F_{2,737}=92.23$, $p<0.0001$
Trap no covariates	No. days	E=1.42, $p<0.0001$	E=0.84, $p<0.0001$			$R^2=0.20$, $F_{1,738}=181.3$, $p<0.0001$
Trap covariates	Hunting time	E=0.45, $p=0.00027$	E=0.02, $p<0.0001$	E=0.01, $p<0.0001$	ns	$R^2=0.19$, $F_{2,737}=87.59$, $p<0.0001$
Trap no covariates	Hunting time	E=0.91, $p<0.0001$	E=0.024, $p<0.0001$			$R^2=0.19$, $F_{1,738}=173.7$, $p<0.0001$

Table 4.5 Minimum adequate models for hunting trip catch, from weekly interviews, as a function of effort measures and covariates. Effect sizes (E) and significance levels of effort measures (*p*) and covariates are indicated.

Catch model	Effort	Intercept	Effort	Hunter age	Season	Model statistics
Total covariates	Reported time	E=0.53, $p<0.0001$	E=0.005, $p<0.0001$	E=0.004, $p<0.0001$	ns	$R^2=0.22, F_{2,3992}=576.7, p<0.0001$
Total no covariates	Reported time	E=0.68, $p<0.0001$	E=0.0047, $p<0.0001$			$R^2=0.22, F_{1,3993}=1153, p<0.0001$
Total covariates	Adjusted time	E=0.53, $p<0.0001$	E=0.006, $p<0.0001$	E=0.004, $p<0.0001$	ns	$R^2=0.24, F_{2,3992}=639.4, p<0.0001$
Total no covariates	Adjusted time	E=0.68, $p<0.0001$	E=0.0061, $p<0.0001$			$R^2=0.24, F_{2,3992}=1279, p<0.0001$
Gun covariates	Reported time	E=0.95, $p<0.0001$	E=0.013, $p<0.0001$	ns	E=-0.24, $p=0.0008$	$R^2=0.08, F_{2,318}=14.71, p<0.0001$
Gun no covariates	Reported time	E=0.85, $p<0.0001$	E=0.012, $p<0.0001$			$R^2=0.07, F_{1,319}=23.33, p<0.0001$
Gun covariates	Adjusted time	E=0.92, $p<0.0001$	E=0.017, $p<0.0001$		E=-0.24, $p=0.001$	$R^2=0.06, F_{2,318}=11.7, p<0.0001$
Gun no covariates	Adjusted time	E=0.83, $p<0.0001$	E=0.016, $p<0.0001$			$R^2=0.05, F_{1,319}=17.62, p<0.0001$
Trap covariates	Reported time	E=0.32, $p<0.0001$	E=0.004, $p<0.0001$	E=0.005, $p<0.0001$	ns	$R^2=0.11, F_{2,3317}=213, p<0.0001$
Trap no covariates	Reported time	E=0.52, $p<0.0001$	E=0.004, $p<0.0001$			$R^2=0.11, F_{1,3318}=422.9, p<0.0001$
Trap covariates	Adjusted time	E=0.31, $p<0.0001$	E=0.006, $p<0.0001$	E=0.005, $p<0.0001$	ns	$R^2=0.10, F_{2,3317}=187, p<0.0001$
Trap no covariates	Adjusted time	E=0.51, $p<0.0001$	E=0.006, $p<0.0001$			$R^2=0.10, F_{1,3318}=373.1, p<0.0001$

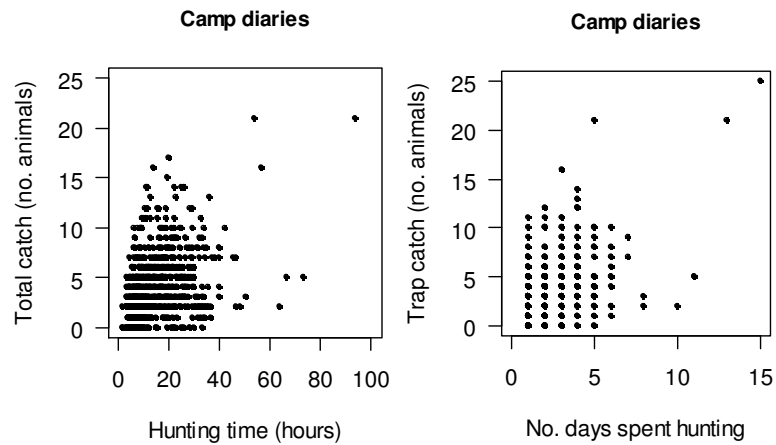
4.4.4 Summary of catch-effort standardisation analyses

The results of these three sets of analyses are now summarised to illustrate the effort measures and covariates that together explain the most variation in catch (Table 4.6, Fig. 4.1). Multiple effort measures are included if they performed equally (within 1%), and covariates are only included if they cause an increase of greater than 1% in the variance explained by the minimum adequate model.

Table 4.6 Summary of models explaining the most variation in catch for the three data sources.

Scale	Catch measure	Effort measure selected	Covariates selected
Follows	Total*	Hunt duration	None
	Gun*	Hunt duration	None
	Trap	Total trap numbers, trap-check time, hunt duration	None
	Duiker	Leg trap numbers	None
	Rodent	Neck trap numbers	None
	Blue duiker	Leg trap numbers	None
	BT porcupine	Small leg trap numbers	None
Camp diaries	Total*	Number of days, hunting time	None
	Gun*	Hunting time	None
	Trap*	Number of days	None
Weekly interviews	Total*	Adjusted time	None
	Gun	Reported time	Season
	Trap*	Reported time	None

*Models with an R^2 above 0.10



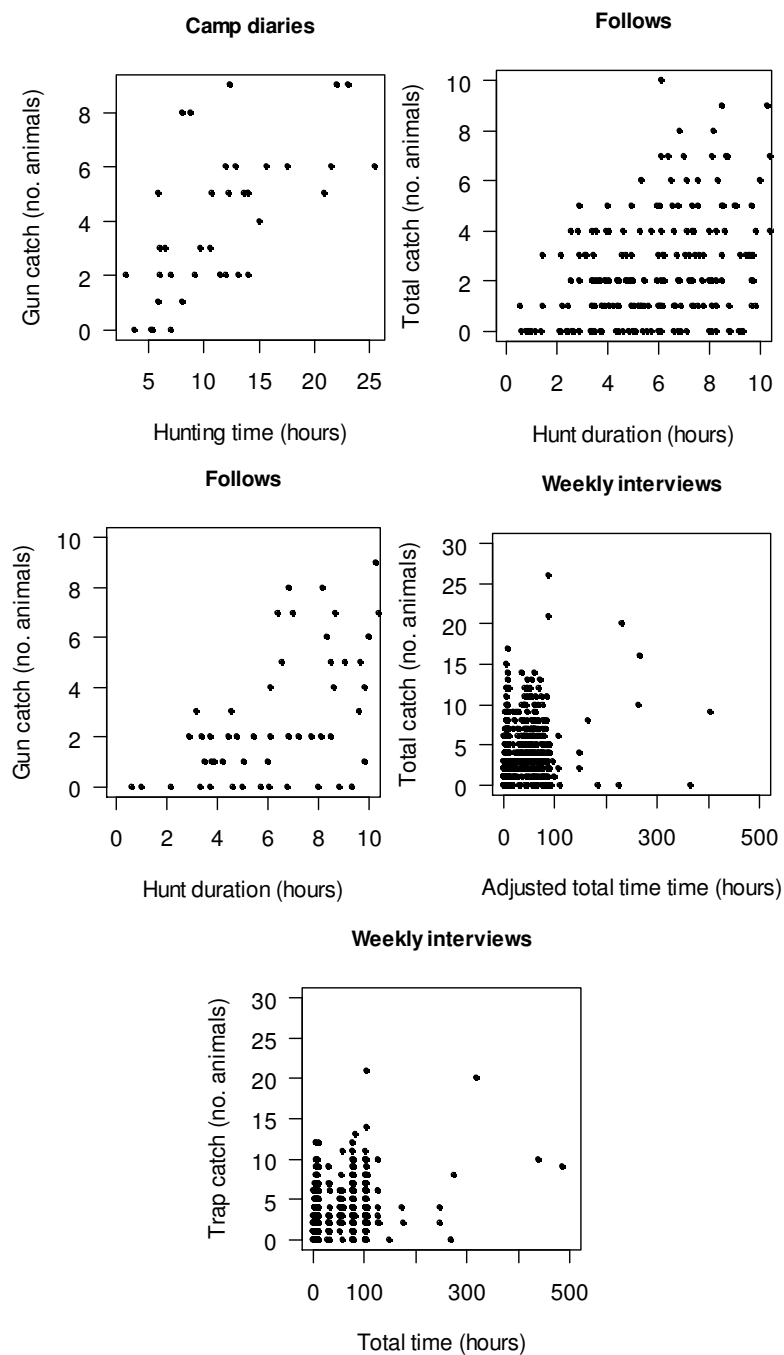


Figure 4.1 Relationship between catch and effort for those models explaining greater than 10% of the total variation in catch, among the three data sources

4.4.5 What explains variance in CPUE between hunts?

This analysis uses aggregate CPUE (all species and methods) calculated using those effort measures identified in the previous analyses to investigate what determines variance in CPUE between hunts, by decomposing variation into spatial, temporal and individual hunter-level components. For camp stay CPUE, spatial, temporal and individual hunter-level components were all significant and retained in the minimum adequate model. Variation due to differences between hunters was the most important and accounted for the greatest proportion of variation in CPUE for camp stays (16%). Changes over time accounted for 8% of variation in CPUE, and differences between sites explained less than 1% of the total variation in CPUE (Table 4.6). In a similar analysis using weekly interview hunting trip CPUE, only temporal and individual hunter-level components were significant and retained in the minimum adequate model. Variation due to differences between hunters was the most important component, accounting for the greatest proportion of variation in CPUE for hunting trips (5%), while changes over time accounted for only just over 1%. The spatial component was excluded during model simplification (Table 4.7).

Table 4.7 Spatial, temporal and individual-level *lmer* variance components of CPUE, for camp stays from camp dairies, and hunting trips from weekly interviews. The percentage of total variation in CPUE explained by each component, and likelihood ratio test results for goodness of model fit are shown.

CPUE	Individual (%)	Temporal (%)	Spatial (%)	Residual (%)
Camp stays (animals/hour hunting time)	16.15 $\chi^2 = 51.30$ $p < 0.0001$	7.74 $\chi^2 = 18.3$ $p < 0.0001$	<1.0 $\chi^2 = 5.32$ $p = 0.021$	76.11
Hunting trips (animals/hour adj. total time)	5.49 $\chi^2 = 114.93$ $p < 0.0001$	1.14 $\chi^2 = 2.78$ $p = 0.095$	ns	92.52

4.5 Discussion

Indices such as CPUE derived from hunting statistics in principle can be used to provide information on levels of species' abundance. However, the use of CPUE is based on the assumption that a linear relationship between catch and effort exists. In reality this may not be the case and is rarely if ever tested. The possible sources of bias that can occur when using different effort measures can be explored and used to give suggestions as to how effort should be quantified (see Table 3.3), however in order to fully establish which effort measures should be used in the calculation of CPUE indices, they need to be tested with catch data. Furthermore, identification of additional explanatory variables that reduce the unexplained variability in catch can be used to adjust or 'standardise' effort so that CPUE observations will more accurately reflect real differences in abundance. Further understanding of the relationship between catch and effort can be obtained by decomposing variance in CPUE into spatial, temporal and individual hunter-level components, allowing recommendations to be made for the design of sampling regimes to obtain estimates of CPUE.

4.5.1 The scale of measurement

The results of this study demonstrate that even after controlling for abundance, for a given level of effort the distribution of catches is highly variable. For the relationship between catch and effort for all species and hunting methods combined, and across data collection methods, effort explained between 11-24% of the total variation in catch. The amount of variation explained and hence the quality of relationship between catch and effort appears to vary with the scale of measurement. When using catch-effort data on individual hunts from hunter follows, effort explained approximately 11% of the variation in catch. However, when the catch-effort information is aggregated into camp stays or hunting trips, then effort explained considerably more variation in catch (19% and 24% respectively), despite the fact that these catch-effort datasets may use somewhat cruder measures of effort. This perhaps surprising result might be due to the highly stochastic nature of hunting (Schmidt et al. 2005), meaning that when using data at a fine scale such as that from individual hunts, the relationship between catch and effort is relatively poor. However at larger scales when data from individual hunts are aggregated some of this variability is reduced and the relationship between catch and effort becomes stronger.

4.5.2 Differences between hunting methods

When catch is separated by hunting method, effort generally explained more variation for gun hunting than for trap hunting. For individual hunts, effort explained only 4% of variation in trap catch and 23% of gun catch, for camp stays effort explained 20% of variation in trap catch and 38% of gun catch. However, for catch-effort data from the largest temporal and spatial scale (hunting trips reported in weekly interviews) this relationship reverses, and more variation in trap catch (11%) is explained by effort than for gun catch (7%). This illustrates the greater difficulties involved in defining a biologically relevant measure of trapping effort at the individual hunt level (see section 3.4.6). When measured at a fine scale such as the individual hunt level, the relationship between catch and effort for trap hunting may be relatively weak. However, once aggregated, the influence of processes acting at this fine level is reduced, resulting in a better relationship between catch and effort.

4.5.3 Selection of effort measures

The fitting of models for multiple effort measures allowed the selection of the measure of effort which explains the most variation in catch and therefore which best equates to the biological impact of hunting.

The hunter follow data set provided the opportunity to explore the suitability of a range of effort measures for specifically quantifying trapping effort, which were not available for the other two data sets. All three effort measures tested explained overall trap catch to the same degree (4%), suggesting that hunt duration can be as good a measure of trapping effort as total trap numbers when aggregate trap catch is concerned. However, in all cases the variation explained in catch for trap caught species was very low. Furthermore for traps, no detectable effect of decreasing efficiency occurred with increasing trap age, and no evidence for trap saturation effects were found. Intuitively one might expect that traps would decrease in efficiency over time, due to deterioration in their component parts with continued exposure to the elements. However, trapping is a dynamic process, with hunters continually augmenting their trap groups with new traps, which might have diluted the effect of trap age when averaged over the entire trap group. This suggests that in order to detect such effects on catch, detailed studies at the individual trap level would be required. Localised depletion would also be expected to have the same effect over time (Hilborn 1992).

The camp diary data set enabled selection between three effort measures: total time spent away from the village, the number of days spent hunting and the total time spent hunting during the camp stay. All three effort measures performed comparably (17-

19% variance explained) in terms of the variation in total catch explained, number of days and time spent hunting performed equally (19%). When broken down by method, of these two measures, time spent hunting was significantly better for gun hunting, and number of days for trap hunting. This is encouraging in terms of facilitating data collection since the number of days on which a hunter went hunting, excluding travelling days, could more easily be recorded than total time spent hunting, when resources for data collection are limited.

Lastly, the weekly interview dataset allowed the direct comparison of economic and biological measures of effort, by comparing models where effort was measured as the total amount of time spent out of the village (an economic measure) with those where effort was also measured as the total time but with an adjustment for the decrease in the percentage of time spent hunting that occurs with distance (a biologically-based measure). The results were mixed with both total time (gun catch, trap catch) and adjusted total time (total catch) explaining the most variation in catch for different models, but in all cases the differences in the amount of variation explained were small (1-2%). These results suggest that total time, even though it is effectively an economic effort measure, may be sufficient to quantify effort at these larger scales.

4.5.4 Covariates for standardisation

I also investigated the effect of a number of covariates on the relationship between catch and effort: hunter age, season, and where the data were available, the use of a dog and hunting party size. No evidence was found for the presence of a dog influencing the catch obtained for a given level of effort. In this study area, dogs are typically used for hunting mandrills (*Mandrillus sphinx*) or cane rats (*Thryonomys swinderianus*) around agricultural fields, and so the effect may only be seen when considering catch-effort data for those species in isolation. Hunting party size was found to have an influence in only one model, that of total catch aggregated by species and method; however the effect size was extremely small, explaining less than one percent of the variation in catch.

No effect of season was found in any of the follow or camp stay models, but for hunting trips from weekly interview models, season was retained once, in the gun model, where gun catch increased in the dry season, by 0.24 animals per hunting trip, explaining 14% of the total variation in gun catch. Increased gun catch in the dry season has also been previously reported in other studies, and suggested to be due to the greater visibility afforded to hunters in the dry season because of reduced vegetation density (Juste et al. 1995; Oates 1988). In addition, the noise caused by rainfall and the tendency of primates to remain still and wait out periods of rain, makes the detection of primate groups difficult for hunters (pers. obs).

It has been previously shown that hunter skill or efficiency increases with age (Walker et al. 2002), but in this study, even though hunter age was retained in some of the minimal adequate models, the effect was minimal (less than 1%) and so age is unlikely to have a substantial influence over the age range of hunters present. It could be that age is a relatively poor proxy for hunter skill or efficiency, and a different measure is required. One previous approach involves using pair-wise comparisons of exploiters to estimate their relative catching power (Salthaug & Godo 2001). Using such an approach, the catch of hunters hunting in the same place and time could be compared for a given unit of effort, however this would require substantial amounts of data.

The goal of standardisation is to remove variation in catch rate that is not attributable to changes in abundance, however the fraction of overall variation explained by catch-effort standardisation here was disappointingly low, this is also often the case in fisheries (Maunder et al. 2006). Some notable examples include a study on Bluefin tuna catch rates, using 12 variables, found that all had very little (>1%) explanatory effect on observed catch rates (Rodriguez-Marin et al. 2003). Battaile (2004) had more success when standardising CPUE for the Alaska walleye pollock, explaining 31-48% of the variation in catch rates using 7 variables, vessel ID alone accounted for 26-40% of the explained variability, suggesting that differences between individual exploiters can have a considerable influence on the relationship between catch and effort.

4.5.5 Implications for the use of CPUE

Of the factors investigated, encouragingly effort best explained catch in all models. However, the distribution of catches for a given level of effort is highly variable and so the amount of variation in catch explained by effort is low. This is especially so for hunting with traps, and the factors influencing this variability are not readily accounted for, with season, hunter age and hunting party size having little or no effect. This lack of a good relationship between catch and effort is also a problem in fisheries, where distributions of catches for a given effort typically show much greater variability than would be expected on the basis of constant catchability models (Cooke & Beddington 1984; De La Mare 1984)

Although my analyses were conducted in discrete spatial areas as a proxy for constant abundance, it is possible that abundance changed on a finer spatial and temporal scale than that on which I measured. In addition, even if abundance is constant, some species may aggregate at any one moment in a small proportion of their total habitat or territory. In this way prey behaviour can lead to catchability coefficient changes over time and space even in localised areas of constant abundance, making CPUE even more stochastic (Cooke & Beddington 1984). Further work on catch-effort standardisation might therefore benefit from the analysis of CPUE data based on even finer temporal and

spatial scales, and the investigation of other variables, such as the weather conditions on the day of the hunt, and particularly from obtaining a measure of relative hunter skill or catching power.

Much attention has been given to the lack of a good catch-effort relationship (Maunder et al. 2006), and the problems of standardising effort in fisheries (Beverton & Holt 1957; Gulland 1964). Given this past experience, the highly stochastic nature of hunting, and the results of this chapter, it is likely that the catch-effort relationship is by nature highly variable, and even if effort is standardised appropriately much of the variation in catch will remain unexplained (Maunder et al. 2006). This might lead to the prediction of a non-linear relationship between CPUE and abundance (Cooke & Beddington 1984), and the conclusion that CPUE is only able to offer limited information on abundance and for the management of hunting. However, in spite of this, some combinations of catch-effort data, and methods of data collection used here have produced reasonable relationships and so perhaps CPUE information will be correlated with abundance, but only for certain species or methods, or when using data at certain scales.

4.5.6 Variance components of Catch per Unit Effort

For camp stays, spatial, temporal and hunter-level components were all significant in explaining variance in CPUE and were retained in the minimum adequate model, explaining a quarter of the total variance in CPUE. Of these components, differences between hunters explained the most variation, followed by changes over time and lastly differences between sites. A very similar pattern was seen in weekly hunting trip CPUE, with hunters explaining the largest amount of variance. If CPUE were to be a reliable index of abundance then one might predict that the most variation in CPUE would be explained by differences between sites, due to different levels of abundance, and then by changes over time due to localised depletion in a site, and then lastly between hunters. However, my results show exactly the opposite pattern.

This suggests that the CPUE for different hunters can be as or more different in a site of constant abundance, than the CPUE of a single hunter in different sites with varying levels of abundance. Individual hunter-level processes are therefore as important in determining the catch obtained for a given level of effort as prey abundance is, and sampling as wide a range of hunters as possible during data collection is going to be crucial when collecting CPUE data.

4.5.7 Conclusion

CPUE, if validated as a method of abundance estimation, could make a significant contribution to the development of sustainable hunting strategies. Currently it has been little used in tropical forest hunting systems relative to commercial fisheries, and its future potential depends upon prior investigation of the assumptions on which it is based. The aim of this Chapter was to test a frequently made but rarely investigated assumption that catch is proportional to effort, and to select and standardise a measure of effort so that subsequent CPUE indices would most closely reflect abundance. My approach illustrates how the analysis of multiple effort measures can enable the selection of that measure which best explains catch, allowing recommendations to be made for the quantification of CPUE. If a measure of overall or aggregate CPUE is required then using a technique such as weekly interviews to record time spent out of the village may be sufficient. However, if more precise CPUE information is required, for example on a species or higher taxon-specific level, then information on trap numbers and composition might be the most appropriate in order to properly quantify effort. However in some cases less precise measures such as total trap numbers and individual hunt duration, can explain equivalent amounts of variation in catch and so may be more cost-effective when resources are limited. I suggest that sampling CPUE using finer spatial and temporal strata and the investigation of hunter catching power would be beneficial to reducing unexplained variation in catch. However, even if catch and effort data are standardised to remove the impact of all known factors, and the sampling strategy adopted is one that gives us the most precise CPUE estimates, there is still no guarantee that the resultant index will be linearly proportional to abundance. The final step in determining the potential of CPUE as an abundance index will be independent CPUE-abundance validation.

Chapter 5

Hunter reporting of Catch per Unit Effort as a monitoring tool: an evaluation of professional versus locally-based methods

5. Hunter reporting of Catch per Unit Effort as a monitoring tool: an evaluation of professional versus locally-based methods

5.1 Abstract

Growing threats to biodiversity in the tropics mean that there is an increasing need for effective monitoring that balances scientific rigor with practical feasibility. Alternative methods are emerging involving locally-based approaches, which may be more sustainable over time, spatially scalable, allow quicker management decisions and lead to increased compliance and shifts in attitudes towards more environmentally sustainable resource use practices. The crucial consideration is whether such methods have the ability to detect changes in population size or patterns of resource use at sufficient resolution. To date there are few studies that compare the findings of locally-based and professional monitoring techniques or that investigate their power for trend detection. I use information from hunter follows, hunting camp diaries and weekly hunter interviews from a study in Equatorial Guinea to evaluate the ability of locally-based monitoring techniques to provide community-level information on the impacts of hunting. I also investigate the ability of such techniques to detect changes in community-level Catch per Unit Effort (CPUE), and examine the influence of hunter sampling strategy and the sample size of hunts. I show that locally-based methods such as weekly hunter interviews provide accurate quantitative and spatial information on hunter catch and effort. I also show that with realistically achievable sample sizes of hunts, and with the appropriate hunter sampling strategy, this method can reliably detect useful levels of change in community-level CPUE. On the basis of these findings I derive practical guidelines and make recommendations for future field studies wishing to use locally-based methods of monitoring CPUE as a tool for the management of bushmeat hunting. Finally, I discuss the implications of my results for the use of CPUE as an index of abundance for tropical forest species.

5.2 Introduction

There is an urgent need to increase the effectiveness of conservation efforts in the tropics (Achard et al. 2002; Dirzo & Raven 2003; Laurance 1999; Pimm et al. 1995). With the growing threat to biodiversity, the need for, and science behind, monitoring is becoming a dominant theme in conservation biology (Bawa & Menon 1997; Brashares & Sam 2005; Field et al. 2005). This is the case for those working to address single threat processes at a local or national scale, such as that of overexploitation (Bennett et al. 2007), right up to those working at a global level on our international commitments to reducing biodiversity loss (UNEP 2002). We will not know if our local or national management interventions are being successful, or whether our global targets are being met, without robust and repeatable systems for monitoring the changing state of nature (Balmford & Bond 2005; Jenkins et al. 2003)

Ideally, monitoring schemes should allow good spatial and temporal coverage, be scientifically rigorous in design, and sustainable over the timescales necessary (Brashares & Sam 2005). For example, to monitor the impact of harvesting on a species, regular estimates of the size of both the stock available, and the harvested offtake are required (Robinson & Redford 1991); however, in practice this level of monitoring is rarely possible (Rowcliffe et al. 2003). Monitoring of biodiversity and resource use by professional scientists faces a number of challenges. It is often costly and therefore hard to sustain, and can be difficult logistically, technically and analytically (Danielsen et al. 2005). This is especially so in developing countries, where the problems associated with biological monitoring are even greater, while the resources available are even smaller (Brashares & Sam 2005; James et al. 1999; Rowcliffe et al. 2003), severely limiting our ability to carry out long-term monitoring and management (Milner-Gulland & Akcakaya 2001; Rowcliffe 2002).

Reliably demonstrating trends in survey data is notoriously difficult (Field et al. 2005), and poor statistical power and bias may mean that simple monitoring schemes can be a waste of time and precious resources (Legg & Nagy 2006). Equally wasteful are programmes so intensive that they cannot be sustained for long enough or at a spatial scale sufficient to address the questions fundamental to management (Sheil & Meijaard 2007). However, even costly and sophisticated monitoring approaches may not provide appropriate or satisfactory information (Plumptre 2000). In addition many monitoring programmes, even if they provide good information, may be unable to contribute to biodiversity conservation because their findings are not considered legitimate by resource users, or they are ineffective at integrating their results into decision making, therefore precluding the development of a system of adaptive management (Royal Society 2003).

Consequently, there is a necessity to identify a methodological 'middle ground' between the need for scientific rigor and the sustainability of a monitoring system

(Brashares & Sam 2005). Indeed, this topic has been the source of much debate (Danielsen et al. 2003a; Danielsen et al. 2003b; Yoccoz et al. 2001, 2003). In light of these difficulties, alternatives are emerging, including locally-based approaches which encompass participatory monitoring, community-based monitoring, hunter self-monitoring and ranger-based monitoring, amongst others. It has been suggested that such locally-based schemes will be more sustainable over time and more spatially scalable. In addition, management decisions from locally-based schemes are often taken promptly, and such schemes can cause shifts in attitudes towards more environmentally sustainable resource use practices, and so may actually be more effective than professional monitoring in arresting overexploitation and the degradation of natural resources, because resource users are more likely to comply with locally agreed decisions (Berkes 2004; Hackel 1999).

One crucial consideration is whether such locally-based methods have the ability to detect changes in populations or patterns of resource use at a sufficient resolution (Taylor & Gerrodette 1993). However, if carefully designed they should be able to yield results as reliable as those from professional techniques (Gaidet et al. 2003; Yoccoz et al. 2003). In a review of published tests Danielsen (2005), found cautious support for the idea that locally-based methods can identify temporal or spatial variation in biological resources, but that compared with professional methods, variance was often higher, or abundance consistently over or underestimated (Uychiaoco et al. 2005). The key issues are those of accuracy (conformity of a measure to its true value) and precision (the degree to which further measurements will show the same or similar results), which together contribute to the fitness for purpose of a measure (Green et al. 2005). Unfortunately, there are few published studies that compare findings between, or employ parallel use of, locally-based and professional monitoring techniques, although there are some notable exceptions: Darwall (1996); Engel (2002); Ericsson (1999); Greenwood (2003); Hellier (1999).

Other studies have used power analyses to examine how far sampling regimes can be reduced and yet still detect key trends with a statistically acceptable degree of confidence. Brashares (2005) showed using Ghanaian ranger-based wildlife data that survey efforts could be decreased by 25-50% before their ability to detect trends in the abundance of large mammals and hunters was substantially reduced, and that a high spatial intensity of sampling may be more important than high temporal intensity. Hockley (2005) using data from harvested crayfish populations in Madagascar, found that a single community would need to invest at least 300 person days a year in monitoring to have an 80% chance of detecting a population decrease of 20% over five years. Such factors are key determinants of whether locally-based approaches will be accepted by conservation scientists and professionals for improving resource management (Danielsen et al. 2003a). A number of authors have made a call for further comparisons of the findings of

locally-based and professional monitoring (Gavin & Anderson 2005; Jones 2004), and of their cost efficiency (Gaidet-Drapier et al. 2006). This is particularly vital in developing countries where the reality is that in many areas the alternative to the use of such schemes will be no monitoring at all (Danielsen et al. 2005).

One specific type of locally-based monitoring method that might prove useful in developing countries, where rural people meet many of their food and livelihood needs by harvesting wildlife (Pimentel et al. 1997), is that of hunter self monitoring. There is a growing body of literature focusing on monitoring in relation to the sustainability of hunting, evaluating changes in wildlife populations or wildlife utilization over time (Crookes et al. 2005; Fa et al. 2000), space (Fa et al. 2002; Noss et al. 2005; Robinson & Bennett 2004), and in some cases also for use in the development of community based management schemes (Hellier et al. 1999; Noss et al. 2005).

It is in this context that I compare locally-based versus professional monitoring, using Catch per Unit Effort (CPUE) as an index of the abundance of hunted species and hence as an indication of the sustainability of harvest (Hill et al. 2003; Puertas 1999; Puertas & Bodmer 2005; Vickers 1991). Assessing the validity of the assumption that a relationship exists between CPUE and abundance, while crucial to the future use of CPUE, is not my purpose here (see Chapter 6). Instead I aim to assess the accuracy of locally-based versus professional methods of collecting CPUE data, and the power of these methods to detect changes in biological community-level CPUE. I use information from hunter follows (professional – hunting activities observed and recorded by researchers and trained research assistants, requiring a high input of training and equipment), hunting camp diaries and weekly hunter interviews (locally-based – hunting activities reported and recorded by hunters, requiring low training input) taken from a study in Equatorial Guinea to ask the following questions: How accurate are hunters at providing quantitative catch-effort information? How spatially accurate are they at reporting their hunting activities? How do the costs of, and effort required for, data collection vary between methods? What is the minimum sampling effort necessary to reliably detect changes in community-level CPUE using hunter interviews as a locally-based method, and to what degree is this influenced by the sampling strategy adopted? What are the implications of these findings for the cost-effectiveness of monitoring? Finally, I derive practical guidelines and make recommendations on the use of locally-based methods using hunting catch-effort data to assess hunting impacts, so that future studies may obtain the most reliable measures of CPUE, and so make the best use of limited conservation resources.

5.3 Methods

5.3.1 Study location

This study was carried out in the village of Midyobo Anvom in the Centro Sur Province of Rio Muni, mainland Equatorial Guinea (1°20N, 10°10E), from January 2005 until March 2006. The village of Midyobo Anvom is 180 kilometres by unpaved road from the mainland's capital Bata, and is one of the most remote communities in mainland Equatorial Guinea (Fig. 2.1). Midyobo Anvom has a population of approximately 150-200 people, who practice shifting agriculture and hunting, and who have little to no access to alternative livelihoods or food sources. For further details on habitat, climate and the development of bushmeat hunting in this area see section 2.3.1, and for further details on the hunting system see section 3.3.2.

5.3.2 Professional methods

Hunter follows were conducted to obtain data on true hunting catch and effort, using a Handspring Visor PDA with Magellan GPS attachment and a customised data collection programme written in CyberTracker (Steventon 2002). Follows were conducted by myself or a local research assistant. A total of 225 hunts were followed, of which GPS positions were captured for 138 (due to the difficulties of obtaining GPS readings under forest cover). For further details on this method, and for information on sample sizes and scheduling see section 3.3.3.

5.3.3 Locally-based methods

Two locally-based methods of catch-effort data collection were used: camp diaries and weekly hunter interviews. Camp diaries were kept by a single hunter in each of the hunting camps in use during the study period, providing detailed information on all hunting activity that occurred in the hunting camp each week, including the duration of hunts and all animals captured. For further details on this method see section 3.3.4.

The second method of weekly hunter interviews involved all hunters in the community being interviewed about their hunting activities at the end of each week throughout the study period, reporting catch and effort information for all of their hunting trips that week. A detailed map of the community and the surrounding area was constructed using participatory mapping (Chambers 1994), and divided into numbered zones to aid hunters in the identification of hunting locations during interviews (see Appendix 8.2). Hunting locations were reported by hunters indicating the main zone out of those used during the hunt. For further details on this method see section 4.3.4.

During such interview techniques, informants may seek to bias their reported activities. Such bias may operate in either direction depending on informant motivations, for example under-reporting to hide illegal hunting activities (Jones 2004; Sheil & Wunder 2002), or over-reporting to impress other community members. However, I am confident that this was not the case during my study and that hunters were honestly reporting their hunting activities. Interviews were done in private as far as possible to limit any effects of hunters inflating catch and effort while in front of their peers, and hunters were referred to by code to preserve their anonymity.

5.3.4 Sampling efficiency

The sampling efficiency of a method depends on the time required, people involved and cost required to cover a sample area, or sampling period (Gaidet-Drapier et al. 2006). In order to compare the sampling efficiency of the three CPUE data collection methods used in this study, I calculate the effort (in people hours) and financial cost involved in obtaining catch-effort data for a sample unit, the hunting trip.

5.3.5 Statistical analyses

All analyses were performed within the R statistical package version 2.5.1 (R Core Development Team 2007). To assess the quantitative accuracy of hunter reporting as a locally-based method I compared matched data from reported hunting catch and effort in camp diaries and weekly interviews against the true catch and effort observed on follows of the same hunting trips. To allow comparison of catch and effort with follows, only hunting trips of a single day in length from camp diaries and weekly interviews were used. For comparisons of mean effort, t-tests were used, and for mean catch, Wilcoxon rank sum tests were used due to non-normal errors (Crawley 2007).

To assess the spatial accuracy of hunter reporting, I compared matched data on true hunting locations recorded during follows with reported hunting locations from weekly interviews for the same hunting trips. The true and reported locations were compared in a GIS (Geographical Information System) using ArcGIS 9.1. (ESRI 2006). The participatory map was digitised and geo-referenced (see Appendix 8.2), and the distance to the centre of each zone reported in the weekly interviews from the village was calculated. For each follow, the distance to the greatest number of GPS points from the village was calculated. The distance between true and reported locations was then calculated, and a Pearson's product-moment correlation test was used to test if the two distances were correlated.

To investigate the ability of locally-based methods to detect changes in biological community-level CPUE, and to determine the influence of sample size and sampling strategy on change detection, I used weekly hunter interview data to simulate three

different hunter sampling strategies from the full data set of 3995 hunting trips available, using code written in R. The three sampling strategies were Random, Minimum and Maximum hunter sampling.

- Random hunter sampling - a random sample of the desired size was taken from the full data set of hunts available.
- Minimum hunter sampling - hunters were randomly selected and all hunts of these hunters were added to the sample until the desired sample size was met. This strategy would be equivalent to selecting a small number of hunters for sampling on a regular basis.
- Maximum hunter sampling - hunters were randomly selected and the number of their hunts that were added to the sample was determined by a moving average (the number of hunts still required to meet the sample size, divided by the number of hunters left in the data set to sample). This strategy would be equivalent to sampling every available hunter.

The sample sizes of hunts were from 20 to a total of 3980 hunts, in increments of 20 hunts, sampling was without replacement for all strategies. For each strategy mean CPUE was calculated for each sample, at each sample size and the bootstrap function *boot* from the *boot* package (Ripley 2007) was used to resample (2000 times) to obtain an estimate of the coefficient of variation (CV) of the mean CPUE estimates.

The equation given by Plumptre (2000), to calculate power for a given CV and detectable difference,

$$2.8 = R / C \sqrt{1 + (1 + R)^2}$$

where R is the % detectable change and C is the coefficient of variation, was used to calculate the detectable differences (% declines) at each sample size, for each hunter sampling strategy, with a power of 80% and with $\alpha = 0.05$. It is not possible to solve for the detectable difference R, but the *optimise* function in the R statistical package can be used to solve it iteratively.

5.4 Results

5.4.1 Do hunters accurately report catch and effort?

A comparison of catch and effort from hunter follows with that recorded in weekly interviews and camp diaries for the same hunts, shows that reported catch and effort are correlated with true catch and effort (Table 5.1). However both locally-based methods overestimated effort, and one overestimated catch. Weekly interviews significantly overestimated effort by 1.05 ± 0.31 hours ($n=69$), or 15 % (Paired t-test, $t=-3.41$, $df=68$, $p=0.001$). Catch was also overestimated, by 0.33 ± 0.28 animals ($n=69$), or 15%, but this difference was not significantly different from zero (Wilcoxon rank sum test, $W=505$, $p=0.19$). Camp diaries significantly overestimated effort by 0.82 ± 0.23 hours ($n=65$) or 17% ($t=-3.49$, $df=64$, $p=0.0009$) and catch was also significantly overestimated, by 0.60 ± 0.20 animals ($n=65$), or 47% ($W=141.5$, $p=0.007$).

Table 5.1 Pearson's product-moment correlations between catch and effort from hunter follows as a professional method, and the two locally-based methods, weekly interviews and camp diaries.

Locally-based method	Catch or Effort	<i>r</i>	df	<i>p</i>
Weekly interviews	Catch	0.47	63	<0.0001
Weekly interviews	Effort	0.69	63	<0.0001
Camp diaries	Catch	0.32	67	0.008
Camp diaries	Effort	0.33	67	0.006

5.4.2 How spatially accurate are hunters?

A comparison of the true distance of hunting locations recorded on hunter follows, with that reported in weekly interviews for the same hunts, shows that reported distances are strongly correlated with the true distances from the village (Pearson's product-moment correlation, $r=0.83$, $df=136$, $p<0.0001$) (Fig. 5.1). There is a tendency to overestimate distance (Paired t-test, $t=-7.91$, $df=137$, $p<0.0001$), however the mean difference between reported and true distance was only 1.66 ± 0.18 km so hunters show a high degree of accuracy in reporting the location of their hunting activities (Fig. 5.2).

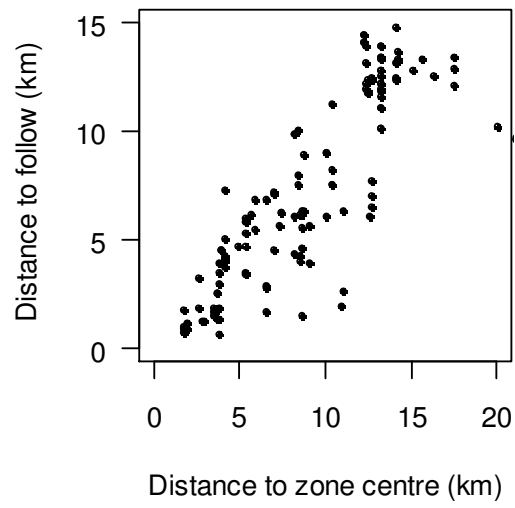
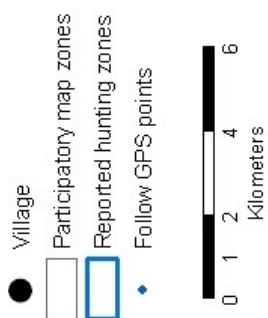


Figure 5.1 Relationship between reported and true distances to hunting locations



Figure 5.2 Map showing the true spatial distribution of hunting activity as recorded from hunter follows in relation to the reported spatial distribution of hunting activity hunting as recorded from weekly hunter interviews. Hunting zones from the participatory village map are colour coded and GPS positions from hunter follows that were reported to have occurred within those zones are coloured correspondingly. The location of the community of Midyobo Anyom, and of the hunting camps are also indicated.



5.4.3 Can changes in community-level CPUE be detected?

The power to detect a decline in CPUE depends strongly on the Coefficient of variation (CV) of the CPUE estimates, and therefore on sample size (Fig 5.3a). Sampling strategy further influences the CV for a given sample size of hunts. Random and Maximum hunter strategies performed comparably in terms of their CV for a given sample size, whereas the CV produced by the Minimum hunter strategy was almost double that of the other two strategies, at all sample sizes.

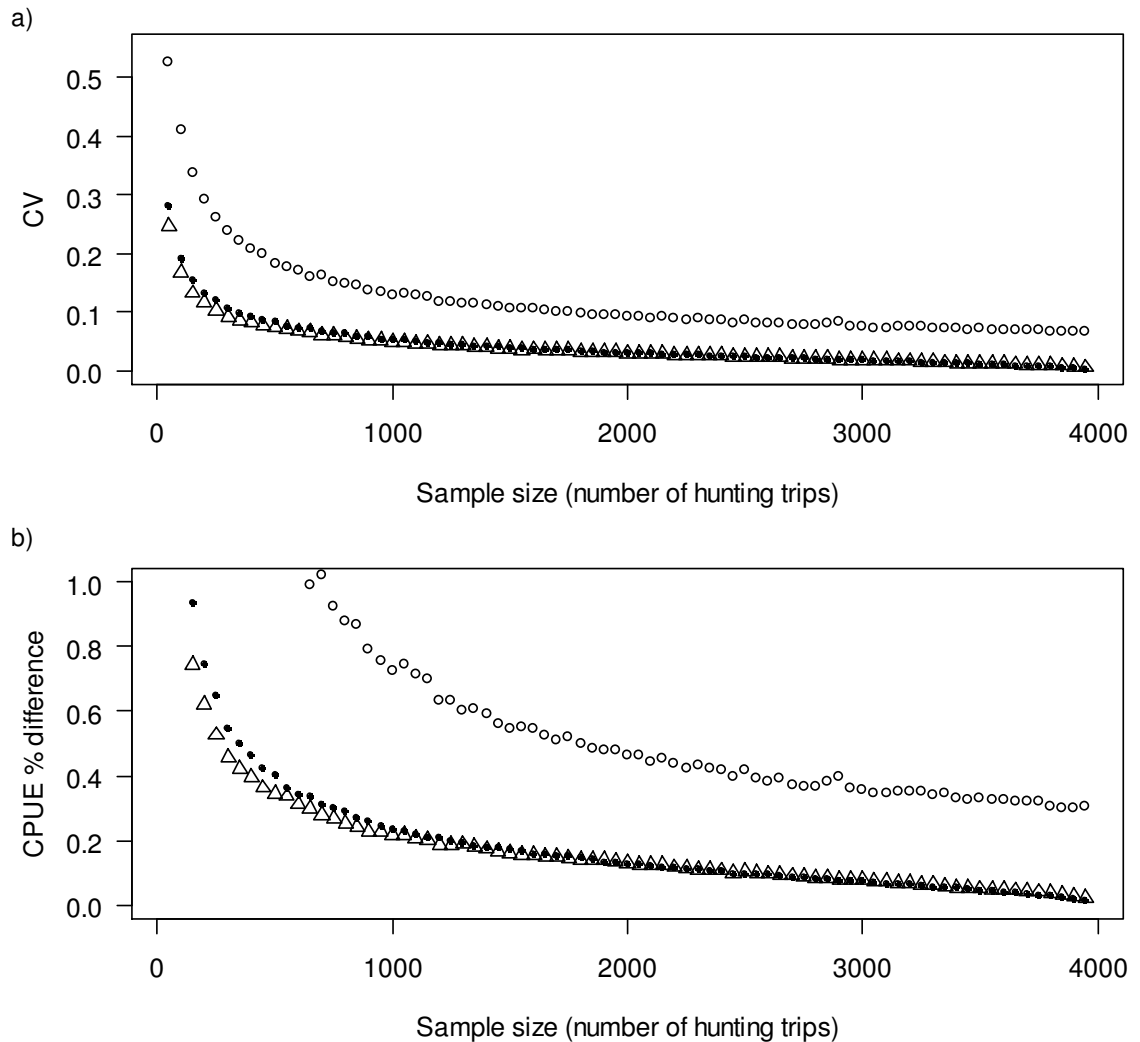
The sampling strategy adopted influences the magnitude of statistically significant change that is detectable for a given sample size of hunts. With a Random hunter strategy, in order to detect a 20% decline in community level CPUE, and hence overall prey abundance, then just over 1000 hunts need to be sampled per year. As sample size decreases, the magnitude of the change detectable in CPUE increases, so that if a sample size of only 500 hunts is possible then a change of approximately 40% will be detected, and with a sample size of 250 hunts then only a change of 60-70% will be detected (Fig. 5.3b).

The Maximum hunter strategy and Random hunter strategy perform almost equally well, with the Maximum hunter strategy detecting a marginally smaller percentage change for the same sample size. This suggests that random sampling of hunters is a sufficiently precise strategy to adopt for estimating mean CPUE at the community level.

In terms of the magnitude of change required for reliable detection, for a given sample size of hunts, the Minimum hunter strategy performs considerably worse than both the Maximum and Random strategies. For a sample size of 1000 hunts, a change of 20% can be detected with a Random or Maximum hunter strategy, but for the same sample size with a Minimum hunter strategy, a change of 70-80% is required in order to be detected, and changes below 35-40% will not be detectable with 80% power.

These results suggest that if Maximum or Random hunter sampling strategies are adopted, a sample size of 1000 hunts per year appears to be sufficient to detect useful levels of change in mean community level CPUE. However, if the detection of smaller changes is required then sampling effort must be considerably increased, for example in order to detect a 10% change between years with 80 % power then sampling effort must increase to around 3000 hunts per year.

Figure 5.3 Effect of sample size and hunter sampling strategy on a) the coefficient of variation (CV) of mean community-level CPUE estimates, and b) the percentage detectable difference in mean community-level CPUE estimates (● Random, ○ Minimum and △ Maximum hunter strategies).



5.4.4 How cost effective, and time efficient are locally-based methods?

The locally-based and professional methods used in this study differ considerably in both the effort required and the cost involved in collecting catch-effort data for a hunt. In terms of the effort involved, the professional technique requires 6 person-hours to collect data on a single hunt, whereas, camp diaries can collect data on 153 hunts in this time, and weekly interviews even more at 240 hunts. A similar pattern is seen in the cost of data collection, a single hunt costs \$9.36 to collect data using a professional method, and for the equivalent cost, information on 50 hunts can be recorded using camp diaries, or on

94 hunts if using weekly interviews. These figures exclude the cost of any equipment, so are likely to underestimate the true cost of the professional method.

The three methods can be compared in terms of the cost and effort required to achieve the minimum sample size of 1000 hunts per year, in order to detect useful levels of change in mean community level CPUE. Using the professional method of hunter follows, 6000 person hours would be required to sample 1000 hunts, at a cost of \$9360 per year. Locally based methods are far more cost and time efficient. If using camp diaries for data collection, 39 hours would be required at a cost of \$200, and if using weekly hunter interviews, then 25 hours would be required at a cost of \$100. These figures illustrate the huge differences in resources required by professional and locally-based methods (Table 5.2).

Table 5.2 Summary of the costs and effort involved in using professional and locally-based CPUE monitoring techniques. Key figures of cost effectiveness and effort efficiency are highlighted and further information is given on data type and coverage, collection frequency and materials.

Method	Hunter follows	Camp diaries	Weekly interviews
Who compiles the data?	Researchers and trained full-time research assistants (RA)	Hunters from the community (part-time RA)	Hunters from the community (part-time RA)
What is monitored?	Recorded directly, data on exact catch, effort, location and method	Recorded in camp at end of day, data on approximate catch, effort, location and method	Reported in village at end of week, data on approximate catch, effort, location and method
Spatial scale. Total size of area monitored (km ²)	Area used by a single hunter, < 5km ²	Hunting camps only, Approx. 30 km ² per camp. Hunting around the village not included so possible that not representative	Whole community hunting catchment area of approx. 300km ²
Interval between bouts of data collection	Daily	Daily	Weekly
Number people surveyed per data recording bout	1 hunter	All hunters in a camp, mean 6.38 ± 1.46 (hunting 4 times a week)	All hunters in community, approx. 80 hunters (hunting 4 days a week)
Time costs for one recording bout (person-hours)	1 observer per follow, Average duration 5.9 \pm 0.2 hours	1 hunter per camp, Approx. 15 minutes per day each	2 hunters for the community, Approx. 4 hours per week each
Effort to sample one hunt (person-hours)	6 hours/hunt	2.35 minutes/hunt	1.5 minutes/hunt
Payment to community members giving data ¹	1,000 CFA (2.08 USD) per hunter followed	None/occasional small gifts	None/occasional small gifts
Payment to community members collecting data ¹	Salary Approx. 17,500CFA (36.4 USD) 5-day working week.	Salary Approx. 2,500CFA (5.2 USD) week	Salary Approx. 7,500CFA (15.6 USD) week
Total cost to sample one hunt	9.36 USD	0.20 USD/hunt	0.10 USD/hunt
Cost for yearly monitoring (detect 20% decline)	9,360 USD	200 USD	100 USD
Time for yearly monitoring (detect 20% decline)	6000 hours	39 hours	25 hours
Additional materials required	PDA with GPS, computer, electricity supply	Pen and paper	Pen and paper

¹ 1000 CFA = 2.08 USD <http://www.xe.com/ucc/convert.cgi>

5.5 Discussion

5.5.1 Quantitative accuracy of locally-based methods

Interviews with local people are frequently used to investigate biological trends, for example in the abundance of endangered species (Anderson et al. 2007), or to quantify levels of resource use (Jones et al. 2006; Ndanyalasi et al. 2007; O'Brien et al. 2003). But the ability of locally-based techniques such as interviews to provide accurate information is rarely tested.

A comparison of true catch-effort data obtained using the professional monitoring technique of hunter follows, with catch-effort data recorded from locally-based methods for the same hunts, revealed a number of differences. Both locally-based methods overestimated effort, while one, the camp diaries, also overestimated catch. In terms of effort, both of the locally-based methods performed almost equally well and the overestimation of effort in both cases was not particularly large. Weekly interviews therefore appear to be the more accurate of the two locally-based methods, since only effort and not catch is overestimated. Consequently, management decisions based on CPUE estimates from weekly interviews will be precautionary (Cooney 2004; Maxwell & Jennings 2005). The greater inaccuracy of camp diaries compared to weekly interviews in reporting catch, suggests that hunters living and working together in close proximity within the same hunting camp are more reluctant to reveal true information on their hunting activities to each other than they are with other hunters in the village. This misreporting could be due to a greater pressure to appear as if they caught more within smaller peer groups of hunters than within the village as a whole. Knowledge of the motivations of resource users such as this could be important in the design of monitoring schemes (Jones 2004; Jones et al. 2006).

Existing investigations of the accuracy of interview data have yielded mixed results. In a study evaluating interview methods for assessing the extent of forest product use in three Amazonian villages Gavin (2005) found that interviews were successful at identifying the majority of species used, but not at determining the quantities collected. Other studies have found that resource use can be well described by interview data but that some degree of overestimation occurs. In a study of crayfish and firewood harvesting activities in a village in eastern Madagascar, Jones (2004) found a general tendency for informants to overestimate both their involvement in harvesting activities and the size of their catches or collections. Such overestimation of resource use has also been shown in marine systems: Lunn (2006) found that fishers consistently over reported both catch and effort when verified with direct observations from researchers on fishing trips.

A certain amount of inaccuracy in reporting is to be expected with the use of locally-based methods, even when participants are reporting to the best of their abilities

and are not actively hiding or biasing information. In addition to this, the variability between true and reported catch and effort may be influenced by resource users having preconceptions or conflicts of interest (Danielsen et al. 2005). In this study, if misreporting was due to the desire of hunters to keep information on good hunting areas to themselves, rather than share information with fellow hunters, then one might have expected to see an underreporting of catch. While this was not the case here, withholding information due to competition for the best hunting locations might occur in other sites and so the direction of any bias should not be assumed. If hunters had preconceptions about, or felt a conflict of interest with, the objectives of the study, then catch could conceivably be misreported. For example, if a hunter feared restrictions, he might underreport his catch if he believes that it is better to appear not to be catching too many animals. If resource users are subject to such pressures and do not honestly report their harvesting catch and effort, then the resulting information will be biased and of limited use for monitoring. The use of locally-based methods such as interviews to collect data on harvesting activities should therefore be accompanied by consideration of the wider context and possible motivations of resource users (Jones 2004).

5.5.2 Spatial accuracy of locally-based methods

In addition to quantitative accuracy, the spatial accuracy of catch-effort reporting is also important if locally-based methods, such as the hunter interviews used here, are to be used for monitoring. The distances of reported hunting locations (from the village) were strongly correlated with the distance of true hunting locations. These results suggest that hunters are generally good at reporting the distance travelled, but alone this does not indicate that they are spatially accurate. For example, they may report a hunting location at a similar distance to that of the true location, but in the opposite direction. My results suggest that this is not the case here, and that only a relatively small amount of error exists between reported and true hunting locations. These results are particularly encouraging, since without reliable information on the area from which animals are taken, assessing the degree of sustainability of a harvest is extremely difficult (Milner-Gulland & Rowcliffe 2007). In addition, if the management of hunting is to involve some form of spatial control or zonation, for example using a mosaic of hunted and unhunted areas (McCullough 1996), then accurate spatial reporting by hunters is essential. To date, very few studies have investigated the feasibility of obtaining accurate spatial information using locally-based techniques, although see Jones (2004). My results provide further support to the findings of Jones (2004), that locally-based monitoring techniques such as interviews can give an accurate representation of the spatial distribution of harvesting effort.

5.5.3 Power to detect changes in community-level CPUE

Given that differences between hunters have been found to be responsible for explaining the largest amount of variation in CPUE (section 4.3.5), it is perhaps not surprising that for a given sample size, the Maximum hunter strategy, very closely followed by the Random strategy, performed the best in terms of the percentage change in CPUE detectable for a given sample size. This illustrates the importance of sampling a wide range of hunters when monitoring community-level CPUE, and suggests that if participation rates by hunters in community monitoring programmes is low then only very large changes in CPUE will be reliably detected (Noss et al. 2005).

This finding is likely to be generalisable to other harvesting systems that involve a large number of individual harvesters, where individuals differ greatly in their harvesting ability and where the exploited area is relatively large. The power of a test is the probability of rejecting the null hypothesis when it is false (Taylor & Gerrodette 1993), which in the case of this study is that community level CPUE is not declining. As discussed by Hockley (2005), the power to detect a decline in CPUE depends strongly on the CV of the CPUE estimates, which in turn can be affected by the strategy for data collection. If the CV is such that the time required to detect a significant decline, or the degree of change in mean community level CPUE required for detection is very large, then management action may not be initiated until a previously unexploited population has become severely depleted, or a small and declining population has become extinct (Wade 1998).

5.5.4 Cost effectiveness and time efficiency of locally-based methods

While the accuracy and precision of results are often compared in the selection of monitoring methods, little attention is generally paid to cost effectiveness, a crucial criterion given the frequent presence of budgetary and logistical constraints (Gaidet et al. 2003; Gaidet-Drapier et al. 2006). My results illustrate that large differences can exist between monitoring methods in terms of both the financial cost and in the effort required for data collection. Using locally-based methods of data collection, a far larger quantity of catch-effort information can be collected for the equivalent time and cost. In this study area, given such large differences in the resources required to monitor an individual hunt, locally-based methods would have to be extremely inaccurate to make the use of professionally based methods cost-effective. It should be noted that in this study community members were paid to act as data collectors, but in order for any monitoring scheme based on these methods to be sustainable in the longer-term then incentives for

participation would ideally be the increased sustainability of bushmeat harvest rather than short-term financial motivations.

5.5.5 Conclusion

I have shown that locally-based methods of collecting catch-effort data such as interviews can be sufficiently accurate, both quantitatively and spatially, but should be compared with professional methods to reveal the magnitude and direction of any biases that may be present (Chapter 3). Tradeoffs are often required between accuracy, precision and the resources available for monitoring. However, here I have shown that locally-based methods, such as interviews, allow catch-effort data for a whole village to be surveyed in a matter of hours and at very low cost, allowing far greater temporal and spatial coverage and giving a better indication of hunting activity and impacts at a landscape scale. Camp diaries did not offer any increased accuracy for the additional investment in data collection, they gave less spatial coverage than weekly interviews and did not incorporate information on hunting activity around the village. While hunter follows provide a true measure of catch and effort, unless locally-based methods are extremely inaccurate the huge increase in resources required by this method may be prohibitive for long-term and large-scale monitoring. Hunter follows are extremely time consuming and without considerable effort spent in the field will generate only small sample sizes which will reveal very little about wider community-level changes in CPUE. Hunter follows also require expensive equipment and considerable technical ability on behalf of the data collector, which might limit the involvement of some resource users.

Monitoring schemes can often be expensive on large scales, and it has been stated that when combined with tight financial constraints, statistical power is often the first casualty (Field et al. 2005). However, I demonstrate that this is not always the case and that using a locally-based method, declines in community level CPUE of a reasonably small size were detectable with a high degree of power. Overall, this suggests that CPUE from weekly hunter interviews could provide a sufficiently accurate and precise locally-based method for both the monitoring and management of bushmeat hunting. Noss (1999) suggested that the use of CPUE would be most useful for generating information on longer term trends; my results suggest that regular annual assessments using this method would also be feasible.

These are encouraging results for the development of CPUE as a monitoring tool. Another benefit of this locally-based approach is that such a scheme would encourage hunters to become more involved in analysing the impact of their hunting and managing their wildlife resources (Bodmer & Robinson 2005). Additionally, the method lends itself to being scaled up, facilitating its use for large-scale wildlife monitoring programmes (Pollock et al. 2002). The concurrent use of similar techniques may prove particularly

useful, for example looking simultaneously at the structure of hunting offtake using prey profiles (Rowcliffe et al. 2003) to provide information on biological community-level responses to hunting that could complement CPUE information.

The aim of this study was to determine whether locally-based methods could be suitable for the monitoring and management of bushmeat hunting. However in order for a locally-based monitoring scheme to work, the benefits of monitoring, for example in terms of future harvests, must be greater than the costs of conducting the monitoring for the communities concerned, and the cost of making management decisions. CPUE as a method is particularly useful since it provides information on trends in the abundance of exploited species, but it also provides information on resource use behaviour and hunting returns, which provides a means of estimating the value of the harvest to local people and therefore the cost of imposing restrictions (Godoy et al. 2000). Another question that has not been answered in this study is therefore, 'will it be worthwhile communities investing in monitoring'? Within this context, even if communities are able to monitor the impacts of their hunting practices, if the results suggest that reductions in hunting are required, this might involve significant economic costs (Bodmer & Lozano 2001; Hockley et al. 2005). Without access to alternative food and livelihood sources, these costs may prevent management action from being taken (Hackel 1999).

Chapter 6

The relationship between hunter Catch per Unit Effort and bushmeat prey species density

6. The relationship between hunter Catch per Unit Effort and bushmeat prey species density

6.1 Abstract

The use of Catch per Unit Effort (CPUE) as an index of abundance has been suggested as a technique for monitoring bushmeat prey species. However, while the use of CPUE is based upon the assumption that it is proportional to population size, a long history of experience from fisheries research suggests that this assumption is not always valid. The nature of the relationship between CPUE and abundance therefore needs to be validated, using un-biased data on CPUE and independent abundance estimates. I use information on bushmeat prey species density from line transect methods, and hunting statistics in multiple sites, taken from a study in Equatorial Guinea, to provide the first test of this assumption in a bushmeat harvesting system. My analyses show encouraging support for the potential of CPUE as an index of abundance, suggesting the existence of a proportional relationship between CPUE and density for some species. Large amounts of error in CPUE and line transect density estimates can make investigation of the relationship problematic and so substantial amounts of temporally and spatially stratified data are required. Reconciling such data needs, with the use of the biologically relevant measures of hunting effort can be difficult, but locally-based methods of CPUE data collection, such as hunter interviews, can offer a practical solution. Further studies of this relationship in additional species, in alternative sites, and of the relationship between community-level CPUE and abundance are now needed to fully assess the utility of CPUE as a monitoring tool for the management of bushmeat harvesting.

6.2 Introduction

Estimation of abundance is an important area of research for population biology and for the management of many exploited species (Jones & Coulson 2006; Novak et al. 1991). However, data on abundance can be expensive, time consuming and difficult to obtain, which can limit our ability for long-term monitoring and management. In fisheries research, Catch per Unit Effort (CPUE) is commonly used as an index of abundance (Hilborn 1992; Quinn 1999). This use of catch-effort data is based on the observation that the size of the catch from an animal population typically increases when either abundance or harvesting effort increase (Seber 1992). So in principle CPUE can be used to detect declines in the same way as abundance itself. It therefore represents a simple and attractive alternative method for measuring the impacts of exploitation. Indeed, the use of hunting statistics has been suggested as a technique to quantify the impact of bushmeat hunting on tropical forest species (Wilkie & Carpenter 1999). While techniques such as capture mark recapture (White & Burnham 1999) and line transect methods (Thomas 2006) have been greatly developed in recent years, the concept of CPUE has received little attention and been relatively little used in terrestrial systems (Dupont 1983), except for the management of some harvested ungulate populations in northern Europe and northern America (Laake 1992; Novak et al. 1991; Weckerly et al. 2005).

The use of CPUE to assess the impacts of hunting on wildlife in the tropics has been very limited to date, but CPUE indices may be particularly useful for this purpose. While line transect methods are feasible in areas of high animal densities, in heavily hunted areas with low densities they become especially problematic due to low encounter rates. Conversely, calculating CPUE is most feasible where hunting effort is fairly high but becomes problematic in areas of low hunting effort because of small sample size (Siren 2004). Tracking the relationship between hunting yield and effort in different locations or over time was first used primarily by anthropologists (Hames & Vickers 1982; Saffirio & Scaglione 1982; Stearman 1990; Vickers 1991), and only more recently by biologists (Auzel 1996; Blake 1994; Hill et al. 2003; Noss et al. 2005; Puertas & Bodmer 2005; Siren 2004).

The CPUE model, despite its long history of use, has a number of shortcomings. Strict proportionality between CPUE and abundance is frequently assumed (Myers & Worm 2003), but it has long been recognized that the assumption that catch is directly proportional to effort may not always be true and that CPUE may not accurately reflect changes in abundance (Harley et al. 2001). A linear relationship might oversimplify the link between CPUE and abundance, due to the influences of exploiter behaviour (Gaertner & Dreyfus-Leon 2004), prey biology (Rose & Kulka 1999), or inappropriate data collection and analysis (Walters 2003). CPUE may change either more (Hyperdepletion) or less (Hyperstability) steeply than abundance, leading to the over- or under-estimation

of population size and therefore problems with the use of CPUE in management regimes (Shelton 2005). It is important to understand the nature of the relationship before relying on CPUE as an indicator of the status of a harvested population.

Validation of CPUE as an index of abundance has rarely been conducted in the fisheries due to the difficulty of obtaining fishery-independent estimates of abundance (but see Connell (1998), Harley (2001) and Richards (1986)). Where validation has been possible, CPUE has often been found to be an inadequate index of abundance (Cooke & Beddington 1984), and strong evidence has been found for hyperstability (Harley et al. 2001). Despite this background, and the suggestion that indices using hunting statistics should be calibrated before use (Seber 1992), few studies have tested these CPUE indices against more accurate abundance estimates. Those that have show mixed evidence: in some cases CPUE has correctly revealed trends in harvested populations (Lancia et al. 1996), while in others no correlation between CPUE and either density (Bowyer et al. 1999a), or other indices of abundance (Pettorelli et al. 2007) has been found.

While CPUE may represent a useful tool for the estimation of the abundance of exploited tropical forest species, its troubled history in the fisheries literature demonstrates that while simple in concept the realities of applying it in practice are very different. The concurrent use of two techniques, CPUE from fisheries science and line transect surveys from terrestrial ecology, offers an opportunity for the evaluation of CPUE as an index to prey abundance. I use this approach to address the following questions: Does prey species density and CPUE vary spatially, and if so then does variation in density explain variation in CPUE? Does the relationship between CPUE and abundance follow theoretical predictions, or are deviations from proportionality present? If deviations from proportionality are present then can they be explained by hunter or prey behaviour? And ultimately how useful might CPUE be, as an index of abundance for exploited tropical forest species? If validated, the use of CPUE could greatly facilitate the development of management strategies for sustainable bushmeat hunting, wider management of other game species, and in the provision of estimates of population size for research in population biology.

6.3 Methods

6.3.1 Study location

The fieldwork for this study was carried out in the village of Midyobo Anvom in the Centro Sur Province of Rio Muni, mainland Equatorial Guinea (1°20'N, 10°10'E), from January 2005 until March 2006. The village of Midyobo Anvom is 180 kilometres by unpaved road from the mainland's capital Bata, and is one of the most remote communities in mainland Equatorial Guinea (Fig. 2.1). Its isolation provides both a large hunting catchment area in which to find variation in abundance, and also allows very accurate quantification of spatial and temporal patterns of hunting effort due to the absence of hunters from neighbouring villages. This makes it an ideal site in which to investigate the use of CPUE as an index of abundance. Midyobo Anvom has a population of approximately 150-200 people, who practice shifting agriculture and hunting, who have little to no access to alternative livelihoods or food sources. For further details on habitat, climate and the development of bushmeat hunting in this area see section 2.3.1, and for further details on the hunting system see section 3.3.2.

6.3.2 Line transects surveys

Line transect surveys were conducted to estimate the abundance of a diverse assemblage of mammal species in six sites located within the total hunting catchment area used by hunters of the Midyobo Anvom community. These consisted of one site around the village, and five hunting camps differing in their distance from the village (Table 6.1, Fig. 6.1). The areas of use around hunting camps were established by accompanying hunters on hunting trips. Hunters typically travelled 2-3 km from the camp to place their traps, or with a gun in search of animals, using an area of approximately 30km² around each camp. In each of the survey sites four 2 km line transects were established in order to estimate abundance within this area (Fig 6.1). The six sites were surveyed in three pairs, each pair being surveyed for a period of 3-4 months during the year-long study period. Survey periods for each pair cut across a wet and dry season, and each pair was comprised of a site located near to, and a site located far from, the village (Table 6.1).

Each transect was walked by a team of observers, comprising a research assistant skilled in mammal identification, and myself or a project volunteer skilled in survey methods, once per week during the survey period. Observers recorded all encounters with animals using the line transect methods of White and Edwards (2000) and Buckland et al. (2001). Duikers were surveyed nocturnally, which has been shown to result in higher encounter rates and therefore more accurate density estimates than

diurnal surveys (Payne 1992; Waltert et al. 2006). Nocturnal surveys were conducted using five D-cell Maglite torches to scan for eye-shine reflections, following the methods of Newing (1994).

Table 6.1 Summary of survey site characteristics showing the distance from the village, survey effort, and the survey period.

Site	Distance from village (km)	Day survey effort (km walked)	Night survey effort (km walked)	Survey period
Midyobo Anvom	0	98	29	Nov 05 – Feb 06
Nseng Midyobo	4.1	160	20	Jul 05 – Oct 05
Esong	7.8	73	17	Mar 05 – Jun 05
Boculu	12.1	116	24	Jul 05 – Oct 05
Miang	12.9	83	18	Mar 05 – Jun 05
Mitong	13.2	81	25	Nov 05 – Feb 06

6.3.3 Distance analysis

Using the abundance survey data, density was calculated using Distance 5.1 (Thomas 2006) for the four most common primate species: the black colobus (*Colobus satanus*), the moustached monkey (*Cercopithecus cephus*), the putty-nosed monkey (*Cercopithecus nictitans*), the crowned monkey (*Cercopithecus pogonias*) and also for the single most common duiker species, the blue duiker (*Philantomba monticola*). Data were truncated prior to analysis to remove observations at extreme distances (Buckland et al. 2001) and minimum AIC (Akaike Information Criterion) was used for model selection (Burnham & Anderson 1998) (see Appendix 8.4 for full Distance outputs, including details of truncation distances and detection function models used). Small sample sizes precluded the estimation of separate detection functions for every species in each survey site. Sightings were therefore pooled for each species across all survey sites to estimate the detection function globally, while cluster size, encounter rate and density were estimated by stratum (i.e. for each species within each site). For some of the more common species, sample sizes were sufficient to estimate detectability at the site level, allowing a comparison of global and stratified detection functions. This comparison showed that the AIC for the pooled detection function across sites was lower than that for separate detection functions for each site, indicating no significant difference in detectability between sites and thus supporting the use of a pooled detection function (Buckland et al. 2001).

6.3.4 Hunting statistics

Catch-effort data were taken from weekly hunter interviews. These interviews measure effort as the time spent out of the village, and although not providing detailed effort measures such as trap numbers and composition (Table 4.2.), time spent out of the village can be successfully adjusted to reflect biologically-relevant hunting effort. As an effort measure, adjusted time spent out of the village has been found to adequately explain variation in hunting catch (section 4.4.3). In addition, weekly hunter interviews have been shown to be accurate, both quantitatively and spatially in the reporting of hunter catch and effort, and to provide the large sample sizes of data required for the validation of CPUE and abundance (Table 5.2).

Weekly hunter interviews were conducted for all hunters in the community at the end of each week throughout the study period. Hunters reported catch and effort information for all of their hunting trips. Interviews typically lasted 10 minutes and were conducted by two hunters employed as part-time local research assistants. A detailed map of the village and the surrounding area was constructed using participatory mapping (Chambers 1994), and divided into numbered zones to aid hunters in the identification of hunting locations during interviews (see Appendix 8.2 for participatory map).

The map used for the weekly interviews was later digitised and geo-referenced and added to a GIS (Geographical Information System), ArcGIS 9.1. (ESRI 2006), containing the locations of the six line transect survey sites and their catchment areas. In this way map zones falling completely within or largely overlapping the survey site catchment areas were identified, and hunts occurring within these zones could be allocated to the survey sites (Fig. 6.1). Hunts and their catch-effort data were matched both spatially and temporally to the six abundance survey sites, to give a finely stratified CPUE dataset (Fonteneau 1999; Walters 2003) (Table 6.2). Temporal stratification permitted the isolation of CPUE data from hunts that occurred within the time period during which the prey abundance surveys took place. The full CPUE data set shall now be referred to as yearly CPUE, while that matched to the abundance survey period will be termed survey CPUE.

Table 6.2 Number of hunting trips per survey site conducted for the year and during the abundance survey period. The number of hunting trips is separated by method and shown in brackets, and the number of hunters contributing to the catch-effort data for each site is shown.

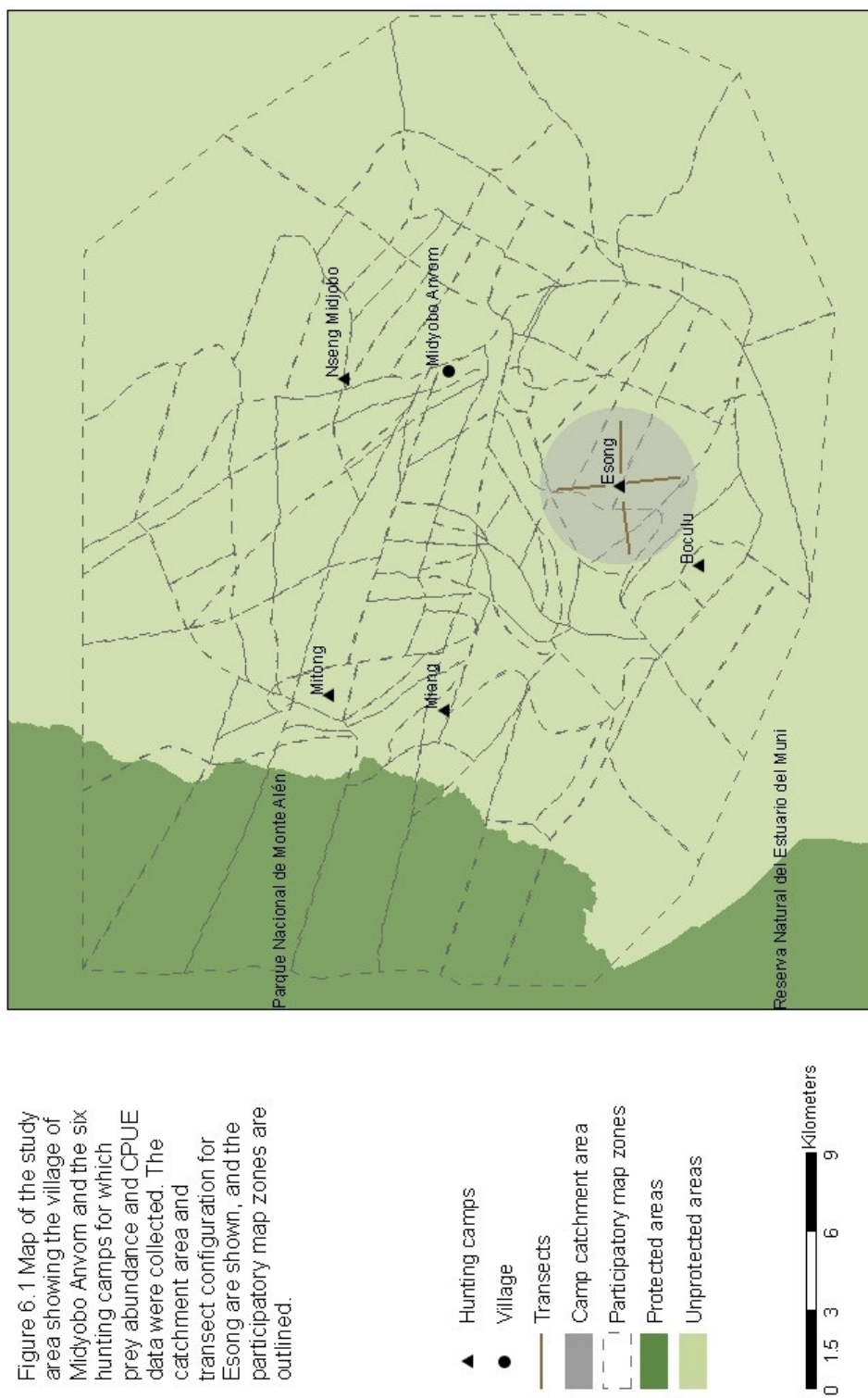
Site	Yearly hunts ¹ (gun/trap)	No. Hunters	Survey hunts ¹ (gun/trap)	No. Hunters	% effort adjustment due to distance ²
Midyobo Anvom	306 (27/287)	27	165 (5/160)	17	0
Nseng Midyobo	230 (22/221)	18	136 (12/132)	11	48
Esong	248 (58/204)	20	35 (4/31)	8	48
Boculu	439 (51/409)	28	208 (26/195)	21	30
Miang	60 (11/54)	11	29 (2/27)	8	22
Mitong	136 (31/122)	23	34 (8/26)	10	17

¹ Totals less than the sum of gun and trap hunts due double use of data from hunts using both methods

² Adjustment factor for bias in reported time with increasing distance to hunting location (Figure 3.4.2)

6.3.5 CPUE calculation

It has been shown that on multi-day hunting trips, the use of total time spent out of the village can be biased and lead to overestimates of effort with increasing distance travelled to the hunting location (Figure 3.2). In order to account for this bias the effort of multi-day hunting trips can be adjusted according to the distance of the hunting location from the village and hence degree of effort overestimation. While a comparison of the variation in catch explained by both raw and adjusted effort data shows that they explain very similar amounts of variation (Table 4.5), suggesting that raw effort data could be used, for the purposes of these analyses I have taken a precautionary approach and used effort measured as adjusted time spent out of the village (see Table 6.2 for adjustment factors). In addition, gun hunting effort was standardised to control for the reduction in catchability during the wet season (0.24 animals/hour), using a multiplication factor of 0.76 (see Table 4.5).



6.3.6 Statistical analyses

All analyses were performed with the R statistical package version 2.5.1 (R Core Development Team 2007). I used generalized linear models of catch with an offset for effort and quasipoisson error structure to account for overdispersion as described by Crawley (2007). Model comparisons using analysis of deviance tests were used to determine if there were significant differences in CPUE between survey sites. This was repeated for each of the five species for which I obtained density estimates: the black colobus monkey, the moustached monkey, the putty-nosed monkey, the crowned monkey and the blue duiker.

When spatial variation in species-level CPUE estimates were found, I tested to see if this was related to spatial variation in species density using log linear regression models. I used t-tests to determine whether slopes for significant relationships were different from proportionality, the assumption of the CPUE model, as described in Crawley (2007). Models were visually inspected using diagnostic plots for violation of model assumptions.

The lack of incorporation of error into survey results, has been a target of criticism (Plumptre 2000). In this analysis of the relationship between CPUE and abundance there are two sources of error: that associated with the abundance estimates, which is typically large (Barnes 2002b; Plumptre 2000), and that which is associated with the CPUE estimates due to variation between hunts, which can also be substantial. In my analyses I purposefully ignore both of these sources of error by investigating the relationships between mean CPUE and mean density (however the extent of this error for both CPUE and density is illustrated in Fig. 6.2) to determine if a relationship between CPUE and density is detectable. My aim here is not to investigate the factors causing variability in CPUE at the hunter level (Table 4.7), nor to use CPUE to predict density, which would both require the inclusion of these two sources of error.

6.4 Results

6.4.1 Prey density estimates

Primate densities differed considerably between survey sites (Table 6.3). For all species (apart from the crowned monkey), densities were lowest in the survey site located around the village (Midyobo Anvom). Of the four species considered, the black colobus and putty-nosed monkeys showed the biggest differences in density between survey sites (10 fold and 9 fold respectively). In contrast the densities of the moustached monkey and crowned monkey were less variable (4 and 2.5 fold respectively). The density of the blue

duiker also varied between sites (3-fold), and similarly to the primates was lowest in density around the village. The error surrounding all estimated densities are large, and overlapping for sites located at similar distances from the village. Statistically significant differences in density are therefore only apparent between sites located a considerable distance from each other, for example the Midyobo Anvom and Mitong survey sites (Table 6.3).

Table 6.3 Density (individuals/km²) of the four most commonly hunted primates, and the single most commonly hunted duiker by survey site. Sites are ordered by increasing distance from the village and one standard error of the mean is shown in brackets

Site	Blue duiker	Black colobus monkey	Moustached monkey	Putty-nosed monkey	Crowned monkey
Midyobo Anvom	13.2 (7.7)	4.7 (3.3)	21.8 (6.5)	11.4 (6.8)	25.8 (14.2)
Nseng Midyobo	28.2 (12.7)	20.3 (9.4)	36.1 (7.6)	20.8 (8.3)	42.4 (14.3)
Esong	41.2 (18.8)	29.9 (12.7)	55.1 (18.2)	27.2 (12.7)	4.9 (6.1)
Boculu	40.1 (14.3)	34.47 (13.1)	47.3 (13.6)	29.1 (7.5)	26.1 (8.2)
Miang	17.8 (7.0)	47.67 (14.3)	87.3 (30.9)	97.7 (31.9)	68.2 (15.1)
Mitong	25.9 (7.4)	42.9 (21.1)	81 (18.5)	91.7 (26.0)	47.3 (26.0)

6.4.2 Catch per Unit Effort estimates

Mean yearly CPUE varies between primate species within a site and also across sites for a single species. Mean yearly CPUE was significantly different between survey sites for all four primates: the black colobus ($\chi^2_5=1000.6$, $p < 0.0001$); the putty-nosed monkey ($\chi^2_5=497.0$, $p = 0.01$); the crowned monkey ($\chi^2_5=398.8$, $p < 0.0001$); and the moustached monkey ($\chi^2_5=241.9$, $p = 0.04$). Of the four species, yearly CPUE is highest for the black colobus monkey in all survey sites apart from the village, where yearly CPUE for the putty-nosed monkey is highest. Yearly CPUE information for the crowned monkey was lower than for all other species in all sites. Visual inspection of aggregate yearly CPUE for these four primate species combined suggests that it was highest in the remotest sites, Miang and Mitong, comparable between Esong, Boculu and Nseng Midyobo, and lowest around the village, Midyobo Anvom (Table 6.4). For the blue duiker, mean yearly CPUE varies significantly across sites ($\chi^2_5= 9597$, $p < 0.0001$), and was greatest in the Esong site (Table 6.4).

Table 6.4 Mean yearly Catch per Unit Effort (animals/hour) of the four most commonly hunted primates, and the single most commonly hunted duiker by survey site. Sites are ordered by increasing distance from the village and one standard error of the mean is shown in brackets

Site	Blue duiker	Black colobus monkey	Moustached monkey	Putty-nosed monkey	Crowned monkey
Village	0.04 (0.006)	0.02 (0.02)	0.04 (0.02)	0.06 (0.02)	0
Nseng Midyobo	0.07 (0.009)	0.07 (0.03)	0.05 (0.02)	0.03 (0.01)	0.01 (0.02)
Esong	0.1 (0.02)	0.09 (0.02)	0.06 (0.02)	0.05 (0.02)	0.02 (0.02)
Boculu	0.08 (0.007)	0.09 (0.03)	0.06 (0.03)	0.03 (0.01)	0
Miang	0.07 (0.01)	0.2 (0.05)	0.1 (0.04)	0.05 (0.02)	0.007 (0.04)
Mitong	0.0 (0.01)	0.2 (0.04)	0.05 (0.02)	0.1 (0.07)	0.01 (0.03)

For the four primate species, trends in survey CPUE among sites or species are less clear. Mean survey CPUE for the black colobus ($\chi^2_5=367.77$, $p=0.02$), putty-nosed monkey ($\chi^2_5=228.57$, $p=0.01$) and crowned monkey ($\chi^2_5=185.03$, $p<0.0001$) are significantly different across sites, but no significant difference was found between sites for the moustached monkey ($\chi^2_5=113.46$, $p=0.58$). Mean survey CPUE for each monkey species in some cases is very similar to mean yearly CPUE (Nseng Midyobo, Miang), in other cases the mean survey CPUE estimates are quite different (Esong, Boculu and Mitong). In all cases the error associated with survey CPUE estimates are greater, due to the smaller sample sizes of hunts available in the short survey period (Table 6.5). Mean survey CPUE for the blue duiker varies significantly between sites ($\chi^2_6=1090.3$, $p<0.0001$), and is relatively comparable to yearly CPUE estimates (Table 6.5)

Table 6.5 Mean survey Catch per Unit Effort (animals/hour) of the four most commonly hunted primates, and the single most commonly hunted duiker by survey site. Sites are ordered by increasing distance from the village and one standard error of the mean is shown in brackets

Site	Blue duiker	Black colobus monkey	Moustached monkey	Putty-nosed monkey	Crowned monkey
Village	0.04 (0.009)	0.05 (0.05)	0.04 (0.04)	0.05 (0.04)	0
Nseng Midyobo	0.06 (0.01)	0.07 (0.05)	0.05 (0.03)	0.02 (0.01)	0.008 (0.008)
Esong	0.2 (0.06)	0.03 (0.03)	0.1 (0.08)	0.03 (0.03)	0.07 (0.07)
Boculu	0.07 (0.007)	0.03 (0.02)	0.07 (0.04)	0.008 (0.005)	0
Miang	0.09 (0.02)	0.3 (0.09)	0.1 (0.1)	0.05 (0.05)	0
Mitong	0.07 (0.02)	0.07 (0.06)	0.03 (0.02)	0.04 (0.04)	0.01 (0.1)

6.4.3 Is there a relationship between Catch per Unit Effort and density?

The investigations of the relationship between CPUE and density that follow use yearly CPUE estimates due to the limited sample sizes of the temporally stratified survey CPUE data (Table 6.2). For the black colobus monkey, mean yearly CPUE showed a significant positive relationship with density (Fig 6.2) (log linear regression: slope=0.86, SE=0.15, t-value=5.9, $p=0.0004$), and the slope of this relationship was not significantly different from the theoretical prediction of one (students t-test: $t = -0.95$, $df=4$). CPUE was also positively related to density for the blue duiker (Fig 6.2), but marginally non-significant, (slope=0.67, SE= 0.26, t-value= 2.6, $p=0.057$), and the slope of this relationship was also not significantly different from one ($t=-1.28$, $df=4$). Therefore in both cases there is no evidence to suggest that for these species that the relationship between CPUE and density is non-proportional (Figure 6.3).

For the remaining three primate species no significant relationships between CPUE and density were found. For the putty-nosed and moustached monkeys, visual inspection of mean CPUE values plotted against density suggests that there may be some evidence of a positive relationship (Fig 6.2), but this was not significant for either species (slope =0.30, SE= 0.26, t value= 1.15, $p=0.32$) and (slope=0.45, SE= 0.22, t value= 2.10, $p=0.10$) respectively. For the crowned monkey, there is some evidence for the existence of a negative relationship between CPUE and density (Fig 6.2) but this is also not significant (slope=-0.46, SE= 7.75, t value= 0.06, $p =0.95$).

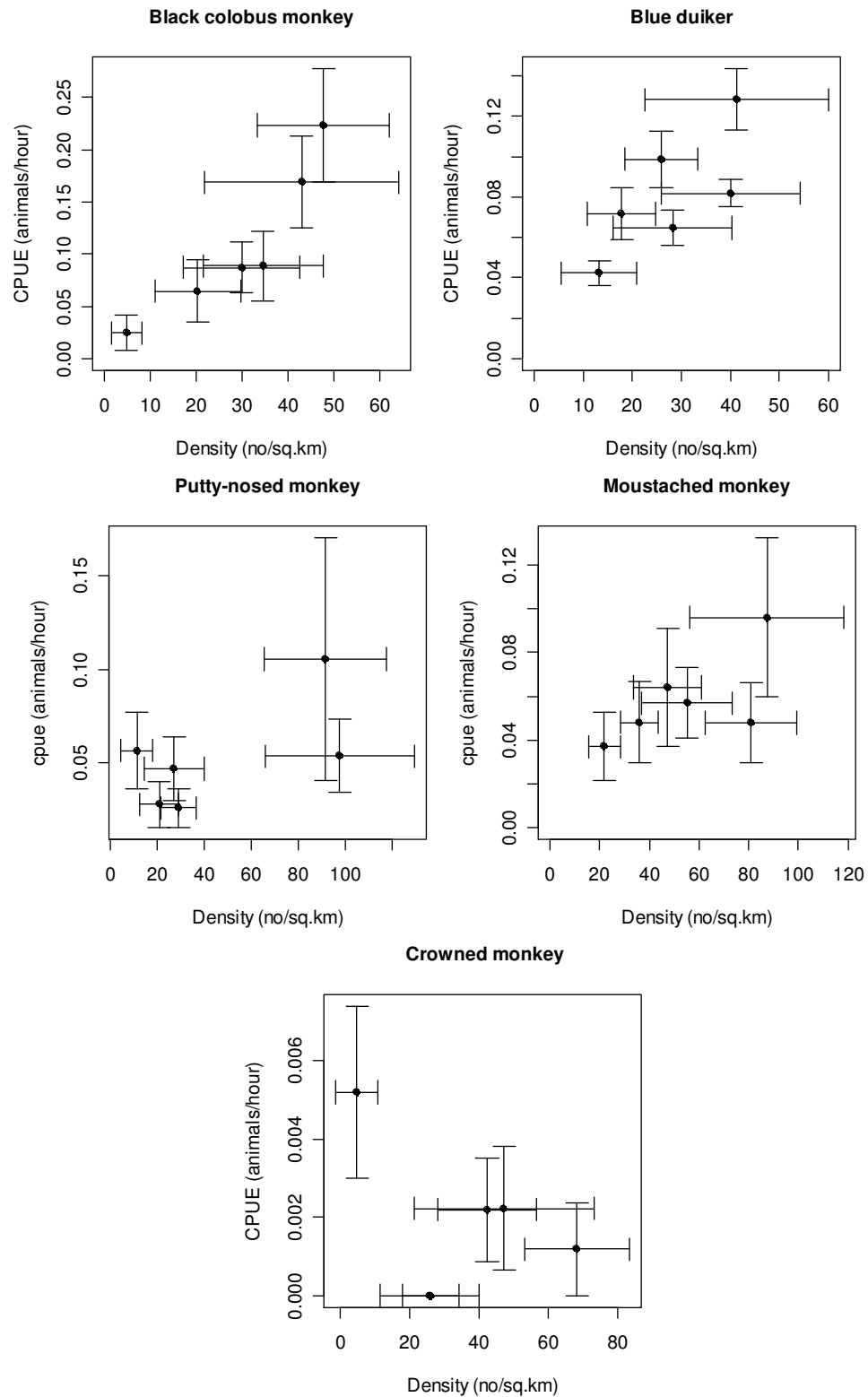


Figure 6.2 Relationship between mean yearly CPUE and density for four most commonly hunted primates, and the single most commonly hunted duiker. Bars indicate one standard error of the mean.

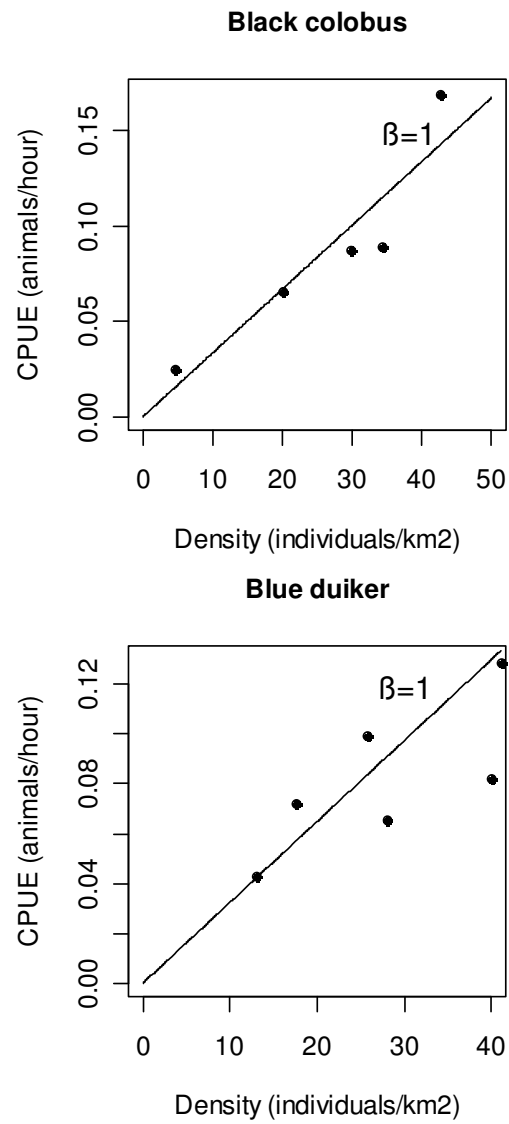


Figure 6.3 Relationships between mean yearly CPUE and density for the black colobus monkey and the blue duiker showing proportionality

6.5 Discussion

The use of CPUE as an index of abundance has been suggested as a technique for monitoring bushmeat prey species. However, the CPUE model is based upon the assumption that CPUE is proportional to population size. In order to test this assumption I have compared CPUE from hunting statistics with prey density estimates from line transect surveys. My findings suggest that CPUE may have potential for use as an index to prey abundance and could act as a low cost alternative to assessing the status of tropical forest species.

6.5.1 Variation in prey density

Differences in density were found both among primate species within a site and among sites for the same species were found. The black colobus was generally the most abundant of the four primate species and also showed the most variation in density across sites. For all primate species, density was generally lowest in the survey sites located close to the village and increased with increasing distance of the survey site from the village. The density of the blue duiker varied less between sites than that of the primates. Similarly to the primates, its density was found to be lowest in the survey site located around the village. But contrastingly, the highest duiker density was found in a survey site located at mid-distance from the village, further demonstrating that habitat factors, in addition to hunting, are important determinants of abundance for duikers (section 2.4.4).

6.5.2 Variation in hunter Catch per Unit Effort

There was also significant variation in levels of CPUE both between species within a site and between sites for the same species. Of the four primate species, CPUE is highest for the black colobus monkey in all survey sites apart from that nearest the village, despite the fact that other primate species are more abundant. Conversely for the crowned monkey, CPUE appears to be considerably lower in comparison to the other species, even when it is equal to or greater than the other species in abundance. This suggests that some degree of active selection by hunters is occurring, or alternatively that these species differ considerably in their catchability. This may have important implications for the relationship between CPUE and abundance for prey that are 'pursuit hunted' with guns. In contrast, for the blue duiker CPUE and abundance appear to follow a similar pattern across sites, suggesting that the mostly 'passive' nature of trapping allows less influence of prey selection by the hunter on the level of CPUE observed (Rowcliffe et al. 2003).

A comparison of yearly CPUE with survey CPUE shows that for some species and some sites the two estimates were very comparable, while for others the differences were quite large. This illustrates the difficulties involved in balancing the need to obtain large sample sizes of hunts, with the need to collect data over short time periods to minimise the influence of temporal changes in abundance or CPUE at a site. The use of spatially stratified CPUE data resulted in far lower sample sizes of hunts, especially for gun hunting, and hence more variable CPUE estimates. This problem is demonstrated by the relatively good match between yearly and survey CPUE for the blue duiker, where a far larger sample size of hunts using traps was obtained. In addition, the nature of the hunting method itself may influence the precision of CPUE estimates. Return rates for gun hunting have been shown to be more stochastic than trapping, and so even with large sample sizes of hunts, the mean CPUE estimates may still be associated with a large amount of error.

6.5.3 The relationship between CPUE and abundance

Significant positive relationships between CPUE and density were found for two out of the five prey species investigated, one which is gun hunted, the black colobus, and one which is trapped, the blue duiker. For the remaining species, there was some evidence for a positive relationship between CPUE and density for the moustached monkey and putty-nosed monkey, and evidence for a negative relationship for the crowned monkey.

Prey selection is an important factor determining the use of CPUE as an index of abundance (Hilborn 1992), and for the primate species it is likely that prey selection was having an important influence on the relationships observed between CPUE and abundance. In order for CPUE to be proportional to abundance, prey must be taken on every encounter; however, hunters may exhibit preferences between prey species due to size, taste, ease of capture and monetary value (Cowlishaw & Dunbar 2000) (Bodmer 1995). Optimal foraging theory can be used to provide insight into these hunter decisions (Stephens & Krebs 1986). The prey choice or optimal diet model ranks prey according to their profitability, and predicts that the most profitable prey species are always taken, but that the decision of whether to take the less profitable species depends on the rate at which the more profitable species are encountered (Charnov 1976; Stephens & Krebs 1986). Foraging theory assumes that foragers will behave to maximize their short-term harvesting rate and a number of studies have found that hunters do indeed make decisions consistent with predictions of foraging theory (Alvard 1995; Alvard 1993; Rowcliffe et al. 2004).

The black colobus has been found to be the preferred monkey species amongst hunters in Equatorial Guinea (Kumpel 2006). The putty-nosed and moustached monkeys are desired but to a lesser extent, while the crowned monkey is the least preferred of the

four primates and is only sold and not consumed in this community (pers obs). In keeping with the low preference for the crowned monkey in my study, lower pursuit rates have been found for this species in other sites in Equatorial Guinea (Kumpel 2006). It is therefore likely that hunters show partial preferences (Krebs & McCleery 1984; Waddington 1982) for this species, so that when hunters are presented with a choice of the crowned monkey and other species the other species are taken first, resulting in no significant relationship between CPUE and abundance. Indeed the inverse relationship with higher CPUE at lower densities may be due to this species becoming more likely to be taken when at lower densities, due to the rarity or absence of other primate species. More subtle preference differences between hunters for the putty-nosed and moustached monkeys might explain the appearance, but lack of significance of, positive relationships between CPUE and abundance.

6.5.4 The practicalities of CPUE as a monitoring tool

I have found evidence to suggest that a proportional relationship exists between CPUE and abundance, across hunting methods, for two prey species: the gun-hunted black colobus monkey and the trap-caught blue duiker. I have also found evidence to suggest that prey selection by hunters may potentially affect the relationship observed between CPUE and abundance. Although not investigated here, it is also possible that species biology can have a further influence, for example if primates regroup at low densities, then CPUE will not decline proportionally with abundance. The existence of a single relationship between CPUE and abundance that holds for all species is therefore quite unlikely.

It is interesting to note that the species for which the relationships between CPUE and density were found are also those species which make up a large proportion of hunting offtake (Table 2.3). Effort is measured at the community level, but may not necessarily be targeted equally among species (Gleeson & Wilson 1986), instead being directed at those species which are preferred, and so resulting in a better CPUE-abundance relationship for preferred species. Therefore a useful approach might be the use of a small number of key preferred prey species as 'indicators' to the state of the community overall.

The species investigated in this study represent a handful of a whole community of species that are exploited for the bushmeat trade. The use of community-level CPUE (Myers & Worm 2003) implies that the catchability coefficient is the same for all species, but different species have different biological characteristics that will make them more or less prone to being caught (Maunder et al. 2006). Therefore it remains to be seen to what extent the relationships found here can be applied to these other species and whether a community-level approach using aggregate levels of CPUE would be valid. The use of

species aggregated CPUE has been an important indicator of the exploitation status of fisheries for two reasons: because it has economic relevance, and also because it reflects community-level responses to exploitation. However, it has also been shown that using aggregate CPUE as an indicator of impacts on exploited communities can be problematic and should be interpreted with caution (Lorenzen et al. 2006; Maunder et al. 2006).

6.5.5 Conclusion

My analyses provide the first validation of the relationship between Catch per Unit Effort and abundance in a tropical forest hunting system, testing the frequently made assumption of proportionality between CPUE and abundance. I find encouraging support for the potential of CPUE as an index of abundance, with proportional relationships being demonstrated in a gun-hunted primate and a trap-hunted duiker species. However, obtaining a sufficient number of sites for comparison combined with the large amounts of error in estimates of both CPUE and density, and the need for large sample sizes of finely temporally and spatially stratified and unbiased CPUE data, makes the investigation of these relationships problematic. Furthermore, given widely varying biology, and prey selection by hunters, the generality of these findings to other species, and hence the utility of community-level CPUE is still to be ascertained. In order to fully evaluate the potential of CPUE, further investigation of the relationship between CPUE and abundance for other species, and for species aggregated CPUE is required. In addition, further comparative studies in other sites and contexts are needed to determine the value of using indices based on hunting statistics to assess and monitor the abundance of bushmeat prey species.

Chapter 7

Discussion

7. Discussion

Achieving the sustainability of bushmeat hunting is a topic of much current interest. Many major conservation NGOs, academic institutions and other organisations have participated in the debate, conducted research or contributed funding. The bushmeat trade, its causes, and likely solutions encompass many of the areas that are most challenging in conservation science, such as the need bring our use of natural resources to sustainable levels (Hutton & Leader-Williams 2003), the need for improved biodiversity monitoring (Balmford et al. 2003; Bawa & Menon 1997), the need to combine community-level with single species approaches (Rowcliffe et al. 2003), and lastly our growing awareness that conservation is essentially a human science with social, economic and political themes being both the root causes and also the likely source of many solutions (Jacobson & McDuff 1998). This thesis touches on all of these subjects as it evaluates both the scientific validity and practical feasibility of bushmeat CPUE as a monitoring tool. I now present a discussion of my main findings, a conclusion of their implications given the wider context of bushmeat hunting, and a brief outline of some areas for future research and some recommendations for the application of a bushmeat CPUE index.

7.1 Hunting as one of many determinants of abundance

Understanding the impact of hunting on wildlife populations is crucial to achieving the sustainability of the bushmeat trade, and requires knowledge of how prey species' abundance responds to different levels of exploitation. Once we know which species are affected and how they are affected by a given level of hunting, in the context of habitat type and threatening processes other than hunting, then we can begin to develop sustainable harvesting strategies. With all the concern surrounding the bushmeat trade, there might have previously been a lack of objectivity in attributing species declines or differences in abundance to hunting. Just because hunting is occurring does not mean that it is the cause of all changes in abundance, or indeed the key threat needing to be tackled (Caughley & Gunn 1995). It is well known that teasing apart the factors that determine abundance is notoriously difficult (White et al. 2007), and species' abundance can be affected by a number of anthropogenic threatening processes (Isaac & Cowlishaw 2004), habitat factors (Peres 1997b), natural stochasticity (Beddington & May 1977), and species interactions (Karanth et al. 2004). But despite this knowledge, many studies of the impacts of bushmeat hunting on wildlife are conducted with a limited spatial or temporal sample size, without controls for habitat, and without consideration being given

to the influence of other types of human disturbance. In Chapter two, I further current understanding in this area by disentangling the independent effects of these factors on the abundance of a diverse assemblage of mammalian species exposed to bushmeat hunting. My findings show that the effects of hunting and habitat on abundance can vary greatly between species and that these factors can sometimes be confounded, requiring an approach that isolates their independent effects, and that also considers the wider context of the hunting system and of individual prey species biology.

In terms of practical conservation in Midyobo Anvom, these results suggest that, while current levels of hunting may be reducing the abundance of some species, for others habitat remains the overriding influence on abundance, in spite of high levels of hunting. Such information will be useful for the development of future sustainable harvesting strategies, facilitating the targeted management of species thought to be most at risk. One important consideration on this subject is the frequently ignored distinction which exists between declines in abundance and unsustainable hunting. Many bushmeat studies demonstrate spatial or temporal declines in abundance, which are used as evidence to suggest that hunting is unsustainable. However, when a population is exploited, population size will be reduced, and does not in itself indicate unsustainable hunting (Milner-Gulland & Mace 1998; Sutherland 2001). Only if populations continue to decline over time, can unsustainable hunting be demonstrated.

This study is therefore limited in its ability to make an assessment of the likely sustainability of current hunting practises in Midyobo Anvom. Declines in abundance due to hunting have been found for some primate species, but without further monitoring over time it is difficult to say whether these indicate that current hunting is unsustainable. This site is rare in its isolation and in the area of forest available to the community for hunting, in comparison to other sites in Equatorial Guinea, and so can probably tolerate high levels of offtake. However, the country is currently undergoing a period of strong economic and population growth, and a wealthier urban population will mean that future demand for bushmeat is likely to increase (East et al. 2005). Midyobo Anvom is currently one of the main sources of bushmeat to the country's capital, and as links to the capital improve, hunters will no doubt take advantage of this opportunity, and pressure on wildlife in this area will rise.

More broadly, these results have practical implications for the management of hunting in other tropical forest areas. Spatial structure is increasingly being recognised as important in determining the sustainability of hunting (Ling & Milner-Gulland 2007; Naranjo & Bodmer 2007; Peres & Nascimento 2006; Salas & Kim 2002), and the use of core hunting zones and no-take areas has been suggested (McCullough 1996; Novaro et al. 2000). My results suggest that conservation managers need to consider and incorporate habitat heterogeneity as well as hunter access when undertaking spatial zonation for management.

7.2 Methodological issues and theoretical assumptions

Many methodological questions need to be answered, and theoretical assumptions tested before CPUE can be reliably used as an index of abundance. These issues are addressed in chapters three, four and six. Chapter three illustrates how terms such as 'hunting pressure' and 'hunting intensity' are frequently used, but rarely defined in many bushmeat studies, and that a diversity of different measures are currently being used by researchers to quantify hunting. In many cases these are economic measures of hunter effort, rather than measures of the likely biological impact of hunting. This distinction is particularly useful, and is one that has not been previously made. Similarly, the biases that may result from the use of economic effort measures have not been previously investigated or identified and Chapter three illustrates how economic measures can result in considerably biased estimates of biologically-relevant hunting effort. The choice of effort measure has important implications not only for correctly attributing observed levels of prey abundance to a particular level of hunting, but also for the use of hunting statistics such as CPUE as indices of abundance.

Chapter four develops this theme further by testing the different effort measures identified in Chapter three against catch data. The relationship between catch and effort was found to be highly variable, as is the case in many other harvesting systems (Cooke & Beddington 1984; Schmidt et al. 2005), and dependent not only upon the particular measure of effort used, but also the hunting method and the scale at which the catch-effort data were collected. Despite the biases identified in economic effort measures in Chapter three, in many cases economic measures explained no less variation in catch than their biologically-relevant equivalents. Furthermore, in many cases the best relationships between catch and effort were found when catch-effort data were aggregated over a number of individual hunts into hunting trips or stays in hunting camps. This suggests that economic measures of effort such as time spent out of the village, can be as good at explaining catch as biological measures of effort, and that 'professional' and detailed methods of collecting catch-effort data such as hunter follows may not always be necessary. This is an important result and suggests that methods of data collection more amenable to larger scale monitoring, and that involve hunters, may be the most promising for use in calculating CPUE indices. This theme is returned to in Chapter five.

Chapter four also investigates the influence of factors other than abundance on the relationship between catch and effort, but with somewhat limited success. A substantial amount of variation in catch remains even once effort and the effect of additional variables has been accounted for. While some unexplained variation in the catch-effort relationship is to be expected, due to the stochastic nature of hunting, it is

probable that additional variables not investigated here will be important in reducing this unexplained variation, for example weather conditions or habitat type. However, given that much of this variability was attributable to the hunter level, differences in individual hunter skill is the most likely cause. However, intrinsic hunter skill is not necessarily strongly related to age and so establishing a method that allows this effect to be quantified is required.

Another critical assumption of the CPUE model is that CPUE is proportional to abundance, but evidence from both fisheries research (Harley et al. 2001), and limited testing in terrestrial harvesting systems, suggests that this assumption may not always be valid (Bowyer et al. 1999a; Pettoirelli et al. 2007). Before CPUE can be used as an index of abundance it needs to be validated using un-biased data on CPUE and independent abundance estimates. Building on the results of chapters three and four, Chapter six uses this approach to present the first validation of CPUE as an index of abundance for tropical forest species. Encouraging support was found for the potential of CPUE as an index of abundance for two out of the five species investigated. However, given widely varying biology and prey selection by hunters, the extent to which these findings can be generalised to other species, and hence the utility of a community-level CPUE index (such as that outlined in Chapter 5), needs considerable further investigation (Hampton et al. 2005; Maunder et al. 2006). Chapter six also shows that large amounts of error can exist in both CPUE and abundance estimates, making investigation of the relationship problematic. If CPUE is to be used for predictive purposes to estimate abundance, then both of these sources of error would need to be incorporated into analyses, requiring considerable amounts of temporally and spatially stratified data. Reconciling such data needs with the use of biologically relevant measures of hunting effort can be difficult as demonstrated in Chapter three. However, Chapters four and five demonstrate that locally-based methods of CPUE data collection can offer a practical solution.

7.3 The practical feasibility of CPUE as a monitoring tool

One of the main factors limiting the achievement of sustainable levels of bushmeat hunting, from a biological knowledge perspective, is our ability to assess the state of the system, and to do this periodically so that management decisions can be formulated, applied and adapted (Krebs 1991; Pollock et al. 2002). There is therefore a need for methods of estimating abundance that are time-efficient, cost-effective and so spatially scalable and temporally sustainable (Danielsen et al. 2005). This need is not only limited to those working on the bushmeat trade but applies to a wide range of other conservation and resource management issues. In addition, there is also a need to engage more with resource users and local communities, by involving them in

management decisions (Bawa et al. 2004). It is in this context that Chapter five builds on the findings of chapters three and four, to examine the feasibility of using CPUE as a locally-based monitoring tool. In this Chapter I show that locally-based monitoring of community-level CPUE has considerable potential as a tool for the assessment and management of bushmeat hunting. It can provide quantitatively and spatially accurate data on local resource use in a relatively short time with limited resources and with sufficient power to detect useful levels of change.

A technique such as this that involves resource users may help to cause a shift in attitudes towards more environmentally sustainable resource use practices, and so be more effective than professional monitoring in arresting unsustainable levels of hunting. This is because resource users are more likely to comply with locally agreed decisions (Danielsen et al. 2005). Even though the CPUE concept forms the core of the sophisticated science of fisheries management, its background originally lies in being a traditional monitoring method used by harvesters to assess the status of natural resources, therefore lending itself to being used as a locally-based monitoring technique (Moller et al. 2004). Furthermore, CPUE relates to the socioeconomic benefits obtained by hunters, and so as well as providing an index of abundance with which to monitor prey species, it can also be used to determine the effects of management interventions on the food and livelihood security of hunting communities (Lorenzen et al. 2006). While there are many avenues for future research in the use of bushmeat CPUE, and while the theory behind sustainable exploitation is extremely sophisticated, Chapter five shows that the greatest success in using CPUE to monitor bushmeat species abundance might be achieved through a relatively simple technique. This might involve the monitoring of CPUE at the species or community level, with the use of threshold values, which when passed, initiate management action so that the required adjustments in hunting activity are made. This is essentially identical to the use of CPUE as a traditional monitoring technique, where informal decisions are made by resource users or communities (Moller et al. 2004).

7.4 Recommendations

The use of CPUE as an index of abundance is a subject central to the sophisticated science of fisheries management, and one that has been at the centre of much debate and research effort over many decades, but very little work exists on the use of this method in terrestrial systems. The research presented here has made substantial progress in answering some of the theoretical, technical and practical questions that surround the use of CPUE for monitoring tropical forest species abundance, providing the first detailed exploration and test of CPUE in this context. However, the findings of this

study raise many further questions, and many opportunities and needs for further research have been highlighted. I now discuss some of these, and make some recommendations for the practical application of this method.

Research recommendations

In this study the CPUE-abundance relationship was investigated for only a small number of species. Although important prey species, they form only part of a whole community of species that are hunted for the bushmeat trade. One of the key research priorities for the development of a bushmeat CPUE index must therefore be the exploration of this relationship for a wider range of species, especially other duiker species and some of the semifossorial species, like pangolins and rodents, which make up a large part of bushmeat offtake. Similarly crucial is the need for exploration of the relationship between community-level CPUE and abundance, and a greater knowledge of species-level relationships will help to address this. Biological community-level responses to exploitation are likely to be important for a number of reasons including the existence of interactions between prey species (May et al. 1979), the distribution of hunting effort between species (Gleeson & Wilson 1986), and the occurrence of 'piggyback' extinction (which is when vulnerable species continue to be exploited due to the presence of alternative prey, Clayton et al. 1997). Our knowledge of these community-level responses to hunting is currently limited (but see Rowcliffe (2003)), and monitoring community level CPUE would help to provide us with this essential information, while also being relatively easy and affordable to implement

This further investigation of both species and community level CPUE-abundance relationships needs to be coupled with investigation at other sites with different hunting systems, prey species and habitat types to reveal the general applicability of this method. Unfortunately, validating the CPUE model first requires the collection of the exact data that the use of CPUE might later negate. While data on both mammal abundance and hunting catch-effort can be difficult and time consuming to collect, this study shows that on a limited budget and time scale, considerable information can be obtained.

When CPUE data is collected and summarized over large heterogeneous areas, it can present a number of new challenges. Therefore if bushmeat CPUE is to be used as a locally-based monitoring tool at the village level, consideration might need to be given to a number of areas highlighted in the background of this thesis (Chapter 1.4), in particular the spatial and temporal stratification of data, changes in the area from which species are harvested, the spatial allocation of effort and efficiency of hunter search and the patterns of prey species distributions.

I would recommend that research effort also be directed at the identification of additional factors that would reduce the unexplained variability in catch shown in this

study. Quantification of hunter skill is likely to prove most fruitful, and exploration of environmental variables such as weather conditions and habitat type may also be beneficial. Additionally, at the level of the hunter, investigation of hunter prey preferences is required to allow the full interpretation of CPUE-abundance relationships and how they differ between species. This would allow the identification of those species for which bushmeat CPUE is most likely to work, so that if biological community-level CPUE is not possible to validate then perhaps trends in the CPUE of a selected number of indicator species, that make up a large proportion of hunting offtake, could be used as a guide to the state of the hunting system and of the prey community as a whole.

Applied recommendations

In terms of the practical application of this method, a number of key questions may be asked: How useful and generalisable are the findings of this study? What potential does bushmeat CPUE as a monitoring method have to make a contribution to the achievement of sustainable levels of bushmeat hunting? What are the considerations for conservation managers wishing to implement this technique?

In order to be useful, this technique will need to be generally applicable in a range of bushmeat hunting systems. Hunting systems can differ in a number of ways, such as in the species hunted, the habitat types present, the motivations for hunting, the methods used, the security of land rights, and the legality of hunting. Since the CPUE model is an intuitive concept (Seber 1992), and there is usually likely to be a biological signal between CPUE and abundance, the method is likely to be broadly applicable in all of these situations. Nevertheless, a conservation manager hoping to implement the bushmeat CPUE method, in order to ensure that CPUE most closely reflects abundance, should give consideration to the various issues identified in the methodological chapters of this thesis, for example the best way to measure hunting effort and the possible influence of prey selection on the CPUE-abundance relationship.

While the application of CPUE may be valid in theory, what is likely to differ greatly between these different systems is the feasibility of implementation in practice. The circumstances surrounding this study, and features of the study site, may make the feasibility of CPUE as a locally-based scheme more likely in Midyobo Anvom compared to other areas. My presence in the village for 15 months conducting a research project and employing a number of community members will undoubtedly have helped to facilitate enthusiasm, participation and accurate data collection. The extent to which a 'professional' presence is needed for successful implementation of bushmeat CPUE as a locally-based monitoring tool therefore remains to be seen. Other factors that would facilitate the use of such a method in this study site, but perhaps not in others, include the existence of a degree of long-term land security and an openness when talking about

hunting. In other systems where hunters may have no long term interest in the preservation of prey species for future hunting, or where hunting restrictions are enforced, their willingness to participate in such a monitoring programme is likely to be much lower.

Equatorial Guinea is a relatively small country and so a national bushmeat monitoring programme involving the use of the bushmeat CPUE index collected using locally-based methods might be feasible. A 'professional' presence would be required for initial implementation of the programme in a number of sites, followed by short visits to facilitate data interpretation and the discussion of management decisions by the communities concerned. Furthermore the supply chain is quite well known in the country, with considerable knowledge of markets, traders and routes of trade existing (Allebone-Webb & Rist, unpublished data; East et al (2005); Kumpel, (2006). Facilitating the targeting of management interventions. However, the socioeconomic barriers to sustainable use must not be forgotten, and the lack of alternative food and livelihood options will need to be simultaneously addressed. As well as the need for a strong and stable land tenure system that motivates communities to participate in monitoring. If successful, such a scheme could serve as a useful model for other tropical forest countries in which the bushmeat trade threatens wildlife.

7.5 Conclusion

The aim of this thesis was to evaluate the potential of CPUE as an index of abundance, with which to monitor prey populations and so aid the sustainable management of bushmeat hunting. In order that bushmeat CPUE as a method fills this requirement, three conditions need to be met. Firstly, CPUE as a method must be scientifically well founded. Secondly, it must be practically feasible given the resources available. Thirdly, resource users must be able to act on the information obtained and adjust their hunting activities accordingly. My thesis shows that the first two conditions can be satisfied, and suggests that the use of bushmeat CPUE for monitoring, while still having considerable further research needs, may be a fruitful area to pursue. However, whether the third condition can be satisfied is not so clear.

For many people living in developing countries the use of wild living resources is an imperative (Hutton 2003), often depending heavily on fishing, hunting and gathering to meet their basic livelihood needs (de Merode et al. 2004; Wilkie & Godoy 2001). Without alternatives, and while there is such a strong imperative for use, it is unlikely that any management recommendations to achieve sustainable levels of use will be acted upon (Hockley et al. 2005). The conclusion of this thesis must therefore be that while the use of CPUE as a monitoring tool may have much to offer those working to bring bushmeat

hunting to sustainable levels, monitoring alone will not be sufficient to achieve sustainability and is only going to be part of the solution. If the other barriers to sustainable use still exist, then conservation will remain an elusive goal (Bawa & Menon 1997).

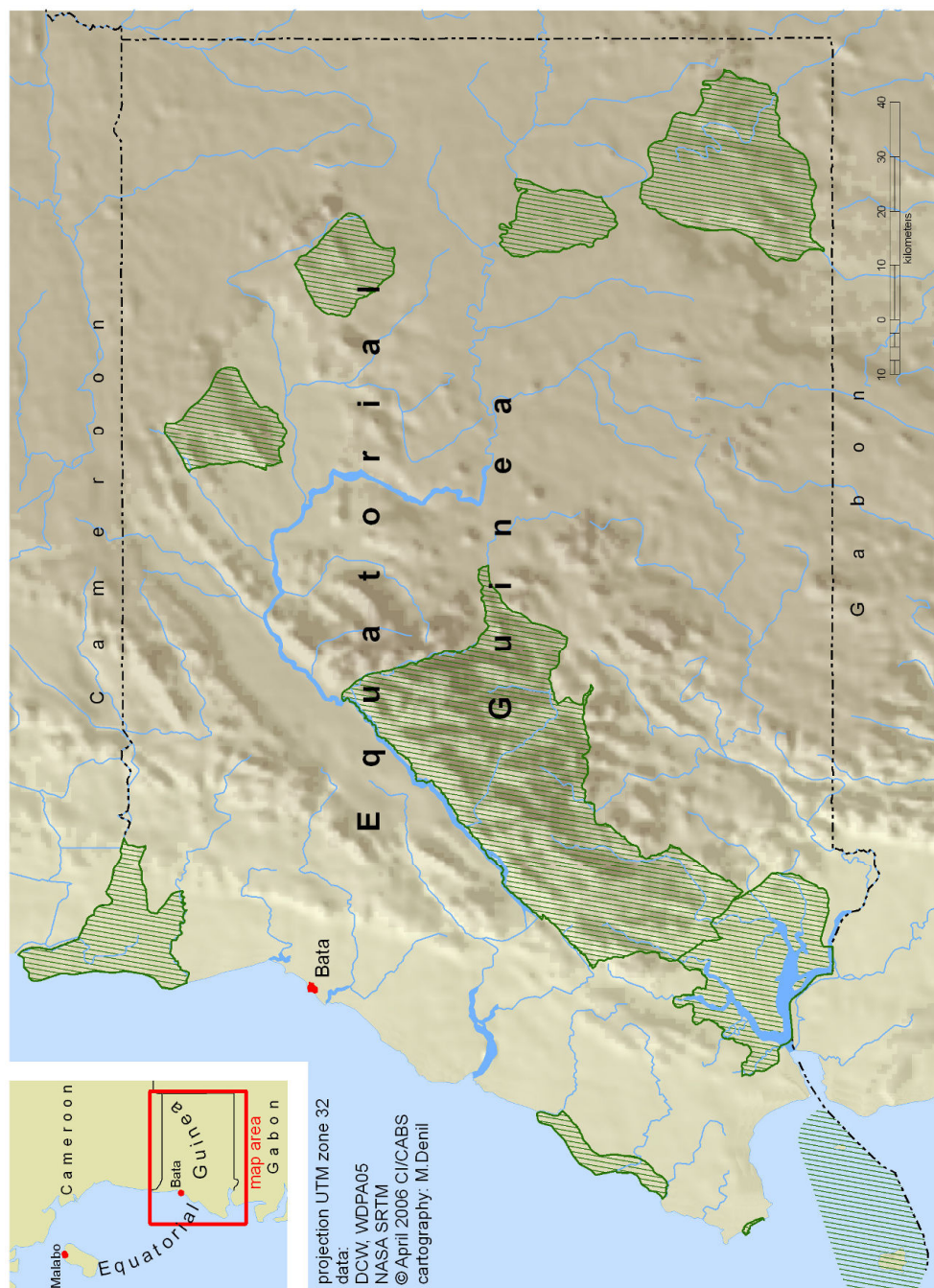
Lord Robert May (2001) articulated this problem well when he said: “Ultimately it is the social and political pressures from growing populations that constrain all choices about conservation. In developing countries these pressures are compounded by legitimate aspirations to the material comforts of the modern world, vividly conveyed by global media in a shrinking world. In the developed world itself, ever more prodigal patterns of consumption counterbalance lower levels of population growth. Any effective plan for the conservation of endangered species must be based not only on the sound understanding of ecology but even more on untidy social and political realities”.

While some may find May’s words dispiriting, they summarise all that is required to successfully address many problems in conservation today. It is undeniable that many of the obstacles to sustainable use in general, and the bushmeat trade in particular, are most likely to be removed by tackling these ‘untidy realities’. However, biological and ecological knowledge is still central to the solution, since without it we cannot understand how species respond to exploitation. Especially needed is research such as this study which provides a link between these human and wildlife dimensions. Monitoring tools such as a locally-based bushmeat CPUE index offer a way of combining these biological and human aspects by involving resource users in monitoring as part of a wider management strategy for wildlife harvesting.

8. Appendices

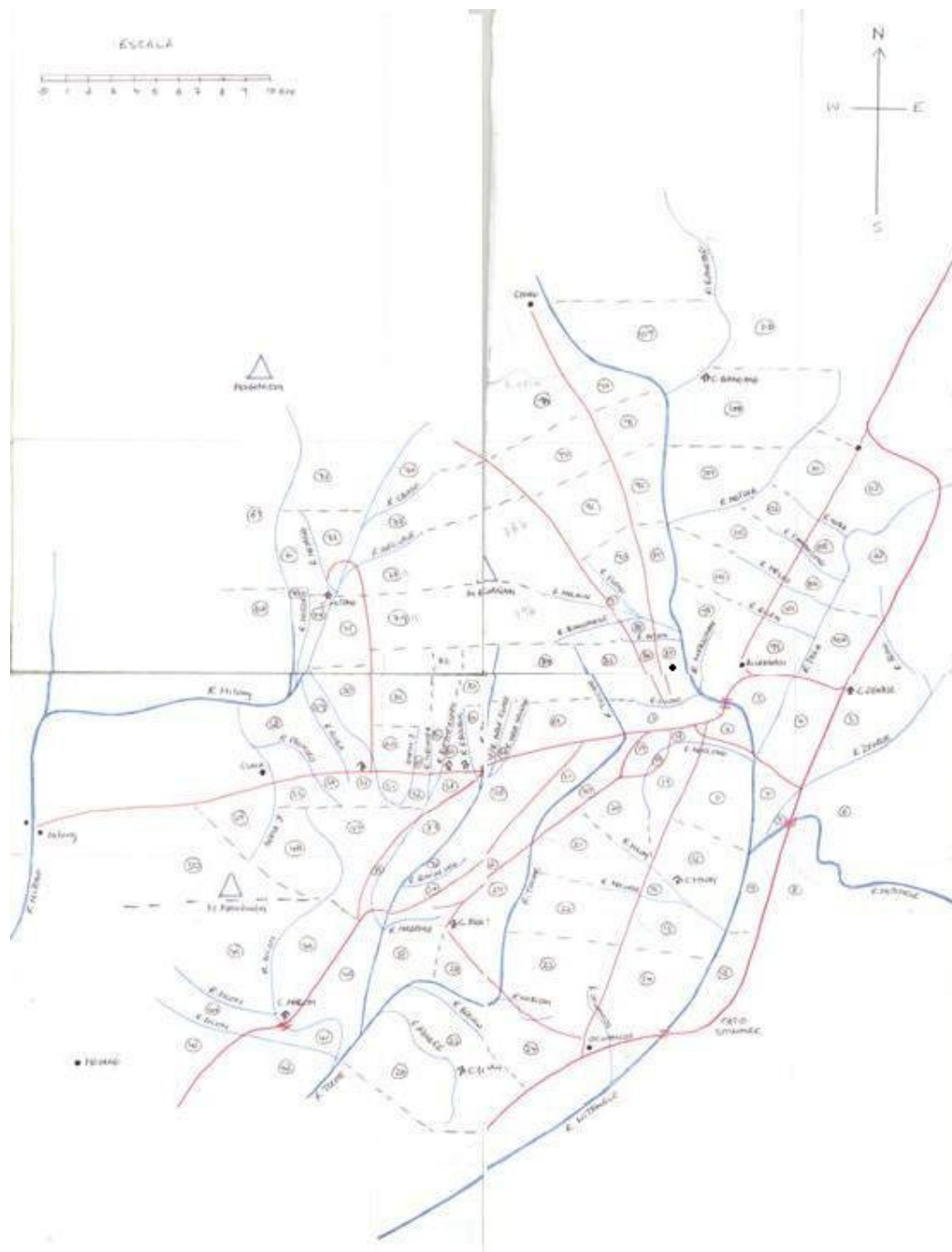
Appendix 8.1

Mainland Equatorial Guinea and its protected areas, clockwise from top left: Reserva Natural de Rio Campo, Reserva Natural de Monte Temelon, Monumento Natural de Piedra Bere, Monumento Natural de Piedra Nzas, Parque Nacional de los Altos de Nsok, Reserva Natural de Estuario del Muni, Reserva Natural de Punta Llende, Parque Nacional de Monte Mitra and Parque Nacional de Monte Alen



Appendix 8.2

Participatory village map of Midyobo Anvom and its hunting catchment, used for weekly hunter interviews



Appendix 8.3

Annual hunting offtake and offtake rates by carcass numbers and biomass. Species contributing over 2% of total biomass are highlighted in bold. Species Red List status (2007) for mammals is shown (Extinct = EX, Extinct in the Wild = EW, Critically Endangered = CR, Endangered = EN, Vulnerable = VU, Near Threatened = NT, Least Concern = LC, Data Deficient = DD, Not Evaluated = NE (IUCN 2007)). Weights are taken from * Kumpel (2006), † Kingdon (1997), ‡ Estimate, § Average for the Genus from Kumpel (2006). Taxonomic classification followed that of Kingdon (1997).

Taxon	Common name	Scientific name	IUCN status	Recorded number of carcasses	Est.annual offtake (carcasses)	Average weight (kg)
Primates	Black colobus	<i>Colobus satanus</i>	VU	506	546.48	9.23*
	Mandrill	<i>Mandrillus sphinx</i>	VU	223	240.84	8.80*
	Putty nosed monkey	<i>Cercopithecus nictitans</i>	LC	355	383.40	5.00*
	Moustached monkey	<i>Cercopithecus cephus</i>	LC	249	268.92	3.60*
	Chimpanzee	<i>Pan troglodytes</i>	EN	23	24.84	34.00*
	Crowned monkey	<i>Cercopithecus pogonais</i>	LC	63	68.04	3.70*
	Unknown guenon	<i>Cercopithecus.spp</i>		5	5.40	9.83§
	De Brazza's monkey	<i>Cercopithecus neglectus</i>	LC	1	1.08	6.00†
	Northern talapoin	<i>Miopithecus onguensis</i>	LC	4	4.32	1.20*
	Potto	<i>Perodicticus potto edwardsi</i>	LC	3	3.24	1.20*
	Golden angwantibo	<i>Artocebus aureus</i>	NT	3	3.24	0.24†
Hyracoidea	Tree hyrax	<i>Dendrohyrax arboreus</i>	LC	3	3.24	2.80*
	Demidoffs galago	<i>Galagoides demidoff</i>	LC	2	2.16	0.06*
Artiodactyla	Blue duiker	<i>Philantomba monticola</i>	LC	2287	2,469.96	4.70*
	Bay duiker	<i>Cephalophus dorsalis</i>	NT	335	361.80	17.00*
	Red river hog	<i>Potamochoerus porcus</i>	LC	29	31.32	29.40*
	Water chevrotain	<i>Hyemoschus aquaticus</i>	DD	30	32.40	9.00*
	Yellow-backer duiker	<i>Cephalophus silvicultor</i>	NT	4	4.32	36.50*
	Sitatunga	<i>Tragelaphus spekei</i>	NT	3	3.24	38.70*
	Bush buck	<i>Tragelaphus scriptus</i>	LC	4	4.32	29.00*
	Ogilby's duiker	<i>Cephalophus ogilbyi</i>	NT	4	4.32	17.00†
	Dwarf antelope	<i>Neotragus batesi</i>	NT	24	25.92	2.30*
	Black-fronted duiker	<i>Cephalophus nigrifrons</i>	NT	1	1.08	16.00†
	Brush-tailed porcupine	<i>Atherurus africanus</i>	LC	1612	1,740.96	3.20*
Rodentia	Giant pouched rat	<i>Cricetomys emini</i>	LC	521	562.68	1.10*
	Marsh cane rat	<i>Thrinomys swinderianus</i>	LC	58	62.64	4.40*
	Red-legged sun squirrel	<i>Heliosciurus rufobrachium</i>	LC	8	8.64	0.33†
	Rope squirrels	<i>Funisciurus.spp</i>	DD/LC	9	9.72	0.15*
	Biafran bight palm squirrel	<i>Epixerus wilsoni</i>	DD	1	1.08	0.56†
	African pygmy squirrel	<i>Myosciurus pumilio</i>	DD	1	1.08	0.02†
	Tree pangolin	<i>Phataginus tricuspis</i>	LC	657	709.56	1.90*
Pholidota	Giant pangolin	<i>Smutsia gigantea</i>	LC	25	27.00	20.40*
	Servaline genet	<i>Genetta servalina</i>	LC	77	83.16	1.70*
	African palm civet	<i>Nandinia binotata</i>	LC	43	46.44	2.40*
	Swamp otter	<i>Aonyx congica</i>	DD	4	4.32	20.00†
	Marsh mongoose	<i>Atilax paludinosus</i>	LC	26	28.08	3.00*
	Cuisimanse	<i>Crossarchus platycephalus</i>	LC	34	36.72	1.10*
	Long-snouted mongoose	<i>Herpestes naso</i>	LC	12	12.96	3.00*
	African civet	<i>Civettictis civetta</i>	LC	5	5.40	6.00*
	Leopard	<i>Panthera pardus</i>	LC	1	1.08	23.00†
	Black-legged mongoose	<i>Bdeogale nigripes</i>	LC	3	3.24	2.00*
	Central african linsang	<i>Poiana richardsoni</i>	LC	1	1.08	0.60†

Reptilia	Forest hingeback tortoise	<i>Kinixys erosa</i>		910	982.80	1.7*
	Dwarf crocodile	<i>Osteolaemus tetrapis</i>		64	69.12	4.44*
	Monitor lizard	<i>Varanus niloticus</i>		21	22.68	3.83*
Aves	Black Guinea fowl	<i>Agelastes niger</i>	LC	231	249.48	0.90*
	Black-casqued Hornbill	<i>Ceratogymna atrata</i>	LC	38	41.04	1.5†
	Vulturine fish eagle	<i>Gypohierax angolensis</i>	LC	5	5.40	4.00‡
	Great blue turaco	<i>Corythaeola cristata</i>	LC	15	16.20	1.30*
	Crowned Hawk-Eagle	<i>Stephanoaetus coronatus</i>	LC	4	4.32	3.00†
	Plumed guinea fowl	<i>Guttera plumifera</i>	LC	8	8.64	1.00*
	Scaly Francolin	<i>Francolinus squamatus</i>	LC	2	2.16	0.50†
	Nkulengu rail	<i>Himantornis haematopus</i>	LC	1	1.08	0.50†
Unknown	Snake			3	3.24	2.00†
	Bird			6	6.48	2.00‡
	Mammal			1	1.08	0.00
Total				8568	9253	

Appendix 8.3 continued.

Taxon	Common name	Estimated annual biomass (kg)	Carcass % of total offtake	Biomass % of total offtake	Carcass offtake rate (carcasses/km ² /yr)	Biomass offtake rate (kg/km ² /yr)
Primates	Black colobus	5,044.80	5.91	11.975	2.14	19.76
	Mandrill	2,119.39	2.60	5.031	0.94	8.30
	Putty nosed monkey	1,917.00	4.14	4.551	1.50	7.51
	Moustached monkey	968.11	2.91	2.298	1.05	3.79
	Chimpanzee	844.56	0.27	2.005	0.10	3.31
	Crowned monkey	251.75	0.74	0.598	0.27	0.99
	Unknown guenon	53.08	0.06	0.126	0.02	0.21
	De Brazza's monkey	6.48	0.01	0.015	0.00	0.03
	Northern talapoin	5.18	0.05	0.012	0.02	0.02
	Potto	3.89	0.04	0.009	0.01	0.02
Hyracoidea	Golden angwantibo	0.76	0.04	0.002	0.01	0.00
	Tree hyrax	9.07	0.04	0.022	0.01	0.04
	Demidoffs galago	0.13	0.02	0.000	0.01	0.00
Artiodactyla	Blue duiker	11,608.81	26.69	27.557	9.67	45.46
	Bay duiker	6,150.60	3.91	14.600	1.42	24.09
	Red river hog	920.81	0.34	2.186	0.12	3.61
	Water chevrotain	291.60	0.35	0.692	0.13	1.14
	Yellow-backer duiker	157.68	0.05	0.374	0.02	0.62
	Sitatunga	125.39	0.04	0.298	0.01	0.49
	Bush buck	125.28	0.05	0.297	0.02	0.49
	Ogilby's duiker	73.44	0.05	0.174	0.02	0.29
	Dwarf antelope	59.62	0.28	0.142	0.10	0.23
	Black-fronted duiker	17.28	0.01	0.041	0.00	0.07
Rodentia	Brush-tailed porcupine	5,571.07	18.81	13.224	6.82	21.82
	Giant pouched rat	618.95	6.08	1.469	2.20	2.42
	Marsh cane rat	275.62	0.68	0.654	0.25	1.08
	Red-legged sun squirrel	2.81	0.09	0.007	0.03	0.01
	Rope squirrels	1.46	0.11	0.003	0.04	0.01
	Biafran bight palm squirrel	0.60	0.01	0.001	0.00	0.00
Pholidota	African pygmy squirrel	0.02	0.01	0.000	0.00	0.00
	Tree pangolin	1,348.16	7.67	3.200	2.78	5.28
	Giant pangolin	550.80	0.29	1.307	0.11	2.16

Carnivora	Servaline genet	141.37	0.90	0.336	0.33	0.55
	African palm civet	111.46	0.50	0.265	0.18	0.44
	Swamp otter	86.40	0.05	0.205	0.02	0.34
	Marsh mongoose	84.24	0.30	0.200	0.11	0.33
	Cuisimanse	40.39	0.40	0.096	0.14	0.16
	Long-snouted mongoose	38.88	0.14	0.092	0.05	0.15
	African civet	32.40	0.06	0.077	0.02	0.13
	Leopard	24.84	0.01	0.059	0.00	0.10
	Black-legged mongoose	6.48	0.04	0.015	0.01	0.03
	Central african linsang	0.65	0.01	0.002	0.00	0.00
Reptilia	Forest hingeback tortoise	1,670.76	10.62	3.966	3.85	6.54
	Dwarf crocodile	306.73	0.75	0.728	0.27	1.20
	Monitor lizard	86.97	0.25	0.206	0.09	0.34
Aves	Black Guinea fowl	224.53	2.70	0.533	0.98	0.88
	Black-casqued Hornbill	61.56	0.44	0.146	0.16	0.24
	Vulturine fish eagle	21.60	0.06	0.051	0.02	0.08
	Great blue turaco	21.06	0.18	0.050	0.06	0.08
	Crowned Hawk-Eagle	12.96	0.05	0.031	0.02	0.05
	Plumed guinea fowl	8.64	0.09	0.021	0.03	0.03
	Scaly Francolin	1.08	0.02	0.003	0.01	0.00
	Nkulengu rail	0.54	0.01	0.001	0.00	0.00
	Snake	6.48	0.04	0.015	0.01	0.03
Unknown	Bird	12.96	0.07	0.031	0.03	0.05
	Mammal	0.00	0.01	0.000	0.00	0.00
Total		42127				

Appendix 8.4

Table of full Distance analyses outputs showing the number of encounters, encounter rate, individual and group density estimates and 95% confidence limits, the effective strip width, the model used to estimate the detection function (HR = Hazard rate, HNCos = Half Normal cosine and HRsim = Hazard rate simple polynomial), the detection probability and the data truncation length.

Species	<i>C. nictitans</i>						<i>C. cephus</i>						<i>C. satanas</i>					
	Pueblo	Nseng Midyobo	Mitong	Miang	Esong	Boculu	Pueblo	Nseng Midyobo	Mitong	Miang	Esong	Boculu	Pueblo	Nseng Midyobo	Mitong	Miang	Esong	Boculu
Survey site																		
Total encounters (n)	9	18	25	26	7	16	9	19	15	25	13	20	4	14	13	17	8	16
Encounter rate (n/L) per km	0.09	0.11	0.31	0.32	0.10	0.14	0.09	0.12	0.19	0.31	0.18	0.17	0.04	0.09	0.16	0.21	0.11	0.14
Individuals/km ² (D)	11.41	20.83	91.74	97.74	27.15	29.10	21.81	36.08	80.99	87.28	55.14	47.28	4.70	20.26	42.89	47.67	29.86	34.47
D Upper 95% Conf. Int.	41.82	49.28	180.97	226.19	82.60	50.56	43.98	58.31	148.03	235.14	127.60	102.96	30.44	62.86	144.26	91.82	76.90	83.67
D Lower 95% Conf. Int.	3.11	8.80	46.51	41.71	8.92	16.75	10.82	22.33	44.31	32.40	23.83	21.71	0.73	6.53	12.75	24.75	11.59	14.21
Clusters/km ² (DS)	1.83	2.26	6.18	6.46	1.92	2.76	1.98	2.58	4.01	6.71	3.85	3.72	0.75	1.62	2.97	3.90	2.02	2.54
DS Upper 95% Conf. Int.	7.15	5.28	12.24	15.17	6.12	4.63	4.11	4.18	7.47	18.65	9.38	8.35	1.11	5.10	10.14	7.45	5.15	6.17
DS Lower 95% Conf. Int.	0.47	0.97	3.12	2.75	0.60	1.64	0.96	1.59	2.15	2.42	1.58	1.66	0.51	0.52	0.87	2.04	0.79	1.05
Cluster size (S)	6.22	9.22	14.84	15.04	14.14	10.56	11.00	14.00	20.20	13.00	14.31	12.70	6.25	12.50	14.46	12.24	14.75	13.56
CS Upper 95% Conf. Int.	13.36	15.07	17.81	17.27	23.39	14.03	15.99	17.88	23.58	15.57	19.25	15.28	44.46	16.16	18.67	14.26	22.88	16.65
CS Lower 95% Conf. Int.	2.90	5.65	12.37	13.10	8.55	7.95	7.57	10.96	17.31	10.85	10.64	10.57	1.00	9.67	11.20	10.50	9.51	11.05
Effective strip width (ESW)	24.96	24.96	24.96	24.96	24.96	24.96	23.09	23.09	23.09	23.09	23.09	23.09	23.09	27.06	27.06	27.06	27.06	27.06
Model used	HR sim	HR sim	HR sim	HR sim	HR sim	HR sim	HR sim	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos	HR	HR	HR	HR	HR
Detection probability (p)	0.42	0.42	0.42	0.42	0.42	0.42	0.38	0.38	0.38	0.38	0.38	0.38	0.50	0.50	0.50	0.50	0.50	0.50
Truncation length (m)	60.00	60.00	60.00	60.00	60.00	60.00	60.00	60.00	60.00	60.00	60.00	60.00	60.00	55.00	55.00	55.00	55.00	55.00

Appendix 8.4 continued.

Species	<i>P. monticola</i>										<i>C. pogonias</i>									
Survey site																				
Total encounters (n)	4	5	8	4	8	4	8	11	10	23	11	19	2	11						
Encounter rate (n/L) per km	0.14	0.25	0.33	0.22	0.47	0.46	0.10	0.14	0.14	0.14	0.24	0.03	0.09							
Individuals/km ² (D)	13.14	28.19	25.94	17.80	41.23	40.09	25.84	42.38	47.26	68.16	4.93	26.07								
D Upper 95% Conf. Int.	58.92	93.63	50.10	44.88	135.22	98.835	112.79	103.07	215.84	119.58	82.28	57.95								
D Lower 95% Conf. Int.	2.93	8.49	13.43	7.06	12.57	16.261	5.92	17.43	10.35	38.85	0.30	11.73								
Clusters/km ² (DS)	8.76	15.66	20.76	14.24	29.98	29.40	1.93	2.73	2.57	4.47	0.52	1.79								
DS Upper 95% Conf. Int.	42.02	53.57	39.85	35.97	102.25	74.11	8.98	6.90	12.31	7.94	6.67	4.14								
DS Lower 95% Conf. Int.	1.83	4.58	10.81	5.64	8.79	11.66	0.41	1.08	0.54	2.51	0.04	0.78								
Cluster size (S)	1.50	1.80	1.25	1.25	1.38	1.36	13.40	15.52	18.36	15.26	9.50	14.55								
CS Upper 95% Conf. Int.	2.75	2.45	1.70	2.35	1.88	1.75	19.04	19.54	24.31	17.83	65845	19.33								
CS Lower 95% Conf. Int.	1.00	1.32	1.00	1.00	1.01	1.06	19.04	19.54	24.31	17.83	1.00	10.94								
Effective strip width (ESW)	7.84	7.84	7.84	7.84	7.84	7.84	26.39	26.39	26.39	26.39	26.39	26.39								
Model used	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos	HN cos								
Detection probability (p)	0.33	0.33	0.33	0.33	0.33	0.33	0.38	0.38	0.38	0.38	0.38	0.38								
Truncation length (m)	24.00	24.00	24.00	24.00	24.00	24.00	70.00	70.00	70.00	70.00	70.00	70.00								

Appendix 8.5

List of species present in the study area, from Kingdon (1997), Perlo (2002)

Taxon	Common name	Scientific name
PRIMATES	Potto	<i>Perodicticus potto edwardsi</i>
	Putty nosed monkey	<i>Cercopithecus nictitans</i>
	Elegant needle clawed galago	<i>Euoticus elegantulus</i>
	Allen's squirrel galago	<i>Galago alleni gabonensis</i>
	Chimpanzee	<i>Pan troglodytes</i>
	Mandrill	<i>Mandrillus sphinx</i>
	Crowned monkey	<i>Cercopithecus pogonais</i>
	De Brazza's monkey	<i>Cercopithecus neglectus</i>
	Grey-cheeked mangabey	<i>Lophosebus albigena</i>
	Golden angwantibo	<i>Artocebus aureus</i>
	Western lowland gorilla	<i>Gorilla gorilla gorilla</i>
	Moustached monkey	<i>Cercopithecus cephus</i>
	Black colobus	<i>Colobus satanus</i>
	Demidoffs galago	<i>Galagoides demidoff</i>
	Northern talapoin	<i>Miopithecus talapoin</i>
UNGULATES	White-bellied duiker	<i>Cephalophus leucogaster</i>
	Red river hog	<i>Potamochoerus porcus</i>
	Buffalo	<i>Synceros caffer nana</i>
	Bush buck	<i>Tragelaphus scriptus</i>
	Ogilby's duiker	<i>Cephalophus ogilbyi</i>
	Peter's duiker	<i>Cephalophus callypigus</i>
	Sitatunga	<i>Tragelaphus spekei</i>
	Yellow-backer duiker	<i>Cephalophus silvicultor</i>
	Black-fronted duiker	<i>Cephalophus nigrifrons</i>
	Dwarf antelope	<i>Neotragus batesi</i>
	Blue duiker	<i>Philantomba monticola</i>
	Bay duiker	<i>Cephalophus dorsalis</i>
	Water chevrotain	<i>Hyemoschus aquaticus</i>
	Hippo	<i>Hippopotamus amphibius</i>
	Elephant	<i>Loxodonta africana cyclotis</i>
RODENTS	Tree hyrax	<i>Dendrohyrax arboreus</i>
	Marsh cane rat/grasscutter	<i>Thriomys swinderianus</i>
	Climbing mice	<i>Dendromys spp.</i>
	Red-legged sun squirrel	<i>Heliosciurus rufobrachium</i>
	Giant pouched rat (emin's rat)	<i>Cricetomys emini</i>
	Biafran bight palm squirrel	<i>Epixerus wilsoni</i>
	Brush-tailed porcupine	<i>Atherurus africanus</i>
	African giant squirrel	<i>Protoxerus strangeri</i>
	African pygmy squirrel	<i>Myosciurus pumilio</i>
	beecrofts/lesser anomalure	<i>A.beecrofti/pusillus</i>
	Common scaly tail	<i>Zenkerella insignis</i>
	Lord Derby's Anomalure	<i>Anomalurus deberianus</i>
	Ribboned rope squirrel	<i>Funisciurus lemniscatus</i>
	Fire footed rope squirrel	<i>Funisciurus pyrropus</i>
	Lady Burtons rope squirrel	<i>Funisciurus isabella</i>
INSECTIVORES	Red cheeked rope squirrel	<i>Funisciurus leucogenys</i>
	Green squirrel	<i>Paraxerus poensis</i>
PHOLIDOTA	Giant otter shrew	<i>Potamogale velox</i>
	Giant pangolin	<i>Smutsia gigantea</i>
CARNIVORES	Tree pangolin	<i>Phataginus tricuspis</i>
	Long-tailed pangolin	<i>Uromanis tetradactyla</i>
CARNIVORES	Golden cat	<i>Felis aurata</i>
	Slender mongoose	<i>Herpestes sanguineus</i>
	Long-snouted mongoose	<i>Herpestes naso</i>

Taxon	Common name	Scientific name
BIRDS	Marsh mongoose	<i>Atilax paludinosus</i>
	Swamp otter	<i>Aonyx congicus</i>
	Black-legged mongoose	<i>Bdeogale nigripes</i>
	Blotched genet	<i>Genetta tigrina</i>
	Servaline genet	<i>Genetta servalina</i>
	African civet	<i>Civettictis civetta</i>
	Spot-necked otter	<i>Lutra maculicollis</i>
	African palm civet	<i>Nandinia binotata</i>
	Leopard	<i>Panthera pardus</i>
	Cuisimanse	<i>Crossarchus platycephalus</i>
	Central african linsang	<i>Poiana richardsoni</i>
	African woodowl	<i>Strix woodfordii</i>
	Vermiculated fishing owl	<i>Scotopelia ussheri</i>
	Fulvous whistling duck	<i>Dendrocygna bicolor</i>
	Vulturine fish eagle (Palm-nut Vulture)	<i>Gypohierax angolensis</i>
	Black Guinea fowl	<i>Agelastes niger</i>
	African grey parrot	<i>Psittacus erithacus</i>
	Nkulengu rail	<i>Himantornis haematopus</i>
	Great blue turaco	<i>Corythaeola cristata</i>
	Brown cheeked hornbill	<i>Ceratogimna cylindricus</i>
	Afep pidgeon	<i>Columba unicuncta</i>
	Shelly's eagle owl	<i>Bubo shelleyi</i>
	Plumed guinea fowl	<i>Guttera plumifera</i>
	African geen pidgeon	<i>Treron calva</i>
	Scaly Francolin	<i>Francolinus squamatus</i>
	Turtle-dove	<i>Streptopelia spp</i>
	Black-casqued Hornbill	<i>Ceratogymna atrata</i>
	Spot-breasted Ibis	<i>Bostrichia rara</i>
	Crowned Hawk-Eagle	<i>Stephanoaetus coronatus</i>
	Plaintain eater	<i>Crinifer piscator</i>
	African fish eagle	<i>Haliaeetus vocifer</i>
	African Goshawk	<i>Accipter tachiro</i>
	Latham's francolin	<i>Francolinus latham</i>
	Helmeted guinea fowl	<i>Numida meleagris</i>
	Red Billed dwarf hornbill	<i>Tockus camurus</i>
	Grey-necked picathartes	<i>picathartes oreas</i>
REPTILES	Woodpecker	<i>Lybius bidentatus</i>
	Forest hingeback tortoise	<i>Kinixys erosa</i>
	African Forest Turtle	<i>Pelusios gabonensis</i>
	Gabon viper	<i>Bitis gabonica</i>
	Slender-snouted crocodile	<i>Crocodylus cataphractus</i>
	Caiman/Monitor lizard	<i>Varanus niloticus</i>
	Dwarf crocodile	<i>Osteolaemus tetrapis</i>
	African rock python	<i>Python sebae</i>
	Cameleon	<i>Chamaleo cristatus</i>
	Goliath frog	<i>Conraua goliath</i>
AMPHIBIANS		

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