Herbivory and Biodiversity Conservation of the Savannah Habitats in Akagera National Park, Rwanda

Callixte Gatali

Department of Biological and Environmental Sciences
Faculty of Science

UNIVERSITY OF GOTHENBURG

Doctoral thesis for the degree of Doctor of Philosophy in Applied Environmental Science

The thesis will be publicly defended on Friday 26th April, 2013, at 14 p.m., in Hörsalen, Department of Biological and Environmental Sciences, Carl Skottbergs gata 22B, Göteborg.

Faculty opponent: Beth A. Kaplin, PhD, Dept. of Environmental Studies, Antioch University New England, USA.
Examiner: Professor Ulf Molau, Dept. of Biological and Environmental Sciences, University of Gothenburg, Sweden.

ISBN: 978-91-85529-56-8
http://hdl.handle.net/2077/32604

ISBN: 978-91-85529-56-8
Summarizing chapter for thesis is available at:
http://hdl.handle.net/2077/32604
Cover page photography: Kjell Wallin

Department of Biological and Environmental Sciences
University of Gothenburg, Sweden
Printed by Ineko AB, Kållered

Herbivory and Biodiversity Conservation of the Savannah Habitats in Akagera National Park, Rwanda

Callixte Gatali
Department of Biological and Environmental Sciences
University of Gothenburg, 2013

ABSTRACT

Savannahs make up about 20% of the world's land surface, whereas African savannahs constitute 50% of the land area and have been used as parks to conserve nature and for outdoor recreation. However, conserving biodiversity in these ecosystems has been challenging due to increasing pressures, potential loss of habitat and species or lack of up-to-date data in some of the protected areas. In this thesis, I investigated the state of biodiversity in Akagera National Park (ANP), Rwanda, and factors affecting its distribution. The work of this thesis is based on the results of large-scale, replicated point counts and presence-absence surveys conducted between August 2009 and August 2011 in the savannah habitats of the park. ANP plays an important role in conserving about 525 bird species known from the park and > 50 species of large mammals. Systematic plots of equally-spaced 1-km^2 (n = 266) were used for both bird and large mammal censuses. The Chao2 estimator and the Simpson index were used to estimate and compare bird species richness and diversity, respectively, between inside and outside the park. Generalized linear models (GLMs) were used to investigate relationships between bird diversity and habitat structure, whereas Distance sampling methods were used for estimating both population sizes and densities of large mammals.

Despite recent important changes in habitats and fauna of the ANP, the results of this thesis show that the park has maintained an important diversity of birds. The 301 bird species recorded during my study represents 43% of Rwanda's checklist of birds (i.e. 697 species), underlining that ANP still contributes to the conservation of birds (Paper I). The results highlight that ANP still maintained special and important ornithological features, including the presence of endemic species of the Lake Victoria region, globally threatened species, those that have not previously been recorded in Akagera and a large number of Palearctic and Afrotropical migrants (Paper I). The abundance of bird species was found to be linked to human influence (Paper II). In fact, this thesis found large human effects on both the grassland habitat (e.g. reduction of grass biomass and the presence of tall grass by 57% and 76%, respectively) and bird species richness which significantly varied between inside and outside the park due to different land use practices between the two types of habitat. However, human activities did not affect species diversity.

This thesis further revealed significant relationships between habitat structure and bird species richness that varied between inside and outside the park (Paper III). However, habitat structure did not correlate with species diversity. Paper III also demonstrated that single savannah species use habitats differently due to individual niche characteristics and niche interactions with other species. Estimates of the total population and density of large mammals varied for each species and the most abundant large herbivores were impalas, buffaloes, topis, baboons and zebras (Paper IV). High population sizes and densities of Ankolé found both inside and outside the park might have an impact on wildlife. Similarly, large population sizes of large mammals that are still outside the park pose a conservation challenge. Compared to previous surveys of the park (e.g. 1990, 1997/1998, 2002 & 2010), the findings of this thesis demonstrate that most large wild herbivores declined between 1990 and 2011 except zebras, warthogs and duikers that rather increased. Habitat structure was also found to affect the distribution and abundance of large mammals. Finally, I hope that my results provide new inputs for further strengthening of efforts to conserve the park's biodiversity and might be useful for further assessment of the relationships between species diversity/richness and community stability as well as ecosystem function.

Keywords: Akagera National Park, biodiversity, birds, East Africa, habitat structure, human impact, landscape and local/plot scales, large herbivores, Rwanda, savannah, species-habitat relationship, species- richness, detectability, diversity.

LIST OF PAPERS

This thesis is based on the following four papers, which are referred to in the text by use of Roman numerals.

I. Callixte Gatali and Kjell Wallin. Bird diversity in the savannah habitats of Akagera National Park, Rwanda, in the post-war recovery period. Accepted with minor corrections (Journal: *Ostrich*)

II. Callixte Gatali and Kjell Wallin. Human impact on vegetation structure and bird diversity in savannah habitats of the Akagera National Park, Rwanda. Submitted manuscript (Journal: *Bird Study*).

III. Callixte Gatali and Kjell Wallin. Avian diversity- habitat structure relationships in *Acacia*-savannah of the Akagera National Park, Rwanda. Manuscript.

IV. Callixte Gatali and Kjell Wallin. Population size estimates of large mammals and effects of vegetation structure in Akagera National Park, Rwanda. Manuscript.

LIST OF ABBREVIATIONS

AIC : Akaike Information Criterion
ANP : Akagera National Park
CBD : Convention on Biological Diversity
CDS : Conventional Distance Sampling
CEESD : Centre for Environment, Entrepreneurship and Sustainable Development
CITES : Convention on International Trade in Endangered Species
GIS : Geographical Information Systems
GTZ : Germany Technical Cooperation
IUCN : International Union for the Conservation of Nature
MINITERE: Ministry of Lands, Resettlement and Environment
NISR : National Institute of Statistics of Rwanda
NUR : National University of Rwanda
ORTPN : "Office Rwandais du Tourisme et des Parcs Nationaux" (presently Rwanda Development Board-Tourism & Conservation Department, RDB- T&C)
RDB : Rwanda Development Board
SIDA : Swedish International Development Agency
WCS : Wildlife Conservation Society

TABLE OF CONTENTS

1. INTRODUCTION

In Africa, most large protected areas, established for the conservation of wildlife, are found in savannah habitats, where they typically support increasing populations of large mammals and birds (Balmford *et al*. 1992, de Klerk *et al*. 2004). According to Shorrocks (2007) different types of savannahs in Africa make up 50% of the land area and create a fascinating network of plant, mammal and bird species interactions. In addition, these savannah ecosystems play important roles as parks and reserves to conserve nature and for outdoor recreation (Child 2004, Wiegand *et al*. 2006, Gottschalk *et al*. 2007). But potential loss of biodiversity in some of the protected areas or lack of data for others has been a big concern for their effective conservation and management (Homewood & Brockington 1999). To optimize conservation efforts within a biogeographical region, quantitative information is needed of the species present, which should be prioritized for conservation, and what their needs are or management interventions these require (Dolman *et al*. 2012).

In Rwanda, significant biodiversity lies within the country's protected areas (Chemonics International 2008). This biodiversity is an important source of ecosystem services for local livelihoods and a significant component of the country's economy through tourism revenues (MINITERE 2003, Twagiramungu 2006, Chemonics International 2008, Nahayo & Yansheng 2009, Republic of Rwanda 2011). However, maintenance of biodiversity in Rwanda is still critical due to progressive disappearance of national parks (reduction in size) and loss of habitats and species (World Bank 2004, Wong *et al*. 2005).

Why did this thesis focus on Akagera National Park (ANP)? As one of the three national parks of Rwanda and the only savannah habitat in the country, ANP has experienced important changes in its habitats and wildlife over the last 22 years, especially following the 1990-1994 war in the country, which culminated into the 1994 genocide with serious consequences not only to human lives and livelihoods but also biodiversity (Kanyamibwa 1998, Lamprey 2002, MINITERE 2003). In fact, losses in biodiversity have been estimated at more than 60% of the park area that was converted into farmland, 50-80% of large mammals and 13% of birds (Kanyamibwa 1998, Plumptre *et al.* 2001, Lamprey 2002, MINITERE 2003, Twagiramungu 2006, Chemonics International 2008). Increasing human population pressures and needs for resettlement were among the main causes of these losses (Kanyamibwa 1998, MINITERE 2003, Chemonics International 2008, Nahayo & Yansheng 2009). During the post-war recovery period, compared to other national parks, Akagera did neither benefit from adequate scientific research nor necessary conservation or human resource support for the revival of its biodiversity (Rutagarama & Martin 2006). However, ANP still has the potential for the protection and conservation of an important diversity of birds (e.g. 525 species known from the park) and > 50 species of large mammals typical of East African savannahs as well as > 900 species of plants of which 6 orchids are internationally protected (Vande weghe 1990, Kanyamibwa 1998, Lamprey 2002, MINITERE 2003:13, Vande weghe & Vande weghe 2011).

Therefore, the main goal of this thesis is to assess the current status of biological diversity in ANP, clarify the impacts of human activities on the structure of habitat and bird diversity, investigate bird diversity-habitat relationships and determine the population sizes and density of large mammals. This thesis applied appropriate methods for estimating the park's biodiversity (e.g. bird species richness and diversity & large mammal population size), quantifying the effects of human influence on bird diversity and analyzing bird diversity-habitat relationships, considering a proper sampling and species detectability.

The methodology used in this thesis might be an appropriate tool for future monitoring of biodiversity in ANP over time and space. This thesis also wants to demonstrate the regional (e.g. East Africa and/or sub-Saharan Africa) and international ornithological importance of ANP and the need to focus conservation priorities.

1.1 Biological diversity: definitions and different measures

'Biological diversity' or 'Biodiversity' has been defined as the 'variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part' (Magurran 2004: 6). It encompasses three components: *genetic diversity* (within-species diversity), *species diversity* (number of species), and *ecological diversity* (diversity of communities, p.6). Malcolm *et al*. (2007) define biodiversity as the variety of life in all its forms (plants, animals, fungi, bacteria, and other microorganisms) and at all levels of organization (e.g. genes, species and ecosystems). The above definition implies that biodiversity includes these structural components and functional components (e.g. ecological and evolutionary processes through which genes, species and ecosystems interact with one another and with their environment, p.33). Another definition of biodiversity which involves abundance pattern is provided by Magurran (2004): 'Biodiversity is the variety and abundance of species in a defined unit of study' (p.8). Buckland *et al*. (2005) have easily defined abundance as total numbers of individuals or the density of individuals, though biomass or percentage ground cover (for terrestrial plants) may also be appropriate measures.

Biodiversity can have a diversity of meanings and it is important to distinguish it from species richness, e.g. the number of species present in a defined geographical unit (Begon *et al*. 2006: 602). The important role of species richness in conservation planning has been recognized by Begon *et al*. (2006:602) who argue that knowledge of the spatial distribution of species richness is a prerequisite for prioritizing conservation efforts both at a large scale and at regional and local scale. The authors further describe a range of factors influencing species richness that include spatially varying factors (e.g. productivity, spatial heterogeneity and environmental harshness) and temporally varying factors such as climatic variation, environmental age and habitat area. The relationship between species richness and habitat or species niche is one of the most consistent of all ecological patterns (Begon *et al*. 2006, Franklin 2009); I investigated this relationship in **Paper III.**

The aim of measuring biodiversity is to determine if one domain is more diverse than another, or whether diversity has changed over time (Magurran 2004:12). Obviously, the community is the natural ecological unit with its boundaries in space and time as well as the interactions among species that make up the community or several communities (p.12). When measure of biodiversity is to be used mainly to assess changes in biodiversity over time, Buckland *et al*. (2005) propose three aspects of biodiversity that are of primary interest: number of species, overall abundance, and species evenness (e.g. high evenness occurs when many species have similar abundance, with no single species dominating).

Species richness is the most commonly used measure of biological diversity in ecology and conservation, therefore estimating species richness is of crucial importance when dealing with the conservation and management of biodiversity (Boulinier *et al*. 1998, Magurran 2004).

But, due to strong dependency on sample size and the presence of rare species in the sample, observed species richness can seriously underestimate actual species richness (Lande *et al.* 2000). A common approach of expressing estimates of species richness is as numerical species richness (e.g. number of species per specified number of individuals or biomass), or species density (Magurran 2004). To estimate species richness from samples, three approaches can be used: (1) species accumulation (species-area) curves; (2) parametric methods (e.g. log series and log normal distributions); and (3) non-parametric estimators like Chao2 (Colwell & Coddington 1994, Magurran 2004), which is used in this thesis. The traditional way of quantifying biological diversity is by using species diversity or heterogeneity measures (Magurran 2004). Heterogeneity measures or diversity indices combine the richness and evenness components of diversity (Magurran 2004:102). They include parametric measures of diversity (e.g. log series α, log normal λ and *Q* statistic) that are based on a parameter of a species abundance model and non-parametric measures such as the Shannon index and the Simpson's index (*D*) that are not linked to any specific species abundance models (pp.102-121). When comparing communities for example, Lande *et al.* (2000) advise the use of the Simpson diversity and species richness, which are applied in this thesis.

Buckland *et al.* (2005) argue that the use of just counts of number of species (species richness) for monitoring changes in biodiversity are prone to bias because detectability changes over time. Alternatively, they suggest the use of presence/absence of each species by quadrat and use the number (or proportion) of quadrats occupied by a species (occupancy) as an index of its abundance, which is used in this thesis. Pollock *et al.* (2002) have also emphasized the design of large-scale monitoring studies of wildlife that incorporate estimating detection probability. Different measures of species richness and diversity are discussed in detail by Magurran (2004) and Magurran and McGill (2011).

In this thesis, I focus attention on two important measures of diversity: Chao2 estimator for species richness and the Simpson's index, which is an estimate of species diversity (Gimaret-Carpentier *et al.*1998, Williams *et al.* 2002, Chiarruci *et al.* 2003, Chao 2005, Begon *et al.* 2006, Gorelick 2006). In ecology, abundance measures with animals and birds are problematic because of movement (Rivera-Milán & Bonilla-Martínez 2007), different life stages and size; therefore, a common measure of abundance is density (Magurran & McGill 2011). Because direct counts of species are often not possible, Distance sampling is one of the methods commonly used to estimate animal density in an area (Buckland *et al.* 2001, Pollock *et al.* 2002, Magurran & McGill 2011). Point transect as one of Distance-based methods for estimating density, has been described for its several logistic advantages over line transect sampling for bird surveys, especially in difficult terrain like Akagera (Buckland *et al.* 2001, Williams *et al.* 2002); I applied it in this thesis for estimating large mammal population sizes and densities.

Another important aspect to consider when estimating biodiversity is the scales at which biodiversity occurs. These have been defined as alpha or local diversity (α), beta diversity or differentiation (β) and gamma or regional diversity (γ), respectively (Koleff *et al.* 2003, Magurran 2004). The total regional diversity of a landscape (γ- diversity) is made up by local (α-) diversity and the difference in species composition (and sometimes species abundance), or turnover, between two or more local communities (β-diversity). Alpha diversity is the diversity of a defined assemblage or habitat and is the property of that spatial unit, whereas β-diversity (also called "species turnover" ψ in terms of ecosystem services) reflects a biotic change or species replacement (a measure of between-habitat diversity, Magurran 2004:162).

Beta diversity, the spatial turnover or change in the identities of species, is therefore a measure of the extent to which the diversity of two or more spatial units differs (local assemblages) or a measure of the difference in species composition between local and regional assemblages (Koleff *et al.* 2003, Magurran 2004, Magurran & McGill 2011). Koleff *et al.* (2003) reviewed different measures of beta diversity, based on presence-absence data. Antonsson (2012) also investigated differences in β-diversity as a measure of similarity and dissimilarity among communities. Magurran (2004:163) further defines delta (δ) diversity as the change in species composition (and abundance) that occurs between units of γ diversity within an area of epsilon (ε) diversity. She argues that the larger the difference of species composition between communities or sites, the higher is the total diversity at landscape scale.

1.2 Importance of biological diversity

The importance of biodiversity is largely recognized for its scientific study (e.g. Rosenzweig 1995) and conservation (e.g. Ranta *et al.* 1999). The value of the Earth's biological resources is also recognized for their contribution to humanity's economic and social development' (CBD 2011a). According to Rands *et al.* (2010), substantial contributions of biodiversity to society include provisions of food, medicines, fiber, timber, climate regulation, nutrient cycling, recreation, agricultural development (e.g. pollination and pest control), carbon storage and sequestration and positive effects on human physical and mental health. In Africa, many poor people directly rely on natural resources for their everyday life (Egoh *et al.* 2012). This is also the case for Rwanda where a large proportion of the population directly depends upon biological resources for subsistence purposes such as the gathering, harvesting or hunting of animals and plants for food, medicine, shelter, fuel, building materials and trade (Republic of Rwanda 2011).

Worldwide, biological diversity is recognized as a global asset of tremendous value to present and future generations (CBD 2011a) which needs to be managed in a sustainable way. This implies that national governments should have clear policies that address conservation and protection of biodiversity, and demonstrate a great commitment for the implementation of these policies as well as different international Conventions they ratified, e.g. the Convention of Biological Diversity (CBD). Conservation priorities should be coupled with the 'Strategic plan for Biodiversity 2011-2020 and the Aichi Targets' as well as the 'Nagoya Protocol (adopted in 2010) on Access and Benefit-Sharing' (CBD 2011a, 2011b). Egoh *et al*. (2012) provide a descriptive review of ecosystem services and their importance across Africa and present new approaches that have been tested in Africa for conserving biodiversity.

Rands *et al*. (2010) recognize that conservation efforts have been increasing worldwide and conservation approaches have been developed to addressing biodiversity loss. They also point out that despite these efforts pressures on biodiversity continue to increase, resulting in massive loss of species. These pressures include overexploitation of species, pollution, climate change, invasive alien species, degradation, fragmentation and destruction of habitats. Lovejoy and Hannah (2005) emphasize for example that climate is now warming rapidly, causing alterations in biodiversity already facing multiple threats. The synergy between climate change and habitat fragmentation is the most threatening aspect of climate change for biodiversity (Lovejoy & Hannah 2005: 4). To reverse biodiversity decline, Rands *et al.* (2010) recommend to: (1) manage biodiversity as a public good; (2) integrate biodiversity into public and private decision-making; and (3) create enabling conditions for policy implementation.

1.3 Characteristics of African savannahs and maintenance of biodiversity in Rwanda

Savannahs are tropical and subtropical grasslands, extremely diverse, with scattered bushes and trees (Shorrocks 2007, Vande weghe & Vande weghe 2011). They occupy a fifth of the earth's land surface and support large proportions of the world's human population, livestock and wildlife (Sankaran *et al.* 2005). Most savannahs occur in Africa (approx. 70%), with a smaller amount in South America, India and Australia (Shorrocks 2007). Savannahs occur around the Equator (between the Tropic of Capricorne and the Tropic of Cancer), where it is warm and relatively dry (Shorrocks 2007: 1). Interrelated factors involved in the formation of savannah vegetation include climate, soils, time, geomorphology, herbivores, hydrology, geology, laterization, natural fire, fire caused by humans and paleoclimate (Goudie, 2006:40). A combination of herbivory browsing and fire for example, can be used as a management tool to control tree cover (e.g. by suppressing tree establishment and density) and facilitate the coexistence of trees and grasses in savannahs (Staver *et al*. 2009).

As Shorrocks (2007) highlighted, the dominant grasses in savannahs tend to be C_4 plants that are capable of utilizing higher light intensities than C_3 plants, have greater maximum photosynthesis and consume less water in the process but are extremely poor quality food for most herbivores. He observes that the photosynthetic efficiency of many savannahs is very high due to these C_4 plants. The climate divides Africa into three main ecosystems: deserts, tropical rain forests and savannahs in between (Vande weghe 1990, Shorrocks 2007). Savannahs are more dynamic than forests in responding quickly and effectively to changes in their physical environment (Vande weghe 1990). Shorrocks (2007) made a detailed description of the biology of African savannahs. The Afrotropical region (Afrotropics) or sub-Saharan Africa, which is continental Africa south of 20ºN, is known to be an area of high richness of resident birds, Afrotropical endemics, intra-African migrants and Palearctic migrants (de Klerk *et al.* 2004).

Shorrocks (2007) also points out that savannah wildlife has an ecological, scientific, financial and aesthetic value but also a cost in terms of loss in human life, loss of property, crops, livestock and income. He argues that frequent conflicts between humans and wildlife might be due to specific interests of people living close to wildlife, that some protected areas are sited in regions of high population density or because of human interference (e.g. hunting, poaching, bush fires and habitat destruction, pp.229-234). In Akagera, similar wildlife-human conflicts have often resulted in farmers losing considerable amounts of their crops to wild animals, deaths of people and killings of livestock. Most damages are due to elephants, buffaloes and hippopotamuses. However, the Rwandan government has put in place compensation mechanisms (e.g. a recent Law on compensation from wildlife damage). Other conservation issues for ANP are related to livestock and wildlife using the same area for grazing, especially outside the protected area, which may result not only in intense competition but importantly in transmission of certain animal diseases (Kock 2004).

Rwanda (26,338 km^2) is covered by diversified natural ecosystems that accommodate an exceptional biodiversity of flora and fauna (Wong *et al.* 2005, Republic of Rwanda 2011, Vande weghe & Vande weghe 2011). As already mentioned these ecosystems are the primary sources of biodiversity and genetic resources and provide health and cultural benefits to people. Savannahs constitute 32% of these ecosystems (Wong *et al.* 2005).

However, maintaining biodiversity within protected areas has been a challenge for Rwanda mainly due to the progressive disappearance of national parks (e.g. reduction in size) and destruction of habitats (World Bank 2004, Wong *et al.* 2005).

Nonetheless, encouraging news is that Africa has registered strong increases in international wildlife tourism and receipts. For example between 2000 and 2005, international arrivals to Africa increased from 28 million to nearly 40 million (e.g. 5.6% growth per year), whereas receipts doubled from US$10.5 billion to US$21.3 billion, and most of this tourism is due to wildlife (Shorrocks 2007). According to the World Tourism Organization (2011), Rwanda registered an income of US$ 202 million in 2010 from international tourism. In his annual State of the Nation Address at the beginning of the New Year of 2013, the President of Rwanda highlighted that by October 2012, the tourism sector in Rwanda (mainly wildlife tourism) has generated US$ 232 million compared to US$ 204 million in 2011 (Kanyesigye 2013) and came to the first position in generating foreign currency for the country. Therefore, it is worthy protecting wildlife for its financial return through tourism, in addition to its aesthetic and scientific value (Shorrocks 2007). Importantly, for its sustainability, Akagera National Park has to generate incomes. Furthermore, conservation issues need to involve surrounding people and revenue sharing mechanisms already in place need regular improvement to ensure that these local people get benefits as well.

1.4 Historical background and conservation importance of ANP

Akagera National Park (ANP) is located in the eastern part of Rwanda along the Tanzanian border. It was established by decree dating from 1934 with an original size of 280,000 ha. In 1957 Umutara hunting area of 30, 000 ha was added (Vande weghe 1990, Kanyamibwa 1998). ANP is part of the 'Akagera ecosystem' extending from Rwanda and north-western Tanzania into south-western Uganda and combines *Acacia*-savannah habitats with open grasslands and flooded plains as well as dry forests (Vande weghe 1990, Kanyamibwa 1998, Averbeck *et al.* 2009). Compared to African standards, ANP is just a small park, however rich and varied with a virtually complete savannah ecosystem, several lakes and swamps (Kanyamibwa 2001). As a result of varied topography, ANP contains an important diversity of habitat types (see Vande weghe 1990, Kanyamibwa 2001, Vande weghe & Vande weghe 2011for a complete description). ANP is the only savannah habitat in Rwanda with a fauna, which is essentially east African and where typical savannah species (e.g. birds and mammals) occur (Vande weghe 1990, Chemonics International 2008, Vande weghe & Vande weghe 2011).

As Kanyamibwa (2001) previously pointed out, the park is currently not heavily populated by large mammals, it lacks massive concentrations of animals as one might encounter in other classical large East African parks in Tanzania, Uganda and Kenya. Key large mammals for the park include three species that are protected by the CITES (Convention on International Trade in Endangered Species) namely the African buffalo *Syncerus caffer*, African elephant *Loxodonta africana* and Eland *Taurotragus oryx* (MINITERE 2003, Twagiramungu 2006).
Other species present include the Giraffe *Giraffa camelopardalis*, Hippopotamus *Hippopotamus amphibius*, at least 8 species of antelope and 2-3 species of primates (Vande weghe 1990, Kanyamibwa 1998, 2001, Plumptre *et al.* 2001, Lamprey 2002). However, the Lion *Panthera leo* (also protected by the CITES), Black rhinoceros *Diceros bicornis* and Wild dog *Lycaon pictus* are thought to be locally extinct (Kanyamibwa 2001, Plumptre *et al.* 2001).

Bird diversity is probably the most important feature of Akagera National Park. Despite recent reduction in its size, Akagera still conserves many ornithological features and has been characterized as having one of the most diverse avifauna of Africa with several breeding residents, Palearctic and Afrotropical migrants, wetland and open water birds as well as endemics of sub-Saharan Africa (Kanyamibwa 1998, 2001, Lamprey 2002, Rutagarama & Martin 2006, Shorrocks 2007, Vande weghe & Vande weghe 2011). Typical savannah species occur in Akagera and include several species which belong to cisticolas, prinias, chats, robin-chats, thrushes, pipits, wagtails, doves, francolins, sunbirds, rollers, buntings, finches, weavers and pigeons that can breed in the park throughout the year (Vande weghe & Vande weghe 2011). However, according to Vande weghe and Vande weghe (2011) the bird fauna of the park has decreased from 525 to 482 species following the consequences of the 1990-1994 conflict and genocide in Rwanda. Factors affecting this diversity of birds may include a variety of landscapes and habitats coupled with good environmental conditions (e.g. tropical climate) and the position of Akagera in relation to major migration flyways (Kanyamibwa 2001, Shorrocks 2007, Vande weghe & Vande weghe 2011). Consequently, ANP still holds 99 species not found in any other protected area in Rwanda (Vande weghe & Vande weghe 2011).

Akagera avifauna also has several biome-restricted species (Kanyamibwa 2001, Vande weghe &Vande weghe 2011). For example, nine of the 11 bird species endemic to the Lake Victoria Basin that occur in Rwanda are present in Akagera (Kanyamibwa 2001). These include the Red-faced Barbet *Lybius rubrifacies*, which seems now to be restricted to ANP (African Bird Club 2011), Papyrus Gonolek *Laniarius mufumbiri* and Ring-necked Francolin *Scleroptila streptophora*. Zambesian elements are also present in ANP and include the Long-tailed Cisticola *Cisticola angusticaudata*, Crested Barbet *Trachyphonus vaillantii*, Broad-tailed Whydah *Vidua obtusa* and Miombo Wren-Warbler *Calomonastes undosus*. In addition, there is only one Somali-Masai species-the Fischer's Lovebird *Agapornis fischeri*, which has been introduced to Rwanda (Vande weghe &Vande weghe 2011). Akagera is also rich in spectacular diurnal birds of prey such as the Bateleur *Terathopius ecaudatus*, Martial Eagle *Polemaetus bellicosus*, Long-crested Eagle *Ictinaetus occipitalis*, Palm-nut Vulture *Gypohierax angolensis*, Lappet-faced Vulture *Torgos tracheliotus* and Brown-Snake Eagle *Circaetus cinereus*. The Akagera bird checklist also includes several rare and globally threatened species, birds with nocturnal habits and dry forest species (Kanyamibwa 2001, Vande weghe & Vande weghe 2011), highlighting again its conservation importance for birds.

Armed conflict in Rwanda since 1990 negatively affected the park's habitats and its fauna as already mentioned (Kanyamibwa 1998). The largest decline in wildlife occurred in 1990 with a reduction in large mammals by 70-80% (Schoene 2003) attributable to direct killing by humans. Important vegetation changes also occurred through sustained grazing pressure, agriculture, production of charcoal, cutting of trees and man-made burning inside the park.
During the post-conflict recovery period after 1994, the resettlement of the returnees and former refugees became increasingly urgent. Therefore, in 1997 the government of Rwanda reduced the park's area from more than 2,500 km^2 to its current size of 1,122 km^2 (African Parks 2012) to meet the population's needs (MINITERE 2003, Kock 2004). This resulted in severe loss of habitat (e.g. 15% of trees and shrubs and 20% of herbaceous species), a drastic decline of all wild fauna species and because of occupation of the park by several pastoralists between 1994 and May 2001, gully erosion increased inside the present park, especially along tracks used by cattle (Schoene 2003).

In 2000, the Germany Technical Cooperation (GTZ) supported the government of Rwanda in rehabilitating the remaining part of the park under the project GTZ-PRORENA-AKAGERA whose mandate was confined to an advisory function (Schoene 2003). But the long-term survival and sustainability of the current park is much dependent on the reverse of the negative impact on its vegetation and wildlife as well as conservation efforts and concrete management decisions.

1.5 Major threats to Akagera NP biological diversity

Rutagarama and Martin (2006) reported that Akagera has suffered more than other protected areas of Rwanda (namely Nyungwe NP and Volcanoes NP) in terms of insecurity, lack of human and financial resources and conflict of interest between conservation and local livelihoods. Growing human population pressures, limited land resources and a decade of war have resulted in increased competition between local livelihoods and wildlife for scarce resources (Kanyamibwa 1998, Nahayo & Yansheng 2009), threatening biodiversity. These pressures to the park's biodiversity are a big hinderance to conservation efforts. Major threats can be divided into natural and man-made.

Natural threats include: (1) *soil erosion* due to the relief of the area, which consists of some high mountains like Mutumba, steep-sloped hills and depressions; (2) *floods*: during some seasons, a heavy rain causes floods which can in turn cause extinction of some species in the valleys and depressions (MINITERE 2003). I observed such floods in July 2012 during my last field trip in Akagera where the rise of rain water was observed in many of the lakes inside the park; (3) *drought:* the eastern part of the country is prone to drought, especially during the dry seasons and the severity of the drought can vary year to year due to the global climate change (MINITERE 2003). In turn drought can cause emigration of animals to other places where water is available for example; and (4) Water Hyacinth *Eichornia crassipes* (alien invasive species), which is spreading and covering important surfaces of the lakes, posing a threat to their biological diversity (Twagiramungu 2006). This species also covers some valley dams and is particularly difficult to eradicate.

Man-made threats include: (1) direct consequences of the 1990-1994 war and the post-conflict period after 1994 to biodiversity (see above); (2) high human population densities (416 people per sq. km, NISR 2012) that increase competition over natural resources as already mentioned, therefore putting much pressure on the park's biodiversity, causing overexploitation of natural resources and exacerbating conflicts with conservation. This leads to the removal of grass biomass and extinction of certain species; (3) Illegal activities such as burning and poaching are still persistent both inside and outside the park, negatively affecting biodiversity and even people. For example, during the time of generating my data, poachers killed two park rangers in ANP. Also my enumerators had to break for 1-2 hours helping in seizing some of the snares set by poachers near Lake Kivumba inside the park. An Impala was also found killed by poachers using snares in a farmland in the former park area. The government of Rwanda at several occasions mobilized the army, police and local people to stop the fire set by poachers, mainly inside the park; and (4) during my data collection, the Managers of the park expressed their concerns about fishing in the lakes inside the park by private companies.

2. AIMS OF THE THESIS

The aim of this thesis was to investigate the current status of biological diversity in Akagera National Park, determine the impacts of human activities on habitat structure and bird diversity, assess bird diversity-habitat relationships and determine population sizes and density of large mammals. Large-scale, replicated point counts based on a systematic design, and presence-absence surveys were used to collect data. The main questions in the work with this thesis were:

1. What is the current status of bird species richness and diversity in Akagera National Park? Does Akagera National Park still contribute to the conservation of birds in the region? (**Paper I).**

2. How does human land use affect the structure of habitat and bird diversity both inside and outside the park? We hypothesized that human activities affect bird species richness and diversity through changes to the structure of habitat (**Paper II**).

3. How do species-habitat relationships affect bird diversity in Akagera National Park? How do single savannah species respond to the variation in densities of different vegetation structures? (**Paper III)**

4. What are the current population sizes and density of large mammals in Akagera National Park? What are the effects of vegetation structures? (**Paper IV**)

3. MATERIALS AND METHODS

3.1 Site description

The study was carried out from August 2009 to August 2011 inside Akagera National Park (1º45'00S, 30º38'00E) and areas adjacent to the park (± 600 km^2) but in the former park's area (Figure 1). The total area sampled inside the park was 1,085 km^2, excluding wetlands, lakes and dry forest. The study sites are described in detail in Paper I- IV. Akagera savannah habitats, as other large protected areas in sub-Saharan Africa, are areas of high biodiversity value as they protect and conserve increasing populations of large mammals and bird species, including threatened birds in Africa (de Klerk *et al.* 2004). The conservation importance of ANP, especially for the avifauna has been emphasized by previous studies (e.g. Vande weghe 1990, Kanyamibwa 1998, 2001, Vande weghe & Vande weghe 2011, BirdLife International 2012a, **Paper I-III**).

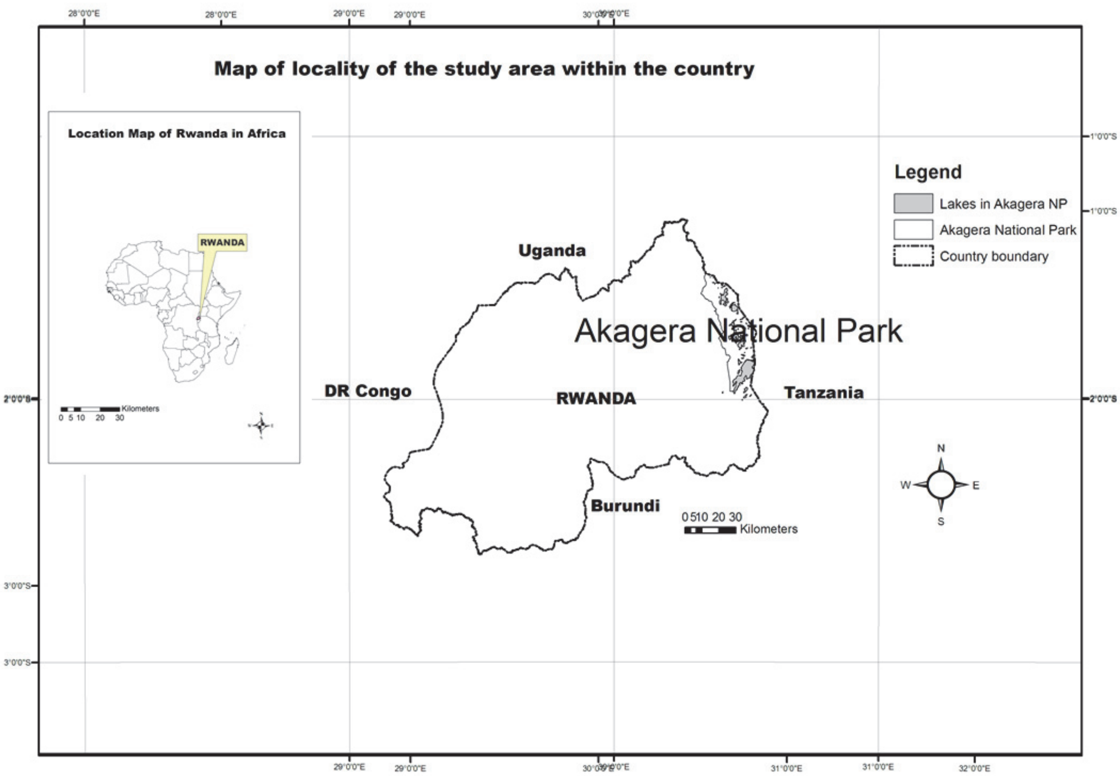


Figure 1. Map of the study area showing location of Rwanda within Africa and location of Akagera National Park (ANP) within Rwanda.

3.2 Sampling design

To get good estimates of the biological diversity in ANP, proper sampling was required. According to Magurran (2004) sampling matters because the number of species and subsequently the diversity of an assemblage tend to increase with the intensity of sampling. As sites are explored more thoroughly or surveyed over longer periods, estimates will increase (Magurran 2004:73). Another consideration when sampling is that species richness is in particular vulnerable to variation in sampling effort (Lande *et al.* 2000). As the primary goal of this thesis was to estimate species richness and diversity, plots of 1km^2 were selected according to a systematic sampling scheme with a random starting-point (Gotelli & Colwell 2001). The sampling was done in such way that different parts of the study area were evenly covered. First, the whole area was divided into 1,662 possible plots or squares (plot and square are used interchangeably throughout this thesis), using shapefiles of this area and ArcMap 9.2 (Figure 2a). Second, a systematic sample size of 266 plots was selected inside the park, including 148 and 118 that were surveyed during 2009–2010 and 2010–2011, respectively. Outside the park, the sample size included 61 plots surveyed during 2009–2010 (n = 32) and 2010–2011 (n = 29), respectively (Figures 2b & c). Figure 2d illustrates a subsample of 20 predefined points in each plot with the numbering of both the plot and points. The four corner points of each plot were used for main bird and large mammal counts (numbered 1, 6, 11 and 16 in Figure 2d). More details on sampling units are provided in **Paper I -IV**.

3.3 Bird surveys

Replicated point counts and a presence-absence approach were used for bird censuses and the methodology is described in detail in **Paper I-III**. Birds were recorded seven times between 2009 and 2011 in 274 plots of which 228 were inside and 47 outside the park. Some plots were measured once (157 and 28 inside and outside the park, respectively), whereas others were visited twice (62 and 18 inside and outside the park, respectively). While surveying birds, double-counting the same species or individual birds at a point was avoided by using careful observation and common sense. The book 'Birds of East Africa' (Stevenson & Fanshawe 2009) was used to identify observed species. All observers received initial training in using the methodology before the survey.

3.4 Large mammal surveys

Distance sampling was used, which is an extension of quadrat-based sampling methods (Thomas *et al*. 2002, Buckland *et al*. 2006), to sample large herbivores inside and outside the park. Both wildlife and livestock (Ankolé and goats) were sampled. As for birds, replicated point counts (a form of quadrat sampling) were used, in which numbers of objects (large mammals) were counted. Conventional Distance sampling methods are described by Buckland *et al.* (2001). For any animal detected from the point, the observation point, species, number of individuals in the cluster and sighting or radial distance to the cluster (in metres) from the point, were recorded. The distribution of these radial distances allowed estimating animal density and abundance (Buckland *et al*. 2001, Thomas *et al.* 2010, **Paper IV**). Population density is then estimated by dividing the total count by the total area surveyed (Thomas *et al.* 2002). Ancillary data (observer's names, plot number, data of the survey, start and end time of the recording) was also recorded.

As described in **Paper IV**, population size estimates of large mammals were also compared with previous surveys of the park conducted between 1990 and 2010.

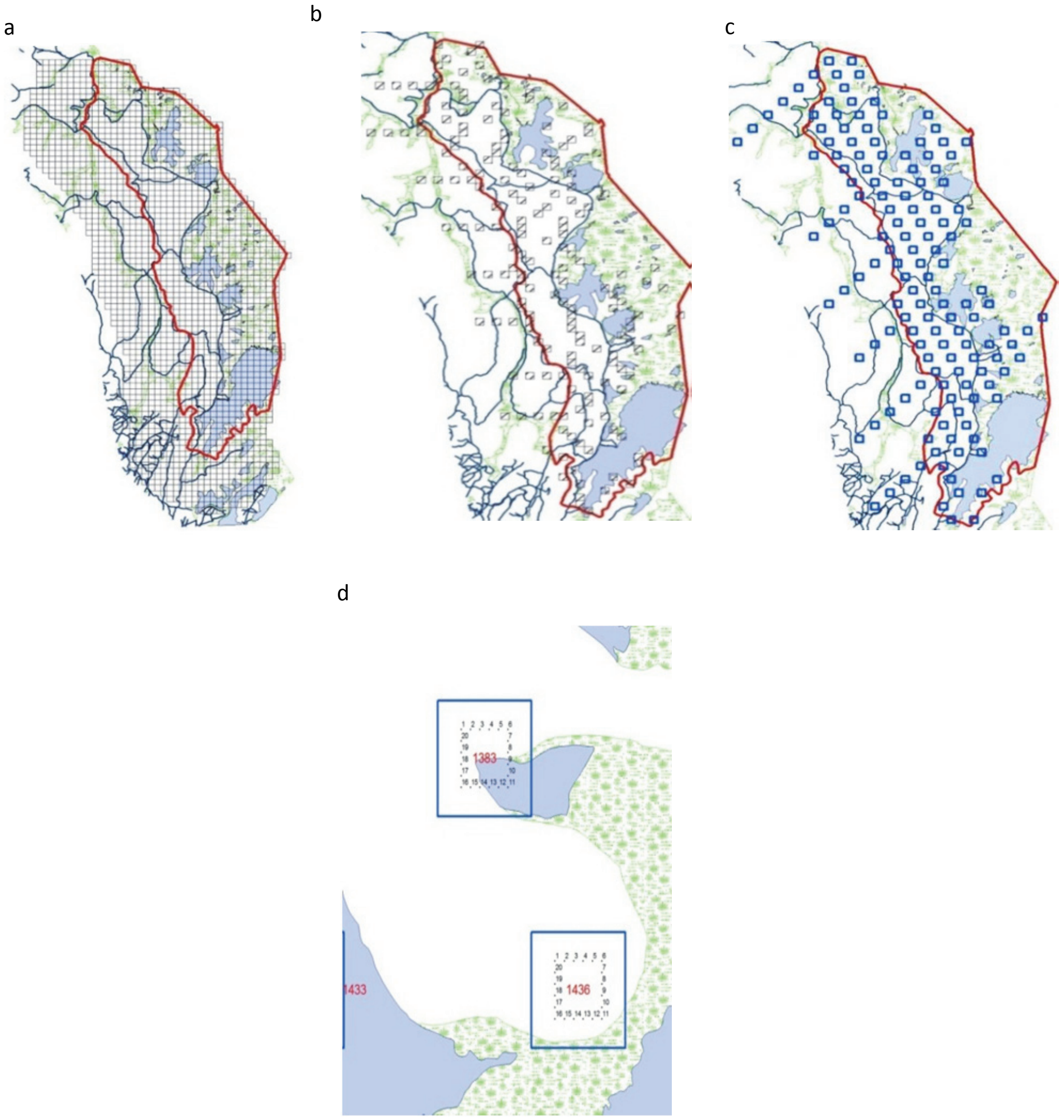


Figure 2. Design of sample units (1-km^2 plots) inside and outside the park. (a) The whole area is divided into 1662 squares; (b) & (c) represent systematic design of sample units in 2009-2010 and 2010 -2011, respectively. Sample size was *n* = 266 plots inside and *n* = 61 outside the park; and (d) subsampling of 20 predefined points in each plot with numbering of both the plot and points. All sample plots were associated with specific IDs, area and Global Positioning System (GPS) coordinates. The red line shows the park border.

3.5 Vegetation measurements

To describe the structure of savannah habitat and assess human influence on habitat structure and bird diversity, vegetation characteristics were measured in the sampling squares/plots (see **Paper I-III** for detailed description); grass heights were measured at every 100 m in each of the 20 points of each plot using the Sward Stick (Rayburn & Rayburn 1998, Stewart *et al.* 2001). In total measurements were taken on 6,861 such sampling points. Where the sward stick was dropped, the presence or absence of various vegetation variables (tall grass, short grass, trees, bushes, bare ground and burned areas) was also noted.

3.6 Data analysis

Survey data were stored into Microsoft Access. All analyses were performed using the software R version 2.7.0 (e.g. species richness & diversity) and Distance 6.0 Release 2. For estimating both species richness and diversity, non-parametric methods, which are not based on the parameter of a species abundance model, were used (Magurran 2004).

3.6.1 Species richness and abundance estimation, checklist and spatial distribution of recorded species

Species richness was estimated based on samples from local communities (referred to as alpha diversity). This was important for comparing bird communities inside and outside the park, assessing the effects of human influence on biodiversity, and providing managers with reliable data upon which to make sound environmental policy decisions (Chao 2005). I used the Chao2 estimator, which is a non-parametric estimator of species richness that uses presence-absence data (often called incidence or occurrence data), by considering the distribution of species amongst samples (Gaston 1996, Magurran 2004:87) and provides a reduction in bias relative to observed species number (Chao 1987, 2005, Colwell & Coddington 1994, Gimaret-Carpentier *et al.* 1998, Bunge & Fitzpatrick 2003, Chiarucci *et al.* 2003, Magurran 2004, Bolwig *et al.* 2006, Magurran & McGill 2011, see also **Paper I- II).**

The classical form of Chao2 is $S_{Chao2} = S_{obs} + \frac{s_1^2}{2s_2}$ where S_{obs} = the total number of species observed in a sample, or in a set of samples; s_1 = the number of species that occur in one sample only (unique species); and s_2 = the number of species that occur in two samples (doubletons). This estimator is based on the concept that rare species carry the most information about the number of missing ones (Chao 2005). However, the Chao2 estimator breaks down when $s_2 = 0$ (no doubletons), therefore this thesis used the bias-corrected form

$$S_{\text{Chao2}} = S_{obs} + s_1 (s_1 - 1) / [2(s_2 + 1)],$$

which is always obtainable (Chao 2005, Magurran & McGill 2011). The precision and accuracy of the estimator were measured by computing its theoretical variance and mean square error, respectively (Hellmann & Fowler 1999). The theoretical variance for Chao2 was calculated using the following formula (Gimaret-Carpantier *et al.*1998, Magurran & McGill 2011):

$$\text{var}(S_{\text{Chao2}}) = s_2 \, [1/2\,(s_1/s_2)^2 + (s_1/s_2)^3 + 1/4\,(s_1/s_2)^4] \text{ for } s_1 > 0 \text{ and } s_2 > 0$$

Chao2 has been widely used, shows low levels of bias and remarkable accuracy, and has the advantage of providing good approximations, being relatively insensitive to number of quadrats (Colwell & Coddington 1994, Magurran 2004, Chao 2005, Bolwig *et al.* 2006). Patterns of bird species richness were measured at different spatial scales: at the park or landscape level and average estimates per plot (local scale). The *z* and Wilcoxon tests were used to test for differences in species richness between inside and outside the park (Quinn & Keough 2002). Species abundance was estimated by determining the number of sampling units in which a species occurs (Magurran 2004:141).

A checklist of the recorded species (see Appendix 1, **Paper I**) was also developed, based on taxonomy (order, family and species). The classification followed the IOC World Bird List, version 3.1 (Gill & Donsker 2012).

Additional information was provided by Vande weghe and Vande weghe (2011), and Stevenson and Fanshawe (2009). The IUCN Red List Category followed BirdLife International (2012b). Values of Chao2 per plots were plotted into GIS, using ArcMap 9.2, to display their spatial distributions across the study area.

3.6.2 Estimates and spatial distribution of bird species diversity

Species diversity is defined as the number and relative abundances of species within a community (Magurran & McGill 2011). Species diversity (referred to as heterogeneity) represents two different aspect of species abundance distribution: 'species richness' and 'evenness', which is the degree to which the relative abundances are similar among species (Magurran 2004, Magurran & McGill 2011). As Magurran and McGill (2011) pointed out, there are two sources of variation in relative abundances among species: the first is variation within a species (within-species component = richness aspect of species diversity) and the second is the variability among species (between-species component = evenness).

To estimate bird species diversity, this thesis used the Simpson's diversity index, which is another non-parametric estimator that takes into account both the abundance (or biomass) patterns and the species richness and makes no assumption about the underlying species abundance distribution (Gimaret-Carpentier *et al.*1998, Magurran 2004, Buckland *et al.* 2005, Begon *et al.* 2006, Gorelick 2006, Kangah-Kesse *et al.* 2007, Magurran & McGill 2011). Advantages of the Simpson's index over other non-parametric estimators of diversity are described in **Paper II**. The theoretical expression of this index is based on the relative frequencies of species in the population, e.g. by determining, for each species, the proportion of individuals or biomass that it contributes to the total in the sample:

$D = 1 - \sum_{i=1}^{S} p_i^{\,2}$, where p_i is the frequency or relative abundance (probability) of the ith species in the sample (e.g. probability of detecting an individual present that belongs to species i), S is the species richness of the population. $\hat{D}$ is an unbiased estimator of the Simpson's index because p^2_i can be estimated by $n_i(n_i-1)/N(N-1)$ (Gimaret-Carpentier *et al.*1998).

$\hat{D} = 1 - \sum_{i=1}^{S_{obs}} n_i(n_i-1)/N(N-1)$ where S_{obs} is the number of species observed in the sample, n_i – the abundance of the ith species in the sample (number of individuals of ith species in the sample) and N-the sample size (total number of individuals recorded).

The theoretical variance of $\hat{D}$ is given by the formula: $\frac{4}{n}\left[\sum_{i=1}^{S} p_i^{\,3} - \lambda^2\right]$. D is derived from the original Simpson's index $\lambda = 1 - \sum(p(1-p))$. As D increases, diversity decreases. Therefore, the Simpson's index is usually expressed as 1-D or 1/D (Magurran 2004).

The Simpson index was found one of the most meaningful and robust diversity measures because when expressed as 1-D or 1/D, the value of the measure will increase as the assemblage becomes more even (Magurran 2004). Lande *et al.* (2000) found the Simpson index more effective than species accumulation curves in ranking communities. Lande (1996) recommends the use of 1-D (which is also used in this thesis) because he found that the overall diversity of a set of communities, measured as 1/D, may be less than the average diversity of these communities.

As for Chao2, the Simpson index is also used in this thesis to compare which site is more diverse than another between inside and outside the park, particularly because the Simpson index has the ability to consistently rank assemblages when sample size varies (Lande *et al.* 2000, Magurran 2004). The Wilcoxon test was used to test for significant differences in species diversity between inside and outside the park (Quinn & Keough 2002). As for Chao2, values of the Simpson index were plotted into GIS using ArcMap 9.2 to display their spatial distributions across the study area.

3.6.3 Effects of human land use on habitat structure and bird diversity

In **Paper II,** I investigated in detail the effects of changes in land use, caused by human activities, on savannah habitat structure and bird diversity. Disturbances are important to investigate as they play a fundamental role in shaping biodiversity patterns and ecosystem processes (Dornelas *et al.* 2011). In fact, disturbances temporarily change the rules that govern community dynamics, therefore affecting biodiversity (p. 238). For simplicity, this thesis focused on anthropogenic disturbances (linked to human actions). To measure the effects of human influence, univariate metrics were used, which are the easiest to use, simple to interpret and the most general even though they retain the least information by concentrating it into a single value (Dornelas *et al.* 2011). Effects of human influence were expressed as differences in total species richness and diversity (Magurran & McGill 2011) between inside and outside the park. These differences were also spatially tested by assessing relationships between the park border and average Chao2 and average Simpson index per plots. Both species detectability (probability of detecting species) and occupancy probability inside and outside the park were also estimated, using occupancy methods (Mackenzie 2005, Mackenzie *et al.* 2006). The Wilcoxon test was used to assess whether there were significant differences between the two types of habitat. Magurran and McGill (2011) recommend detectability to be readily estimated as an integral part of a monitoring scheme to avoid bias in comparative investigations of biodiversity. The assessment of the effects of human influence on bird diversity in this thesis referred to similar studies in tropical savannah habitats (Sinclair *et al.* 2002, Thiollay 2006, Konečný *et al*. 2010, Nkwabi *et al.* 2011).

3.6.4 Relationships between bird diversity and habitat structure

Each census-plot was first of all described in terms of habitat structure using seven vegetation variables: grass biomass, presence of tall grasses, short grasses, trees, bushes, bare soil and burns. Total and mean values of each variable were computed at both the landscape and the plot level and were compared between inside and outside the park (**Paper II-III**). To investigate relationships between habitat structure and bird species richness, a generalized linear model (GLM), with Poisson as the probability distribution, was used (Quinn & Keough 2002, Krook *et al.* 2007, Franklin 2009, **Paper III**). Predictors were the seven habitat structure variables mentioned above, whereas the response variable was mean Chao2 per plot. Polynomial transformations of the predictors (squared transformations) and the factor 'Park' were included in the GLM (Franklin 2009). As for Chao2, I investigated the same relationships with the Simpson index, using the Binomial distribution. I also assessed the effects of habitat structure on single savannah species by plotting bird species density counts against average values of each predictor per plot. Chi-squared, Wilcoxon and z tests were used to assess significant effects and differences between inside the park and outside (Quinn & Keough 2002, Magurran & McGill 2011).

3.6.5 Large mammal density and vegetation structure

Shorrocks (2007) classified savannah large mammals into ungulates, carnivores and primates and further described ungulates according to their feeding specialization. In this thesis, I mainly focused on herbivores (ungulates and primates). I used the Distance sampling methodology developed by Buckland *et al.* (2001) for estimating both the population density (number of individuals/km^2) and population size (total number of individuals in surveyed area) of large herbivores in Akagera National Park. Estimates were mainly based on observations made inside the park but I also selected some species and compared their estimates inside and outside the park. I did the same for livestock (cattle and goats). Program R and Distance 6.0 Release 2 (Thomas *et al.* 2010) were used for parameter estimation. The CDS (conventional distance sampling) analysis engine was used to estimate separately the detection function, encounter rate and cluster size and combined their results to estimate density (Buckland *et al.* 2001: 52, Thomas *et al.* 2009, **Paper IV**). Other parameters estimated for each species included detection probability, low and upper confidence intervals for the population size, number of observations and mean group size or mean cluster size (Buckland *et al.* 2001, Thomas *et al.* 2009, Thomas *et al.* 2010, **Paper IV).** As for birds, I also assessed the influence of vegetation structure on density counts of large mammals.

4. RESULTS AND DISCUSSION

4.1 Paper I

In this Paper I estimated and described the bird species richness and diversity of the Akagera National Park. I also compared Akagera bird species richness with that of other savannah parks in East Africa.

A total number of 22,358 individual birds belonging to 324 species were recorded. These included 16,380 individual birds belonging to 301 species recorded inside the park and 5,978 individuals belonging to 223 species detected outside the park. The number of species recorded inside the park (301) represents 57% of the total number of species previously known from Akagera National Park (ANP) before its reduction in size (e.g. 525 species) and 62 % of the current observed species richness after reduction (e.g. 482 species) according to Vande weghe and Vande weghe (2011). The complete checklist of species recorded within the park is provided in Appendix 1 of **Paper I**. It is clear from Appendix 1 that 75% of the observed birds are resident, 22% are seasonal migrants and 3% are rare or accidental species (see **Paper I** for details**.** The number of species recorded inside the park was further classified into 22 orders and 71 families. The Passeriformes order was the largest with 32 families and 154 individual species (Appendix 1). As expected, the majority of recorded richness was savannah species and this confirmed that Akagera is the only protected-savannah habitat in Rwanda where typical savannah birds occur (Vande weghe & Vande weghe 2011). Importantly for conservation, the large diversity of birds recorded in this thesis included several biome-restricted species. These included five (four endemic & one near-endemic) of the eleven species of the Lake Victoria region that occur in Rwanda (nine of these 11 species were previously reported to occur in Akagera, Kanyamibwa 2001) such as the red-faced Barbet (Figure 3) now restricted to ANP.

Figure 3. Red-faced Barbet *Lybius rubrifacies* – a Lake Victoria region endemic, occurring as a common breeding resident in Akagera National Park (Photo by Kjell Wallin).

Other biome-restricted birds recorded in this work were four species of the Zambesian region and one species of the Somali-Masai dry savannah region (Vande weghe & Vande weghe, 2011, **Paper I**). The conservation importance of the savannah habitats in ANP is also highlighted by the detection of 13 threatened bird species of which four are classified as globally threatened and nine as near-threatened according to the IUCN Red List Category (Birdlife International 2012a, **Paper I**).

The results of this thesis also demonstrated that the savannah habitats of Akagera still hold a large number of birds of prey with 30 species that were recorded (Appendix 1, **Paper I**) out of the 44 species of raptor known from the Park (Kanyamibwa 2001). These included the Lappet-faced Vulture *Torgos tracheliotus* (Figure 4) - a globally threatened species, according to the IUCN Red List Category (BirdLife International 2012b). According to Vande weghe and Vande weghe (2011) this decline in the number of birds of prey in ANP was most related to frequent poisoning of animal carcasses by local farmers.

Figure 4. Lappet-Faced Vulture *Torgos tracheliotus*– an endangered bird species (BirdLife International 2012b) and one of the large raptor species occurring in Akagera National Park (Photo by Kjell Wallin).

My data also confirmed that Akagera is a major destination for migrant birds (Table 1, **Paper I**, Appendix 1). Of the 89 Palearctic visitors known in Rwanda (Vande weghe & Vande weghe 2011), 35 (39%) were recorded in this study. Migrant numbers might vary year to year and are probably dependent on suitable habitats and local weather conditions (Vande weghe & Vande weghe 2011). The findings of this thesis also show the presence in Akagera of several species such as the Helmeted Guineafowl *Numida meleagris*, turacos, woodhoopoes, bushshrikes, oxpeckers and helmetshrikes that are known to be endemic to sub-Saharan Africa (Shorrocks 2007). In addition, my data demonstrated that habitats in ANP also support a large number of wetland birds, even though I did not pay special attention to this habitat, including several species of cranes, egrets, fish eagles, herons, ibises, kingfishers, jacanas, lapwings, pelicans and storks (Vande weghe 1990, Vande weghe & Vande weghe 2011). These birds are in particular found on many islands in different lakes like the so-called '*Nyirabiyoro*' island in Lake Ihema which attracts several birds.

One of the features of this thesis is the detection of a number of species not previously recorded in Akagera National Park (**Paper I**). These species are resident of neighbouring countries of Burundi, Tanzania and Uganda (Stevenson & Fanshawe 2009, BirdLife International 2012c); therefore there might be a regular movement of these species between ‘interlacustrine’ savannahs, which are similar in species composition as previously highlighted by Vande weghe (1990). These new species offer interesting monitoring opportunities for ornithologists and conservationists to ensure that whether they are resident or whether they are just accidental in ANP.

Another feature of this work is that, due to the adequate survey methodology used (e.g. systematic design, sampling effort, accounting for species detectability, emphasis on visual identification of individual species…), my surveys were able to detect several ‘interesting’ savannah species, but not accidental, that have been overlooked by previous studies (see **Paper I** for details). Vande weghe and Vande weghe (2011) argue for example that some of the species recorded in this thesis such as the Little Weaver *Ploceus luteolus* (detected in n = 3 plots), Nubian Woodpecker *Campethera nubica* (n = 5, see Figure 6 of Paper I) and Variable Indigobird *Vidua funerea* (n = 1) were not previously accepted on Rwanda’s bird checklist or were just mentioned by mistake. Also, according to Vande weghe and Vande weghe (2011: 290), the African Firefinch *Lagonosticta rubricata* (n = 20) was previously totally absent from Akagera habitats. Other overlooked species include the Black Kite *Milvus migrans* (n = 7), which is a Palearctic migrant, the Northern Puffback *Dryoscopus gambensis* (n = 4) and Singing Cisticola *Cisticola cantans* (n = 13), all that inhabit the savannah of Akagera (BirdLife International 2012b).

However, my surveys failed to detect some key species, previously known from the park, either because their habitats were not sampled (e.g. those restricted to swamps and dry forests) or that some species no longer occur in the park due to local extinction (e.g. Kanyamibwa 2001, Vande weghe &Vande weghe 2011, see **Paper I** for details). Furthermore, my investigations showed that both observed and estimated species richness was different among different sampling units. Overall, the number of species observed in a plot varied between 3 and 44, whereas the estimated species richness by Chao2 per plot ranged between 9 and 200 (mean = 42 ± 3.98). At the landscape level (study area within the park) Chao2 estimates was 346 ± 12 (SE) species. Chao2 estimates per plots as well as individual bird records were plotted into GIS to display their spatial distribution (Figure 5).

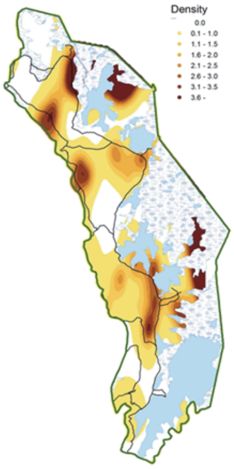
This thesis also compared the bird species richness of Akagera National Park with that of other savannah parks in East Africa, including Ruaha NP, Serengeti NP, Mkomazi Game Reserve, Mikumi NP, Maasai Mara NP, Murchison Falls NP, Meru NP, Ngorongoro Conservation Area, Ruvubu NP, Lake Mburo NP and Amboseli NP, based on two variables: the number of species and park area. Akagera was found to be one of the richest parks in East Africa with regard to the number of bird species, independently of the size of the park (**Paper I**). These findings support previous studies that the avifauna of Akagera is very comparable to that found in other East African savannah parks such as the western Serengeti and Maasai Mara (Vande weghe 1990:29). As mentioned in **Paper I**, the semi-arid savannahs of Akagera National Park, together with those of southern Uganda, northwestern Tanzania and northern Burundi, constitute ‘interlacustrine’ savannahs that are similar in species composition (Vande weghe 1990).

Table 1: Seasonal migrant bird species recorded inside Akagera National Park. Migratory status (BW= Palearctic migrant and winter visitor**,** AM= Afrotropical migrant, V= Vagrant). IUCN Red List Category follows BirdLife International (2011 b): LC= Least concern, NT= Near-threatened.

Common name (English)	Scientific name	No. of plots species was observed	Migratory status	IUCN Red list Category
Willow Warbler	*Phylloscopus trochilus*	54	BW	LC
Barn Swallow	*Hirundo rustica*	42	BW	LC
Red-chested Cuckoo	*Cuculus solitarius*	38	AM	LC
Violet-backed Starling	*Cinnyricinclus leucogaster*	31	AM	LC
Woodland Kingfisher	*Halcyon senegalensis*	20	AM	LC
Red-billed Quelea	*Quelea quelea*	17	AM	LC
European Bee-eater	*Merops apiaster*	15	BW	LC
Levaillant's Cuckoo	*Clamator levaillantii*	12	A M	LC
Yellow Wagtail	*Motacilla flava*	12	BW	LC
Dideric Cuckoo	*Chrysococcyx caprius*	11	AM	LC
Wattled Starling	*Creatophora cinerea*	7	AM	LC
Eurasian Reed-Warbler	*Acrocephalus scirpaceus*	7	BW	LC
Blue-cheeked Bee-eater	*Merops persicus*	6	BW	LC
Wahlberg's Eagle	*Aquila wahlbergi*	6	AM	LC
Eurasian Nightjar	*Caprimulgus europaeus*	5	BW	LC
African Cuckoo	*Cuculus gularis*	4	AM	LC
Glossy Ibis	*Plegadis falcinellu*s	4	AM	LC
Madagascar Bee-eater	*Merops superciliosus*	4	AM	LC
Sand Martin	*Riparia riparia*	4	BW	LC
Steppe Eagle	*Aquila nipalensis*	4	BW	LC
White-throated Bee-eater	*Merops albicollis*	4	AM	LC
Broad- billed Roller	*Eurystomus glaucurus*	3	AM	LC
Common Sandpiper	*Actitis hypoleucos*	3	BW	LC
Wood Warbler	*Phylloscopus sibilatrix*	3	BW	LC
Palm-nut Vulture	*Gypohierax angolensis*	3	AM	LC
African Golden Oriole	*Oriolus auratus*	2	AM	LC
Bronze-winged Courser	*Rhinoptilus chalcopterus*	2	AM	LC
European Roller	*Coracias garrulus*	2	BW	NT
Garden Warbler	*Sylvia borin*	2	BW	LC
Northern Wheatear	*Oenanthe oenanthe*	2	BW	LC
Semi-collared Flycatcher	*Ficedula semitorquata*	2	BW	NT
Southern Carmine Bee-eater	*Merops nubicoides*	2	AM	LC
Thick-billed Cuckoo	*Pachycoccyx audeberti*	2	AM	LC
Tree Pipit	*Anthus trivialis*	2	BW	LC
Whinchat	*Saxicola rubetra*	2	BW	LC
Icterine Warbler	*Hippolais icterina*	2	BW	LC
Lesser Grey Shrike	*Lanius minor*	2	BW	LC
Lesser Spotted Eagle	*Aquila pomarina*	2	BW	LC
Verreaux's Eagle	*Aquila verreauxii*	2	V	LC
Alpine Swift	*Tachymarptis melba*	1	BW	LC
Black Coucal	*Centropus grillii*	1	AM	LC
Black-billed Wood-Dove	*Turtur abyssinicus*	1	AM	LC
Cardinal Quelea	*Quelea cardinalis*	1	AM	LC
Common Cuckoo	*Cuculus canorus*	1	BW	LC
European Honey-buzzard	*Pernis apivorus*	1	BW	LC
Fischer's Lovebird	*Agapornis fischeri*	1	V	NT
Great Reed-Warbler	*Acrocephalus arundinaceus*	1	BW	LC
Great Spotted Cuckoo	*Clamator glandarius*	1	AM	LC
Great White Pelican	*Pelecanus onocrotalus*	1	BW	LC
Grey-headed Kingfisher	*Halcyon leucocephala*	1	AM	LC
Isabelline Shrike	*Lanius isabellinus*	1	BW	LC
Isabelline Wheatear	*Oenanthe isabellina*	1	BW	LC
Namaqua Dove	*Oena capensis*	1	AM	LC
Northern House-Martin	*Delichon urbica*	1	BW	LC
Osprey	*Pandion haliaetus*	1	BW	LC
Pallid Harrier	*Circus macrourus*	1	BW	NT
Pennant-winged Nightjar	*Macrodipteryx vexillarius*	1	AM	LC
Red-backed Shrike	*Lanius collurio*	1	BW	LC
Red-footed Falcon	*Falco vespertinus*	1	BW	NT
Sooty Falcon	*Falco concolor*	1	BW	NT
Splendid glossy-Starling	*Lamprotornis splendidus*	1	AM	LC

Red-faced Barbet *Lybius rubrifacies*

Population size	1 143
Density (km²)	1.96
Present at random location	16%
Chance to be seen at random location	4.8%
Detection probability	30%



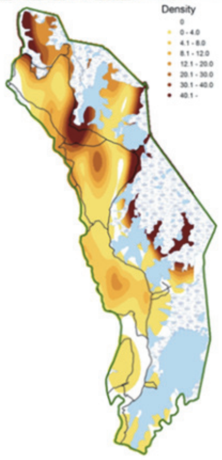
Distribution:
Restricted to parts of the Albertine Rift - southern Uganda and eastern parts of Rwanda and Burundi.

World status:
It is on the IUCN Red List considered as Near Threatened because of its small and restricted population size which is believed to be declining due to habitat loss. Important part of this loss is due to the reduced size of Akagera National Park.

Habitat:
Lives in mixed woodlands, wooded grasslands as well as cultivated areas with scattered trees.

Yellow-throated Longclaw *Macronyx croceus*

Population size	4 499
Density (km²)	7.72
Present at random location	43%
Chance to be seen at random location	6.4%
Detection probability	15%



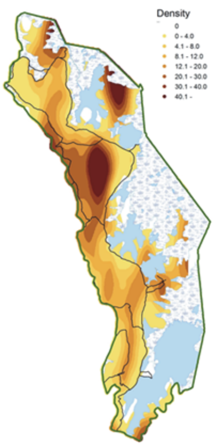
Distribution:
The species has a large distribution - but is restricted to Africa.

World status:
The population size is unknown, but is classified as scarce or even rare. The population is believed to be fairly stable.

Habitat:
It lives in wet and flooded grasslands and savannah is assumed as its natural habitat.

Sooty Chat *Myrmecocichla nigra*

Population size	10 228
Density (km²)	17.5
Present at random location	82%
Chance to be seen at random location	13%
Detection probability	16%



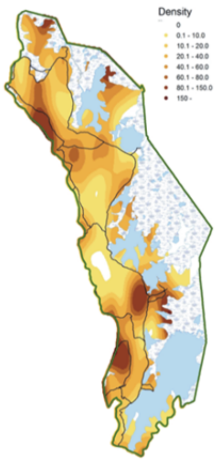
Distribution:
An African species inhabiting sub-Sahara region from Senegal to western Kenya and south to Zambia and Angola.

World status:
Fairly common and no urgent threats.

Habitat:
Lives in sparsely wooded grasslands.

Marico Sunbird *Nectarinia mariquensis*

Population size	61 200
Density (km²)	104.9
Present at random location	100%
Chance to be seen at random location	15%
Detection probability	4.6%



Distribution:
The species has a wide distribution, restricted to sub-Saharan Africa.

World status:
Fairly common and no urgent threats.

Habitat:
It lives in a wide variety of habitats from woodlands to grasslands.

Figure 5. Sample species distribution map showing in which parts of the Akagera National Park the species were recorded. The information displayed in these maps might be useful for guiding both park managers and tourists.

The results of this thesis also confirmed the following ornithological features of Akagera previously highlighted by Vande weghe (1990): (1) the detection of the Red-faced Barbet as already mentioned which is a unique species that only exists in Akagera, extreme south of Uganda, extreme northwest of Tanzania and eastern part of Burundi; (2) the presence of species, which are typical, even endemic to the swampy and aquatic environments of the Lake Victoria region such as the Eastern Grey Plantain-eater *Crinifer zonurus* and the Red-chested Sunbird *Nectarinia erythrocerca;* and (3) the detection of species linked with Miombo woodlands but that have colonized the *Acacia-Combretum* savannah in Akagera such as the Crested Barbet *Trachyphonus vaillantii*, White-headed Black-Chat or Arnot's Chat *Myrmecocichla arnoti* and Long-tailed (Tabora) Cisticola *Cisticola angusticaudata*.

The above findings show that bird watching as a newly launched ecotourism product in Akagera should really be a key area in which the park can successfully compete with larger savannah parks in East Africa. Here the small size of Akagera becomes an advantage because the whole park can easily be covered in 2-3 days. Some data published on the internet reported for example that just during 1-2 days of birding in Akagera, some experienced bird watchers could detect over 100 species (African Bird Club 2011). My data may be useful for bird watching development as a new ecotourism[1] product for the park by providing baseline information to park managers and policy-makers for prioritizing conservation and management decisions as well as improving community conservation. Collected data include for example several pictures taken during data collection that can be used to produce species distribution maps (Figure 5) that can guide both tourists and conservationists, as well as for building a website for advertising bird watching. In turn, ecotourism should contribute to the sustainability of the park. However, there is still a lot to do to reach the full potential of bird watching as an ecotourism product. In fact, I agree with Arun and Redford (2006) that ecotourism studies emphasize the importance of conserving biodiversity, enhancing local incomes and producing sustainable development.

4.2 Paper II

In Paper II, I investigated the effects of human impacts of the structure of habitat and bird species richness and diversity. These effects were expressed as differences in species richness and diversity between inside (undisturbed) and outside the park (disturbed) at different spatial scales (at the landscape and plot level). I also assessed the influence of species detectability.

4.2.1 Differences in species richness between inside and outside the park

My findings demonstrated that human activities had large effects on bird species richness and the savannah habitat both inside and outside the park through changes to the structure of vegetation. This is shown through differences between the two types of habitat in the total species richness at the landscape scale (study area) and mean observed and estimated (Chao2) species richness as well as species diversity (the Simpson index) at the census-plot or local scale (Figure 6, **Paper II**).

[1] One of the definitions of ecotourism is that it is a "travel that generates financial support for protection and management of of natural areas, economic benefits for residents living near natural areas, and support for conservation among these residents." (Buckley 1994 cited in Arun & Redford 2006). As Arun and Redford (2006) point out, ecotourism should generate low visitor impact and help conserving biodiversity and generating socio-economic benefits for local populations to help reducing poverty (e.g. revenue sharing and other incentive mechanisms for local people).

Figure 6 shows that at the local scale, the mean observed and estimated number of species per plot was significantly higher outside than inside the park. The latter relationship is also shown spatially in Figure 7 and **Paper II**.

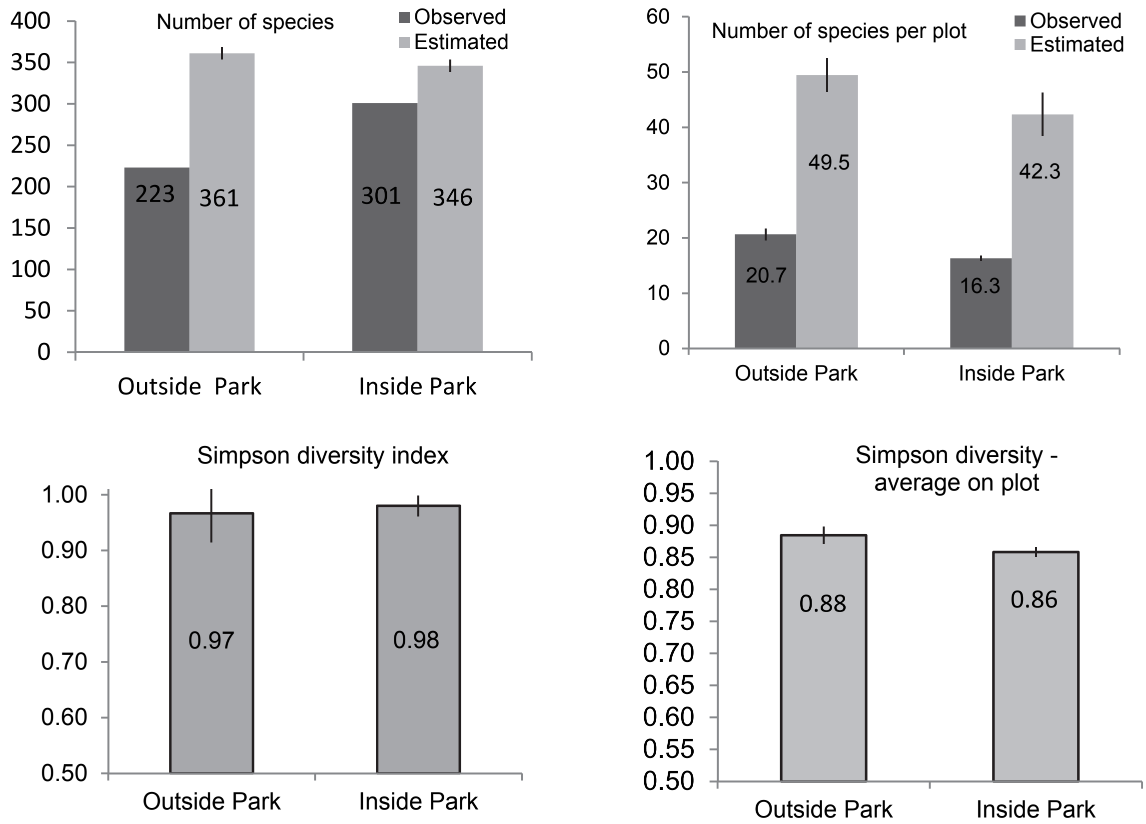


Figure 6. Bird species richness and diversity compared between inside and outside of the park across the savannah habitat in Akagera National Park: upper left- estimated number of species (Chao2) at the landscape level; upper right- average observed versus estimated number of species per plot; lower left-Simpson diversity index at the landscape level (β-diversity); and lower-right average Simpson index per plot (α-diversity). Values of Chao2 estimates and the Simpson index are plotted with their standard errors.

At the landscape level, the total number of species observed was higher inside than outside the park, whereas the estimated number of species was higher outside than inside but this difference was not significant (z = -0.45, P = 0.67). Different land use practices outside the park are affecting vegetation structure mainly through conversion of grass biomass and tall grasses into short grasses and/or bare soil, creating more open habitat. However, human activities did not show any significant impact on bird species diversity as shown by the Simpson index. Contrary to my expectations, my results showed that these large human effects on grassland habitat had a positive impact on bird species richness outside the park, e.g. an increase in generalist species (e.g. Sinclair *et al*. 2002, Shahabuddin & Kumar 2006, **Paper II**). My findings are consistent with previous studies showing changes in bird species richness, following anthropogenic disturbance (Svensson *et al*. 2009, Konečný *et al*. 2010, Nkwabi *et al*. 2011).

Observed human-related activities during the work of this thesis such as crop production, cattle grazing, grouped housing development (known as '*Imidugudu*'), wood harvesting and small-scale mining were being intensified in the former park area, increasing competition with wildlife conservation (Nahayo & Yansheng 2009). Other anthropogenic influences both inside and outside the park included, despite law enforcement, intensification of poaching activities which sometimes resulted in death of people. During the time of generating my data, fire, set by poachers, destroyed large areas of vegetation inside the park as well as arthropods and grassland birds (Figure 10, upper right). At some occasions also, my field workers helped seizing several snares set up by poachers to attract wildlife.

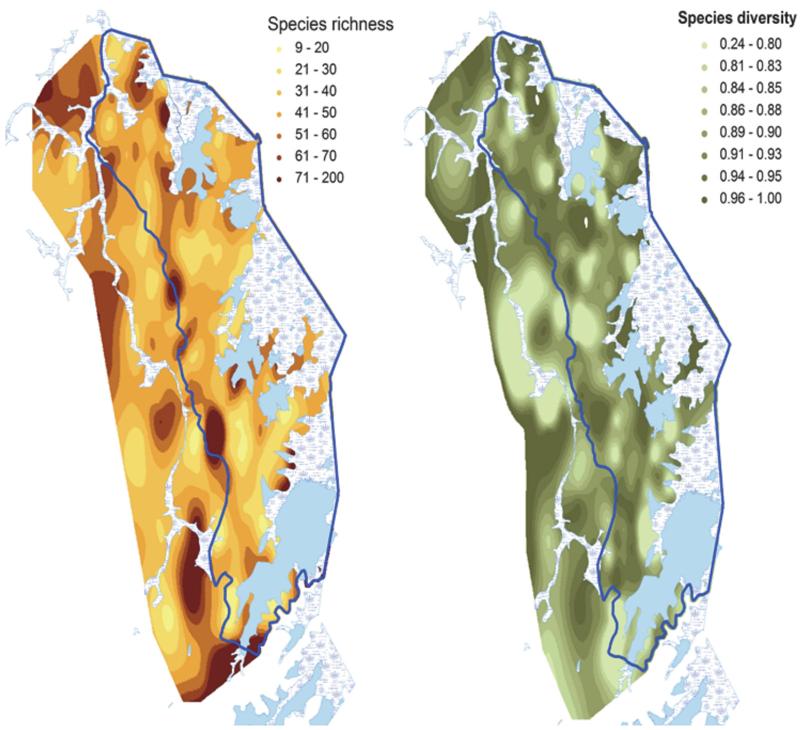


Figure 7. Spatial distribution of: left-bird species richness inside and outside the park indicating estimated number of species by computing Chao2 estimator (mean values per plots); right-bird species diversity indicating values estimated by computing the Simpson index per plot in Akagera National Park. Values of Chao2 and the Simpson index are plotted into GIS. The blue line indicates park border.

4.2.2 Influence of species detectability

My findings demonstrate that modification of the structure of habitat resulted in higher species detectability outside than inside the park, causing more species to be observed outside the park than inside (observation bias, **Paper II**). When detectability was taken into account, I did not find any difference between the two types of habitat. Surveying birds within dense vegetation inside the park was extremely difficult in some places and it is likely that some species were missed. As pointed out by Pacifici *et al.* (2008) and Lloyd *et al.* (2012), avian detection probabilities are highly dynamic and differ between habitats. Unseen species are a detectability issue and when not estimated, variable species detectability may introduce bias in many comparative investigations (Magurran & McGill 2011).

Based on my results, I recommend species detectability to readily be estimated as an integral part of monitoring bird diversity in Akagera National Park, especially when estimating species richness from counts (Lande *et al.* 2000, Magurran & McGill 2011).

4.3 Paper III

In this Paper I aimed to determine how different habitat structure variables affect bird species richness and diversity in ANP. I used GLMs to investigate these relationships. I also assessed how this structure of habitat affects single savannah species.

My results showed that habitat structure had significant effects on bird species richness and these effects significantly varied between inside and outside the park but did not affect species diversity (**Paper III**). The overall effect of biomass and bushes on species richness was negative, while that of tall grasses, short grasses and bare soil was positive. The factor "park" was highly negatively correlated with the species richness. As described in **Paper III**, the increase in densities of grass biomass and bushes resulted in bush encroachment (Roques *et al.* 2001, Sankaran *et al.* 2005, Blaum *et al.* 2007, Sirami *et al.* 2009, Angassa *et al.* 2012), which is widespread in large parts of ANP like the "Giraffe area", threatening grassland habitat and birds. Previous studies have linked bush encroachment with different land use management practices that have mostly been attributed to anthropogenic disturbances (Gottschalk *et al.* 2007, Sirami *et al.* 2009, Seymour & Dean 2010, **Paper II-III**). My findings show that bush encroachment in Akagera National Park is mainly caused by a mixture of bushes and *Acacia sieberana*, subspecies *kagerensis* (e.g. in 'Giraffe area', Vande weghe 1990) and it negatively affects the majority of grassland birds. It will be profitable for the park to remove *Acacia sieberana* from key places (e.g. 'Giraffe area') and create more open habitat not only for the benefits of open-savannah birds but also for the promotion of ecotourism. In **Paper III** I have proposed some management practices aimed at reducing this woody plant cover.

I also tried to explain how single savannah bird species differently respond to changes in habitat structure. Using niche theories, I integrated the Grinnellian and Eltonian niche to describe the complexity of the relationships between species' distribution and niche characteristics (Begon *et al.* 2006, Soberon 2007, Hirzel & Le Lay 2008, Devictor *et al*. 2010). The importance of acknowledging the difference between Grinnellian and Eltonian niche concepts for conservation implications was also highlighted (Hirzel & Le Lay 2008).

4.4 Paper IV

In this Paper I estimated the population sizes and density of large mammals within the park and made a comparison of these estimates with previous surveys of the park. Wildlife occurring outside the protected area as well as livestock present both inside and outside the park was also estimated.

I found that Akagera NP currently holds 18-20 species of large herbivores contrary to more than 50 species previously mentioned (e.g. Kanyamibwa 2001, Plumptre *et al.* 2001, **Paper IV**). These include megaherbivores such as elephants, giraffes and hippopotamuses, other large herbivores such as the buffalo, eland, zebra, topi and roan antelope as well as medium sized mammals (impala, oribi and klipspringer).

At least eight species of antelopes occur within the park boundaries. Three species are also protected by the CITES, including African elephant and African buffalo (Figure 8). The total population of wild herbivores estimated inside the park was 61519 individual animals. Additionally, there were 16950 impalas estimated outside the park.

Figure 8. African elephant *Loxodonta africana* (left) and African buffalo *Syncerus caffer* (right) are both protected by the CITES. These two species are part of the big five and responsible of most wildlife attacks to local people and their crops in Akagera National Park (Photo by Kjell Wallin).

Population sizes and densities varied greatly but the most abundant species in the park are impalas, buffaloes, topis, zebras and baboons. However, my estimates of elephants and roan antelope were not reliable as they were based on only a few observations but I saw at least 30 elephants outside my survey plots, meaning that their population size within the park should be above 100 individuals. Compared to previous surveys, my estimates markedly differ from the 1997/1998, 2002 and 2010 population estimates (Paper IV) probably due to different methodologies used (aerial surveys versus ground counts) but they are more similar to the 1990 estimates by Vande weghe and Dejace (cited in Lamprey 2002, **Paper IV**) before the reduction of the original size of the park. My results demonstrated that in general most species declined between 1990 and 2011 except few species (zebras, warthogs and duikers) that increased during the same period. Most of the decline in wildlife was attributed to human impact (Kanyamibwa 1998, Plumptre *et al.* 2001, Lamprey 2002, Schoene 2003). Figure 9 illustrates some of the negative influences of humans on biodiversity in ANP.

My findings also highlighted that the presence of a large population of cattle both inside and outside the park as well as that of wildlife outside the protected area is a conservation challenge through competition between domestic livestock and wildlife (e.g. pasture and water), animal disease transmission (see **Paper IV**) and conflicts between wildlife conservation and local human population (Vande weghe 1990).

Figure 9. Impala *Aepyceros melampus* killed by snares set by poachers in Akagera National Park (left) and grazing by cattle (Ankolé, right) showing the negative impacts of humans on wildlife (Photo by the author).

My results also revealed that diversity of landscapes and structure of habitats is one important factor affecting abundance patterns of large mammals in Akagera, supporting previous studies (Vande weghe 1990, Kanyamibwa 1998, Lamprey 2002, Vande weghe & Vande weghe 2011, Figure 10). In particular, I found that habitat structure is a key predictor of the distribution and abundance of large mammals (Paper IV). My data emphasize again the importance of the savannah habitat in ANP for the conservation of large mammals and the need to minimize interactions and conflicts between cattle grazing and wildlife conservation.

Figure 10. Diversity of both landscapes and structure of habitats as one important factor affecting large mammals in Akagera National Park. Upper left- Kilala plain, a more open grassland in the north that attracts several animals and birds; upper right-recently burned area that attracts zebras; middle left-Mutumba hills, the highest altitude in the park (1825 m a.s.l.); middle right- overgrazed area outside the park near Rwisirabo showing some traces of gull erosion; Lower left-differences between recently burned vegetation on the left and unburned vegetation on the right; and lower right- a dry forest habitat (Photo by the author and Kjell Wallin).

5. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

1. The finding of this thesis established that Akagera National Park, despite its reduction in size and loss of habitat, still greatly contributes to the conservation of an important diversity of birds and large herbivores in this species-rich part of Africa, reflecting varied landscapes and habitats, and the importance of conserving these habitats (Kanyamibwa 2001, Vande weghe &Vande weghe 2011, **Paper I & IV**). Human land use and habitat structure were found to affect both bird species richness and large mammal population sizes (**Paper II, III & IV**), underlining that any changes in habitat structure may affect the abundance patterns of these species. My data confirmed that, unlike large savannah parks of Kenya, Uganda and Tanzania, Akagera does not hold massive concentrations of large herbivores, but it still conserves an interesting number of two elements of the big five (e.g. the buffalo and elephant), and other large herbivores typical of eastern African savannahs such as the giraffe, roan antelope, hippopotamus, zebra, topi and the widespread impala (Lamprey 2002).

2. I stressed the conservation importance of Akagera National Park for bird diversity, especially in hosting large numbers of typical savannah and biome-restricted species, globally threatened species, Palearctic and Afrotropical migrants, species endemic to sub-Saharan Africa, rare species, several breeding resident and wetland birds (Shorrocks 2007, Vande weghe &Vande weghe 2011, **Paper I**). My data confirmed previous findings that Akagera still conserves several ornithological features and is one of the richest savannah parks in East Africa with regard to avifauna (Kanyamibwa 2001, Vande weghe &Vande weghe 2011). I emphasize the importance of promoting the newly launched bird watching in Akagera and priorities should be fixed according to management objectives.

3. This thesis revealed new bird species coming into Akagera National Park from neighbouring countries of Uganda, Tanzania and Burundi where they are resident (**Paper I**). I also confirmed the presence of certain species such as the Nubian Woodpecker, Little Weaver and Variable Indigobird that seem to have been overlooked by previous studies (e.g. Vande weghe & Vande weghe 2011).
   I recommend monitoring all these species to ensure that they are not just accidental in Akagera and determine the patterns of their probable movement between 'interlacustrine' savannahs (Vande weghe 1990).

4. My findings demonstrated that anthropogenic activities have had an important impact on the park's biodiversity through modification of the structure of habitat (e.g. conversion of savannah habitat into agricultural and grazing lands, and burning), resulting in proliferation of certain bird species outside the protected area (e.g. increase of generalist species) and a little decline in specialists that require specific habitat types (**Paper II**). These findings support previous studies that the introduction of agriculture in the vicinity of wildlife, especially elephants, buffalos, hippos and baboons inevitable creates a conflict between the large fauna and the farmers (Vande weghe 1990: 25). The presence of a large population of wildlife outside the park as well as that of cattle inside the park represents a conservation challenge too (Lamprey 2002).

I recommend government policies to favor joint conservation and management actions to ensure that farmers in adjacent areas maximize their production for food security, while minimizing negative consequences on wildlife conservation and vice-versa.

5. My results demonstrated that the structure of habitat affects bird species richness. Effects differed significantly between inside and outside the park due to different land use practices **(Paper II).** My findings have also shown that single savannah bird species use habitat differently according to their individual niche requirements and niche interactions with other species and this should have important conservation implications (Hirzel *et al.* 2008, Devictor *et al.* 2010). Modification of the structure of habitat also resulted in woody cover increase in different parts of the park including the 'Giraffe area', forming bush encroachment, which is threatening open savannah and grassland bird species. I proposed a number of strategies for woody plant removal (Roques *et al.* 2001, Krook *et al.* 2007, Angassa *et al.* 2012) and creation of more open habitat like the Kilala plain in the north of the park, which would benefit both conservation and tourism.

6. This thesis emphasizes that, to be sustainable, Akagera National Park has to generate income through tourism/ecotourism. Carefully orcherstrated interventions, based on conservation priorities and objective monitoring are necessary for the sustainability of the park (Child 2004). Conservation should be equally important as tourism. This implies that some of the money generated by tourism should be invested back into conservation activities. To achieve this, a close cooperation with local people is necessary as highlighted above. I therefore recommend a combination of ecological knowledge, economic benefits and effective government policies (Begon *et al.* 2006) as well as the application of adaptive management to solve complex local problems (Martin 1999). I also want to underline the importance of strengthening community conservation, capacity building, improving existing revenue-sharing and other incentive mechanisms as well as law enforcement (CBD 2011b).

7. Due to the large number of bird species present outside the park, I recommend to pay specific attention to their conservation by ensuring for example that their habitats are kept intact. Community conservation can be linked with the 'Nagoya Protocol' on Access and Benefit-Sharing and the 'Aichi Targets' of the CBD Strategic Plan 2011-2020 (CBD 2011b, **Paper II**).

6. ACKNOWLEDGEMENTS

I would like to thank all people and institutions that contributed to my doctoral studies in various ways:

My PhD studies were financially supported by the Swedish International Development Agency (SIDA) through SIDA/SAREC-National University of Rwanda (NUR) Cooperation. Thanks to NUR authorities, the staff of NUR-SIDA project and the Centre for Environment, Entrepreneurship and Sustainable Development (CEESD). My thanks also go to the donation and travel grants from the Philosophical Faculties of University of Gothenburg and *Therese Palmer*.

I gratefully thank my main supervisor, *Dr Kjell Wallin* for his valuable inputs in the design of this study, field work kick off, statistical analyses and the scientific guidance during the whole programme. Special thanks to my co-supervisor *Prof Bengt Gunnarsson* for comments and review of my papers and the thesis.

I want to express my gratitude to my field research assistant *Etienne Zibera* for the good job done in a difficult terrain of Akagera National Park.

I thank *Bryan Havemann, Jes Gruner, Eugene Mutangana* (the Chief Park Warden), *Fidele Ruzigandekwe*, Rwanda Development Board (RDB) and the former ORTPN for permission to conduct this study. I want to address special thanks to all the staff of Akagera National Park and Akagera Management Company for collaboration during my field research, especially *Charles Nsabimana, Patrick Buda, Roger Gakwerere, Fidel Sebatware* and those who directly participated in data collection (mentioned in paper I-IV).

My gratitude is extended to *Prof. Ingela Dahllöf*-the Head of the Department Biological and Environmental Sciences (BioEnv) and all the staff and PhD students of BioEnv. at University of Gothenburg, especially *Henrik Aronsson, Sven Toresson, Ingela Lyck, Inga Groth, Niclas Siberg*, *Hans Alexandersson, Brigitte Nyirambangutse, Erik Heyman*, *Delilah Lithner*- and many others for conducive work environment, facilitation in handling administrative matters and friendship.

I cordially thank *Prof. Hans Egneus* who initially coordinated my PhD program in Sweden.

I am indebted to *Prof. Ulf Molau*, *Göran Wallin*, *Thomas Appelqvist, Bernard Pfeil, Anne Magurran, Marie Adamsson, Tage Vowles* and *Henrik Antonsson* for comments on my papers and the thesis.
Special thanks to *Prof. Staffan Höjer* from the Department of Social Work at University of Gothenburg.

I also thank Elizabeth Földi for handling administrative matters at the beginning of my PhD programme.

Special thanks to my beloved wife *Epiphanie Mukundiyimana* for supporting me in several issues.

Finally, I thank all the Rwandan Community in Gothenburg and encourage every member of this Community to be successful.

7. REFERENCES

African Bird Club. 2011. Rwanda. Available at: http://www.africanbirdclub.org/countries/Rwanda/news.html [accessed 21 June 2011].

Angassa, A. Oba, G. & Tolera, A. 2012. Bush encroachment control demonstrations and management implications on herbaceous species in savannas of Southern Ethiopia. *Tropical and Subtropical Agroecosystems* 15: 173-185.

Antonsson, H. 2012. Plant species composition and diversity in Cliff and Mountain Ecosystems. PhD thesis, University of Gothenburg.

Arun, A. & Redford, K.H. 2006. Poverty, development, and biodiversity conservation: Shooting in the dark? WCS Working Paper No. 26: 1-48. Available at: http://archive.wcs.org/wcspubs/science.html [accessed 18 January 2013].

Averberck, C., Apio, A, Plath, M. & Wronski, T. 2009. Environmental parameters and anthropogenic effects predicting the spatial distribution of wild ungulates in the Akagera savannah ecosystem. *African Journal of Ecology* 47: 756-766.

Balmford, A., Leader-Williams, N. & Green, M.J.B. 1992. The protected area system. In Sayer, J.A, Harcourt, C.S & Collins, N.M. (eds) *The conservation Atlas of tropical forests: Africa*. 69-80. Gland and Cambridge: IUCN.

Begon, M., Townsend, C.R. & Harper, J. L. 2006. *Ecology: from individuals to ecosystems*, 4th edn. Oxford: Blackwell Publishing.

BirdLife International. 2012a. Country profile: Rwanda. Available at: http://www.birdlife.org/datazone/country/rwanda [accessed 03 December 2012].

BirdLife International. 2012b. IUCN Red List for birds. Available at: http://www.birdlife.org [accessed 08 November 2012].

BirdLife International. 2012c. Important Bird Areas factsheet. Available at: http://www.birdlife.org [accessed 08 November 2012].

Blaum, N., Rossmanith, E., Popp, A. & Jeltsch, F. 2007. Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecologia* 31: 86-92.

Bolwig, S., Pomeroy, D., Tushabe, H. & Mushabe, D. 2006. Crops, trees, and birds: biodiversity change under agricultural intensification in Uganda's farmland landscapes. *Danish Journal of Geography* 106: 115-130.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines J.E. & Pollock, K.H. 1998. Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* 79: 1018-1028.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2001. *Introduction to Distance Sampling: estimating abundance of biological populations*. Oxford: Oxford University Press.

Buckland, S.T., Magurran, A.E., Green, R.E. & Fewster, R.M. 2005. Monitoring change in biodiversity through composite indexes. *Philosophical Transactions of the Royal Society* B 360: 243-254.

Buckland, S.T., Summers, R.W., Borchers, D.L. & Thomas, L. 2006. Point transect sampling with traps or lures. *Journal of Applied Ecology* 43: 377-384.

Bunge, J. & Fitzpatrick, M. 2003. Estimating the number of species: a review. *Journal of the American Statistics Association* 88: 364-373.

CBD (Convention on Biological Diversity). 2011a. Convention on Biological Diversity: text and annexes. Montreal: The Secretariat for the CBD.

CBD (Convention on Biological Diversity). 2011b. Nagoya Protocol on access to genetic resources and the fair and equitable sharing of benefits arising from their utilization to the CBD: text and annex. Montreal: The Secretariat for the CBD.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783-791.

Chao, A. 2005. Species richness estimation. In Balakrishnan, N., Read, C.B. & Vidakovic, B. (eds) *Encyclopedia of Statistical Sciences*, 2nd edn. 7909-7916. New York: Wiley.

Chemonics International Inc. 2008. Rwanda environmental threats and opportunities assessment (ETOA) 2008 update. Produced for review by the United States Agency for International Development.

Chiarruci, A., Enright, N.J., Perry, G.L.W., Miller, B.P. & Lamont, B.B. 2003. Performance of non-parametric species richness estimators in a high diversity plant community. *Diversity and Distributions* 9: 283-295.

Child, B. (ed.). 2004. *Parks in transition: Biodiversity, rural development and the bottom line*. South Africa: IUCN (World Conservation Union).

Colwell, R.K. & Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B* 345: 101-118.

de Klerk, H.M., Fjeldså, J., Blyth, S. & Burgess, N.D. 2004. Gaps in protected area network for threatened Afrotropical birds. *Biological Conservation* 117: 529-537.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villeger, S. & Mousquet, N. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47: 15-25.

Dolman, P.M., Panter, C.J. & Mossman, H.L. 2012. The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology* 49: 986-997.

Dornelas, M., Soykan, C.U. & Ugland, K.I. 2011. Biodiversity and disturbance. In Magurran, A.E & McGill, B.J. (eds) *Biological diversity: frontiers in measurement and assessment*. 237-251. Oxford: Oxford University Press.

Egoh, B.N., O'Farrell, P.J., Charef, A., Gurney,L.J., Koellner,T., Abi, H.N., Egoh, M. & Willemen, L. 2012. An African account of ecosystem service provision: use, threats and policy options for sustainable livelihoods. *Ecosystem Services* 2: 71-81.

Franklin, J. 2009. *Mapping species distributions: spatial inference and prediction*. Cambridge: Cambridge University Press.

Gaston, K.J. 1996. Species richness: measure and measurement. In Gaston, K.J. (ed.) *Biodiversity: a biology of numbers and difference*. 77-113. Oxford: Oxford University Presss.

Gill, F. & Donsker, D. (eds). 2012. IOC World Bird List (version 3.1). Available at: http://www.worldbirdnames.org/ioc-lists/classification/updates-of-ioc-classification-2-0 [accessed 25 September 2012].

Gimaret-Carpentier, C., Pelissier, R., Pascal, J.P. & Houllier, F. 1998. Sampling strategies for the assessment of tree species diversity. *Journal of Vegetation Science* 9: 161-172.

Gorelick, R. 2006. Combining richness and abundance into a single diversity index using matrix analogues of Shannon's and Simpson's indices. *Ecography* 29: 525-530.

Gottschalk, T.K., Ekschmitt, K. & Bairlein, F. 2007. Relationships between vegetation and bird community composition in grasslands of the Serengeti. *African Journal of Ecology* 45: 557-565.

Gotellli, N.J. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-391.

Goudie, A. 2006. *The human impact on the natural environment: past, present and future* (6th edn.). Oxford, UK: Blackwell Publishing.

Hellmann, J.J. & Fowler, G.W. 1999. Bias, precision and accuracy of four measures of species richness. *Ecological Applications* 9: 824-834.
Hirzel, A.H. & Le Lay, G. 2008. Habitat suitability modeling and niche theory. *Journal of Applied Ecology* 45: 1372-1381.
Homewood, K. & Brockington, D. 1999. Biodiversity, conservation and development in Mkomazi game reserve, Tanzania. *Global Ecology and Biogeography* 8: 301-313.
Kangah-Kesse, L., Attuquayefio, D., Owusu, E. & Gbogbo, F. 2007. Bird species richness diversity and abundance in the Abiriw sacred grove in the eastern region of Ghana. *West African Journal of Applied Ecology*, vol.11, no1.
Kanyamibwa, S. 1998. Impact of war on conservation: Rwandan environment and wildlife in agony. *Biodiversity and Conservation* 7: 1399-1406.
Kanyamibwa, S. 2001. Rwanda. In Fishpool, L.D.C. & Evans, M.I. (eds) *Important Bird Areas in Africa and associated Islands: priority sites for conservation*. 703-710. Newbury and Cambridge, UK: Pisces Publications and BirdLife International (BirdLife Conservation series No.11).
Kanyesigye, F. 2013, January 01. Rwanda on the right track-Kagame. *New Times*. Available at: http://www.newtimes.co.rw/news/index.php?i=15224&a=62387 [accessed 7 January 2013].
Kock, M.D. 2004, October. Ecosystem health in Akagera National Park: health and disease Issues at the interface. A draft report. Wildlife Conservation Society (Field Veterinary Program).
Koleff,P., Gaston, K.J. & Lennon, J.T. 2003. Measuring beta diversity for presence absence data. *Journal of Animal Ecology* 72: 367-382.
Konečný, A., Koubek, P. & Bryja, J. 2010. Indications of higher diversity and abundance of small rodents in human-influenced Sudanian savannah than in the Niokolo Koba National Park (Senegal). *Africican Journal of Ecology* 48:718–726.
Krook, K., Bond, W.J. & Hockey, P. A. 2007. The effect of grassland shifts on the avifauna of a South African savanna. *Ostrich: Journal of African Ornithology* 78: 271-279.
Lamprey, R. H. 2002. Akagera-Mutara aerial survey, Rwanda. Final Report (Unpublished report No. C4/02PRO/R.L.). Kigali, Rwanda: GTZ (German Technical Cooperation).
Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76: 5-13.
Lande, R., deVries, P.J. & Walla, T. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos* 89: 601-605.
Lloyd, H., Rios, S.S., Marsden, S.J. & Valdes-Velasquez, A. 2012. Bird community composition across an Andean tree-line ecotone. *Austral Ecology* 37: 470-478.
Lovejoy, T.E. & Hannah, L. (eds) 2005. *Climate change and biodiversity*. London: Yale University Press.
MacKenzie, D.I. 2005. What are the issues with presence-absence data for wildlife managers? *The Journal of Wildlife Management* 69:849-860.
MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Amsterdam: Elsevier Academic Press.
Magurran, A.E. 2004. *Measuring biological diversity*. Oxford: Blackwell Publishing.
Magurran, A.E. & McGill, B.J. (eds) 2011. *Biological diversity: frontiers in measurement and assessment*. Oxford: Oxford University Press.
Malcolm, L., Hunter, G.R. & Gibbs, J. 2007. *Fundamentals of conservation Biology* (3rd edn). Oxford: Blackwell Publishing.

Martin, R.B. 1999. Adaptive management: the only tool for decentralized systems. In *Proceedings of the Norway/UN Conference 'The ecosystem approach for sustainable use of biological diversity,* 1-14. Trondheim, Norway.

MINITERE (Ministry of Lands, Resettlement and Environment). 2003. National strategy and action plan for the conservation of biodiversity in Rwanda. Kigali, Rwanda: Republic of Rwanda.

Nahayo, A. & Yansheng, G. 2009. Local livelihoods and protected area conservation in Rwanda: a case study of Akagera National Park. *J. of Amer. Sci.* 5:171-178.

NISR (National Institute of Statistics of Rwanda). 2012. The third integrated household living conditions survey (EICV3). Main indicators report. Kigali, Rwanda: National Institute of Statistics of Rwanda.

Nkwabi, A.K., Sinclair, A.R.E., Metzger, K.L. and Mduma, S.A.R. 2011. Disturbance, species loss and compensation: wildfire and grazing effects on the avian community and its food supply in the Serengeti Ecosystem, Tanzania. *Austral Ecology* 36: 403-41.

Pacifici, K., Simon, T.R. & Pollock, K.H. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *Auk* 125: 600-607.

Plumptre, A.J., Masozera, M. & Vedder, A. 2001. *The impact of civil war on the conservation of protected areas in Rwanda*. Washington, DC: Biodiversity Support Program.

Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L & Sauer, J.R. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13: 105-119.

Quinn, G. & Keough, M. 2002. *Experimental design and data analysis for biologists*. Cambridge,UK: Cambridge University Press.

Rands, M.R.W., Adams, W.M., Bennum, L., Butcart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge,I., Kapos,V., Scharlemann,J.P.W., Sutherland, W.J. & Vira, B. 2010. Biodiversity conservation: challenges beyond 2010. *Science* 329: 1298-1303.

Ranta, P., Tanskanen, A., Niemelä, J & Kurtto, A. 1999. Selection of islands for conservation in the urban Archipelago of Helsinki. *Finland Cons. Bio*. 13:1293-1300.

Rayburn, E.B. & Rayburn, S.B. 1998. A Standardized Plate Meter for Estimating Pasture Mass in On-Farm Research Trials. *Agronomy Journal* 90: 238-241.

Republic of Rwanda. 2011. Rwanda biodiversity policy. Kigali, Rwanda: Republic of Rwanda.

Rivera-Milán, F.F. & Bonilla-Martínez, G. 2007. Estimation of abundance and recommendations for monitoring White-Cheeked Pintails in wetlands of Puerto Rico and Territorial Islands. *Journal of Wildlife Management* 71: 861-867.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of bush encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38: 268-280.

Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.

Rutagarama, E. & Martin, A. 2006. Partnerships for protected area conservation in Rwanda. *The Geography Journal* 172: 291-305.

Sankaran, M., Hanan, N.P., Scholes, R.J. et al. 2005. Determinants of woody cover in African savannas. *Nature* 438: 846-849.

Schoene, C. 2003. Rwanda conservation in a haunted country. "Projet de Protection des Ressources Naturelles" (GTZ-PRORENA-AKAGERA). Available at: http://www.sawma.co.za/images/wildnews_2003_jan_a23.pdf [accessed 30 November 2012].

Seymour, C.L. & Dean, W.R.J. (2010) The influence of changes in habitat structure on the species composition of bird assemblages in the southern Kalahari. *Austral Ecology* 35: 581-592.

Shahabuddin, G. & Kumar, R. 2006. Influence of anthropogenic disturbance on bird communities in a tropical dry forest: role of vegetation structure. *Anim. Conserv*. 9: 404-413.

Shorrocks, B. 2007. *The biology of African savannahs*. Oxford: Oxford University Press.

Sinclair, A.R., Mduma, S.A. & Arcese, P. 2002. Protected areas as biodiversity benchmarks for human impact: agriculture and the Serengeti avifauna. *Proceedings Biological Sciences* 269: 2401–2405.

Sirami, C., Seymour, C., Midgley, G. & Bernard, P. 2009. The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Diversity and Distributions* 15: 948-957.

Soberon, J. 2007. Grinnellian and Eltonian niches and geographica distributions of species. *Ecology Letters*, 10: 1115-1123.

Staver, A.C., Bond, W.J., Stock, W.D., van Rensburg, S.J. & Waldram, M.S. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications* 19: 1909-1919.

Stevenson, T. & Fanshawe, J. 2009. *Birds of East Africa: Kenya, Tanzania, Uganda, Rwanda and Burundi*. London: Christopher Helm.

Stewart, K.E.J., Bourn, N.A.D. & Thomas, J, A. 2001. An Evaluation of Three Quick Methods Commonly Used to Assess Sward Height in Ecology. *Journal of Applied Ecology* 38:1148-1154.

Svensson, J.R., Lindegarth, M. & Pavia, H. 2009. Equal rates of disturbance cause different Patterns of diversity. *Ecology* 90: 496–505.

Thiollay, J.M. 2006. Large bird declines with increasing human pressure in savanna woodlands (Burkina Faso). *Biodiversity and Conservation* 15: 2085–2108.

Thomas, L., Buckland, S.T., Burnham, K.P., Anderson, D.R., Laake, J.L., Borchers, D.L. & Strindberg, S. 2002. Distance sampling. In El-Shaarawi, A.B. & Piegorsch, W.W. (eds) *Encyclopedia of Environmetrics*, Volume 1. 7909-7916. Chichester, UK, John Wiley & Sons, Ltd.

Thomas, L., Laake, J.L., Rexstad, E., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Burt, M.L., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., and Marques, T.A. 2009. Distance 6.0 Release 2. Research Unit for wildlife Population Assessment, University of St Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. & Burnham, K. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47: 5-14.

Twagiramungu, F. 2006, July 6. Environmental profile of Rwanda. A report prepared for the National Authorising Officer of FED and the European Commission. Kigali, Rwanda: European Commission and Republic of Rwanda.

Vande weghe, J.P. (ed.) 1990. *Akagera: land of water, grass and fire*. Belgium: World Wide Fund for Nature (WWF-Belgium).

Vande weghe, J.P. & Vande weghe, G.R. 2011. *Birds in Rwanda: an atlas and handbook*. Kigali, Rwanda: Rwanda Development Board (RDB).

Wiegand, K., Saltz, D. & Ward, D. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics* 7: 229-242.

Williams, B.K., Nichols, J.D. & Conroy, M.J. 2002. *Analysis and management of animal populations: modelling, estimation and decision making*. London: Academic Press.

Wong, C., Roy, M. & Duraiappah, A. K. 2005. Connecting poverty and ecosystem services: a series of seven country scoping studies. Focus on Rwanda. Manitoba, Canada: United Nations Environment Programme (UNEP) and the International Institute for Sustainable Development (iisd).

World Bank. 2004. *Environmental assessment and social management analysis*. Washington, D.C: World Bank.

World Tourism Organization (UNWTO). 201. UNWTO tourism highlights 2011edition. http://mkt.unwto.org/sites/all/files/docpdf/unwtohighlights11enlr.pdf [Accessed 17 December 2012].