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Antelope Conservation

From Diagnosis to Action

Edited by Jakob Bro-Jørgensen and David P. Mallon

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Antelope Conservation

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Preface and Acknowledgements

From hot deserts to snowy plains, from lowland rainforests to mountain peaks, antelopes form a critical part of natural ecosystems throughout Africa and Asia. They are distributed in every country of mainland Africa and across the Arabian Peninsula, Middle East to Central Asia, extending west of the Caspian Sea in Russia, eastwards to Mongolia and northern China, and southwards to the Indian subcontinent and all the way to the Indochinese peninsula. They occur at elevations from 150 m below sea level at Lac Assal in Djibouti to more than 5,000 m above on the Qinghai-Tibet Plateau. Their habitats encompass hyperarid deserts, high-altitude cold desert, semi-deserts, steppes, open bush, dry scrub, deciduous woodland, humid rainforest, wetlands, swamps, rocky outcrops as well as mountains.

However, this fascinating and diverse group of animals is under increasingly severe threat of further species extinctions and tends to slip under the conservation radar compared to many other aspects of biodiversity. The addax and dama gazelle are currently very close to becoming extinct in the wild, and a few other species have been reduced to perilously low numbers. At the other end of scale, wildebeest and Mongolian gazelle still number over one million, and the annual migration of the common wildebeest remains one of the world's most impressive wildlife spectacles. But for most species, the vast herds of the recent past have disappeared, and almost everywhere antelope numbers are declining and their ranges shrinking and fragmenting in the face of over-harvesting, conversion of land to agriculture-and over-grazing.

Although important work is being done by passionate conservationists and researchers, as a community antelope specialists appear less vocal compared to many other interest groups - and conservation concerns relating to this magnificent facet of the wild are often overlooked even though they are in many ways central to the current conservation debate. To galvanize the community of antelope researchers, we brought together leading experts in antelope conservation at a highly stimulating two-day symposium at Zoological Society of London (ZSL) in November 2011. The meeting included researchers and conservationists as well as students and lay people from across the globe. The forum enabled engaging discussions and exchange of views on a range of topics, from common best practices in conservation to specific concerns pertaining to antelopes. This book is inspired by the meeting and

reflects its key themes, even if the priority of getting a balanced book addressing general conservation issues means that the contributing authors do not correspond exactly with the speaker list at the meeting.

We would like to extend our deepest gratitude to the Zoological Society of London who made the meeting possible by providing an atmospheric venue and financial support. The organizational team, especially Linda DaVolls and Joy Hayward, were a pleasure to work with. Likewise, we are indebted to Wiley-Blackwell whose patience and support during the preparation of this book have been critical in our efforts to ensure that the coverage of the topic became as comprehensive as possible; Ward Cooper, Kelvin Matthews and Kavitha Chandrasekar and her team here deserve a special mention. All chapters have undergone rigorous scientific peer review by experts in the various topics covered, and we are indebted to all the reviewers, who shall remain anonymous, for their often extremely thorough and insightful reviews. We are also deeply grateful to all the photographers who kindly allowed their exquisite photos to be reproduced on the colour plates. Finally, we would like to thank all the speakers at the 2011 meeting and all the contributors to this volume for their thought-provoking contributions.

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Jakob Bro-Jørgensen
David P. Mallon

Foreword

The outlook for conservation of antelopes and other large mammals in this century depends on the willingness of mankind to provide safe havens for wildlife. Maintaining and increasing existing protected areas is essential. The words of the Triennial Report of the IUCN Antelope Specialist Group (ASG) in 1988–1990 hold just as true today, a quarter of a century later: '*Preservation of any substantial areas of wildlife habitat outside of existing parks and reserves depends on making use of antelope and other wildlife on a sustainable basis more rewarding than other land uses. If their value can be demonstrated in time, it would still be possible to set aside buffer zones surrounding parks that would be accepted as inviolate sanctuaries necessary for renewing stocks of species to be hunted for food or trophies in designated hunting areas.… Nearly all problems of wildlife conservation stem from the continuing uncontrolled growth and impoverishment of the human population.*' In Africa – a continent of paramount importance for antelope conservation – the human population has now passed one billion and continues to increase at 2–3% a year. Huge amounts of natural habitat have already been transformed to meet human needs. Even parks and game reserves set aside for wildlife are under pressure, and development between and around them is turning them into islands. Hemmed in by settlement, wildlife in these protected areas will be unable to extend their range in response to climate change.

Faced with this advanced stage of habitat attrition, the present book is a valuable source of information on central issues in antelope conservation, and the varied contributions provoke reflections on how best to safeguard biodiversity for the future. Reflecting on my own experience as Chair of the ASG between 1978 and 2005, three priorities appear particularly important to slow or even stop the elimination of wildlife habitat in the antelope range states: making wildlife utilization more valuable than competing forms of land use, supporting the growing number of Transboundary Conservation Areas (TBCAs) jointly managed by neighboring countries, and combatting climate change.

The willingness of landowners to save natural habitat and tolerate wildlife ultimately depends on whether the benefits outweigh the costs. Most antelopes live in developing countries occupied by people living at subsistence level. How can communal and private landowners be persuaded to share their property with antelopes and other large herbivores that compete for forage and space with their livestock and crops? One option to make wildlife a more valuable resource is giving landowners increasing ownership. In 1975, Zimbabwe passed a Parks and Wildlife Act that conferred custodianship of wildlife on their land to landholders, followed in 1982 by the CAMPFIRE program that allowed rural communities to benefit economically from their wildlife. The success of these programs led neighboring countries to follow suit. By the end of the 1980s, most of South Africa's larger antelope species were more numerous than at any time since the 1800s (Estes & East, 2009). Neighboring landowners formed large wildlife conservancies and hunting blocks by taking down dividing fences, both in southern and eastern Africa.

Moreover, a guaranteed share of income from wildlife-based tourism should benefit the communities bordering parks and game. Communal and private landowners may also be persuaded to protect wildlife by subsidy, ideally implemented by an effective new international agency. It will be merely one of the expensive but essential commitments by mankind to safeguard natural habitat otherwise sure to be transformed by the ever-growing human footprint. World Heritage Sites and Man and Biosphere Reserves should head the list.

Incorporating vast landscapes encompassing both protected and unprotected areas, TBCAs could play a key role in restoring fragmented ecosystems of migratory ungulates. In southern Africa, TBCAs (here also known as 'Peace Parks') are intended not only for the conservation and sustainable use of biological and cultural resources; they also have the objective of facilitating and promoting regional peace and cooperation and socioeconomic development. Since the Global Transboundary Conservation Network was formed at the 2003 World Parks Congress, over 200 TBCAs have been catalogued in the UNEP/WCMC database.

With such initiatives, there is hope that we can also restore mutually beneficial, harmonic associations between wild and domestic ungulates on open rangelands including buffer zones bordering parks, reserves and game-controlled areas (Marshall, 1990; Homewood *et al.*, 2001; Reid, 2012). Livestock and wildlife have shared the savannas for thousands of years; why give up hope that they can do so again? Transhumance worked and can work again if livestock numbers can be controlled to prevent habitat degradation. Instead of counting wealth in the number of livestock however, pastoralists stand to gain far greater wealth by satisfying the demand for meat in cities, where much poached bushmeat is currently marketed. Combining wildlife and livestock production on private property, as is common in southern Africa, can be very profitable and could work for pastoralists on public land and within some protected areas, the Ngorongoro Conservation Area offering a possible model (Estes, 2014). Where projections of increasingly arid regional climates come true, farmers may indeed find their land better suited to pastoralism than agriculture.

But all these measures may be too little, too late. Suddenly we find that global warming is proceeding faster than predicted. President Obama of the United States, the world's leading economic power and second-largest emitter of greenhouse gases, has sounded the alarm, seconded by Pope Francis: '*Human activity is disrupting the climate in many ways faster than we previously thought. The science is stark. It is sharpening. It proves that this once distant threat is now very much in the present. It is happening here, it is happening now. Already disrupting our agriculture and ecosystems, our water and food supplies, our energy, our infrastructure, human health, human safety, now, today*' (Obama, 2015). Maintaining biodiversity needs to be closely linked with efforts to combat global climate change. Conservation of antelopes and the other large charismatic mammals of Africa's and Asia's rangelands would go a long way toward conserving the planet's biodiversity, given their role as umbrella and keystone species. The Bovidae, the last and greatest mammalian radiation, can show the way.

Richard D. Estes

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1

Our Antelope Heritage – Why the Fuss?

Jakob Bro-Jørgensen

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Introduction

Why a book dedicated to antelope conservation? Our planet has witnessed a decrease of more than 50% in its vertebrate populations since 1970, and this drastic decline has hit antelopes particularly hard, according to the Living Planet Index (BBC, 2008; McLellan, 2014; see also Craigie *et al.*, 2010). Many will agree that antelopes constitute an outstanding aspect of the world's biodiversity and that the prospect of losing this heritage is a concern in its own right. A savanna bereft of flickering herds of gazelles (Figure 1) or a rainforest where duikers no longer lurk in the understorey may be likened to bodies that have lost their souls. But leaving subjective sentiments aside, antelopes are also of fundamental importance for the functioning of many ecosystems across Africa and Asia. They have important roles as architects of habitats, as dispersers of seed, as the prey base for endangered carnivores and indeed in nutrient cycling in general (Sinclair & Arcese, 1995; Sinclair *et al.*, 2008; Gallagher, 2013). Maintaining healthy antelope populations is therefore vital for the management of many ecosystems, and the motivation for this book comes from an urgent concern not only at the species level but also relating to wider repercussions at the ecosystem level.

Antelopes moreover provide a well-suited model to obtain insights into the operation of threat processes affecting wildlife populations more generally. Because they share the same basic biology, yet display a striking variation in habitats and threats, this species-rich group presents an extraordinary opportunity to pinpoint how human impact on wildlife populations depends on the interaction between threats and specific species traits. Many of the issues facing antelopes are central to

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Figure 1 **Thomson gazelles and impalas in Maasai Mara National Reserve, Kenya (© Jakob Bro-Jørgensen).**

the current conservation debate, including the sustainable use of wildlife (for meat and trophies), protection of migratory as well as highly habitat-specific species in a world of climate change and habitat fragmentation, and the coexistence of wildlife with people and their livestock without conflict. Typically, antelope conservation takes place in developing countries with growing human populations and severely under-resourced wildlife authorities, which brings the issue of how to integrate conservation and development to the forefront. Valuable long-term data sets are present for several antelope species, placing them in a strong position to provide some general lessons for conservation biology, especially in relation to the particular challenge of preserving large mammals (MacDonald *et al.*, 2013).

However, following a surge in pioneering field studies of many antelope species in the 1960s and 1970s, the reality is that antelope research seems to have lost its general appeal, and the attention from the general public is modest compared to that received by many of their mammalian relatives, such as carnivores and primates, which are widely seen as more charismatic. This book is intended to reinvigorate the interest in antelope research and give a deeper understanding of the threat drivers facing antelopes today, thereby providing a basis for reflection on common best practices in conservation. As a background, this introductory chapter will first take an evolutionary perspective to understanding the ecological importance of global antelope biodiversity and then outline the current conservation status of this world heritage.

Antelopes – an evolutionary success story … so far

A green world presents a tremendous opportunity for the evolution of efficient plant-eaters, and here antelopes have been an extraordinary success story. A major evolutionary breakthrough took place in the Eocene some 50 Myrs BP when the compartmentalized ruminant stomach evolved (Fernández & Vrba, 2005). This enabled a more efficient breakdown of fibrous plant material by chewing cud and using microbial symbionts to digest cellulose. The antelopes are members of the ruminant family Bovidae, characterized by permanent horns consisting of a bone core covered by a sheath of keratin. The first known bovid fossil, *Eotragus,* dates back to the early Miocene some 20 Myrs BP (Gentry, 2000; Fernandez & Vrba, 2005), and since then, an astonishing adaptive radiation has taken place as bovid species have evolved to occupy a wide range of ecological niches. The majority of these species are antelopes: 88 extant species are represented by 14 species in Asia and 75 species in their main stronghold in Africa, with only the dorcas gazelle (*Gazella dorcas*) found on both continents. Antelopes vary in size from the 1.5 kg of a royal antelope (*Neotragus pygmaeus*) (Plate 3) to nearly a ton in a full-grown giant eland bull (*Tragelaphus derbianus*) (cover).

So what distinguishes antelopes? Treating antelopes as a group is questionable from a strict evolutionary perspective because it violates the ideal of keeping together all species descending from a given distinctive ancestor. The group is created by cutting off two distinct monophyletic branches from the bovid tree: (i) the wild oxen *Bovini,* characterized by their heavier build and water-dependence, and (ii) the wild goats and sheep *Caprinae*, characterized by their extreme adaptation to rocky habitats (Figure 2). However, antelopes are not defined only by what they are not (i.e., as a bovid that is neither an oxen nor a goat). They can be succinctly described as horned ruminants lightly built for swift movement in habitats with predominantly even ground. This has resulted in a characteristic graceful and elegant morphology, often adorned with spectacular ornaments and weapons due to strong sexual selection in the more social species (Stoner *et al.*, 2003; Bro-Jørgensen, 2007).

The broad array of ecological adaptations in antelopes is apparent when considering the variety between the 12 tribes (Plates 1, 2, & 3). The spiral-horned antelopes of Africa **Tragelaphini** (elands, kudus, nyalas and allies), together with their Asian relatives **Pseudorygini** (saola *Pseudoryx nghetinhensis*) and **Boselaphini** (nilgai *Boselaphus tragocamelus*, four-horned antelope *Tetracerus quadricornis*), represent a highly diverse ancient line from within which the wild oxen descended. Except for the browsing saola, they are mixed feeders; that is, feeding on both browse and grass. They vary more than ten-fold in size and are found from dense forests (bongo *Tragelaphus eurycerus*, saola) to semi-deserts (common eland *Tragelaphus oryx*), and from swamps

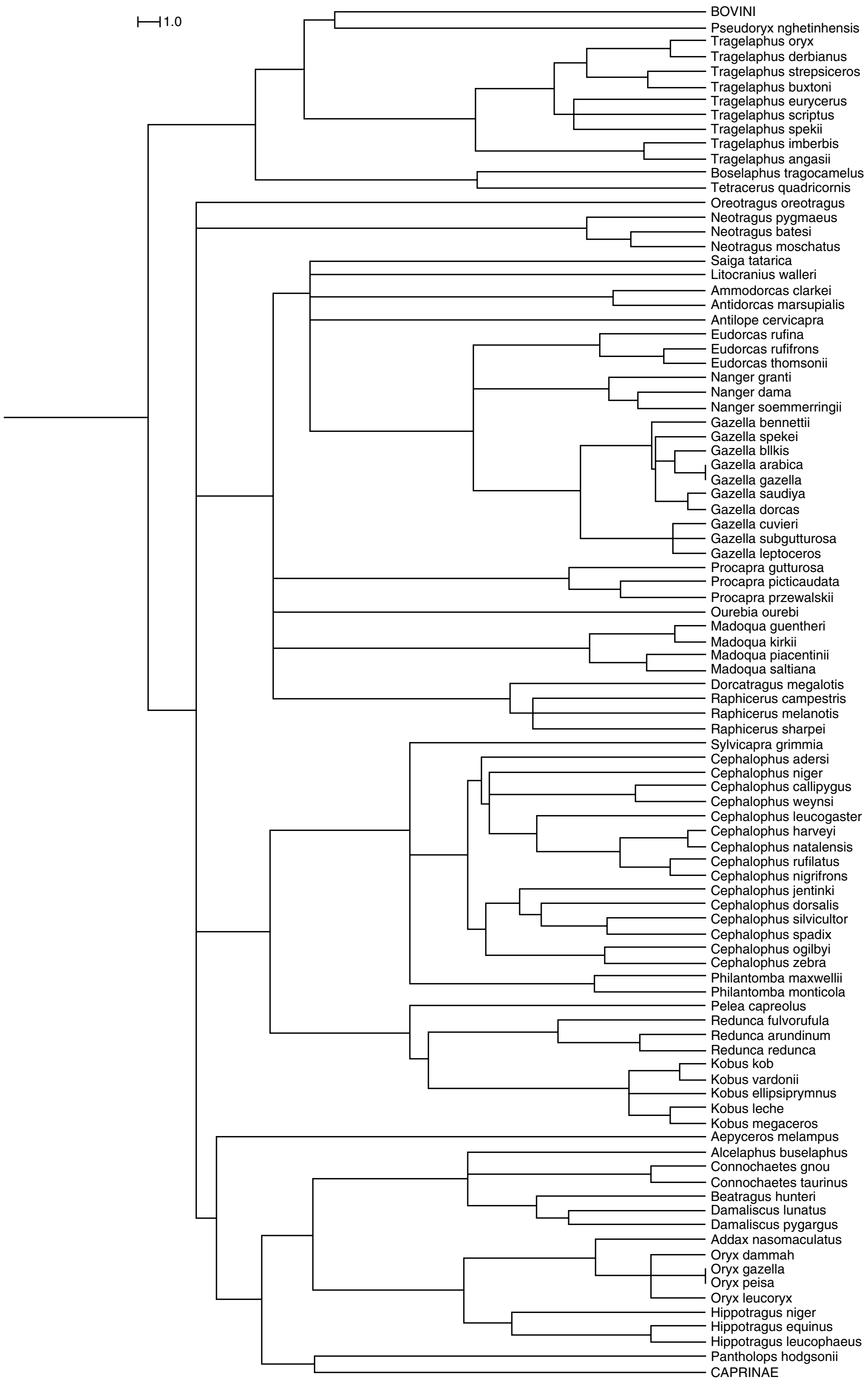

Figure 2 **The evolution within Bovidae since the divergence from deer 32 million years ago (for common names, see the Appendix). Bar indicates one million years. Based on Fernández & Vrba 2005; drawn in Dendroscope, Huson & Scornavacca 2012.**

(sitatunga *Tragelaphus spekii*) to mountains (mountain nyala *Tragelaphus buxtoni*). Other mixed feeders include the arid-adapted gazelles **Antilopini** which span from hot to rather cold regions, and the horse antelopes **Hippotragini,** which predominantly graze and occur from relatively moist savannas (roan *Hippotragus equinus* and sable antelope *Hippotragus niger*) to semi-deserts (oryxes) and deserts (addax *Addax nasomaculatus*). Both the latter tribes have representatives in Africa as well as Asia. Also mixed-feeders, the African impala (*Aepyceros melampus*) and rhebok (*Pelea capreolus*) are the only living representatives of the tribes **Aepycerotini** and **Peleini** respectively. The grazing tribes include the reduncines **Reduncini** (lechwes, reedbucks and allies), adapted to relatively moist savannas and wetlands, and the alcelaphines **Alcelaphini** (wildebeests and allies), adapted to drier savannas; both are exclusively African. The Tibetan antelope (*Pantholops hodgsonii*), the only representative of the caprine-related **Pantholopini**, also feeds on grass, as well as herbs, on the often snowy steppes of the Tibetan Plateau. Smaller antelopes include the duikers **Cephalophini,** which are adapted to the ecology of African forests, where they feed on high-quality browse and fruits, and the dwarf antelopes **Neotragini** which are ecologically diverse, mainly browsers and frugivores, but some also feeding on grass (notably the oribi *Ourebia ourebi*), and inhabiting a wide range of habitats spanning from forests (royal antelope) and thickets (suni *Neotragus moschatus*, dik-diks), to rocky outcrops (klipspringer *Oreotragus oreotragus*, beira *Dorcatragus megalotis*) and fairly open savannas (oribi); several neotragines are actually likely to be more closely related to gazelles than to the genus *Neotragus*. In contrast to the gregarious species of the open land, the smaller species in dense habitats are usually solitary or found in groups of minimal size (Jarman, 1974; Brashares *et al.*, 2000).

Antelopes as an integral part of the structure and function of ecosystems

In an evolutionary and ecological sense, antelopes have thus been an immensely successful group, occupying a remarkable range of habitats. Moreover, within each habitat, a proliferation of species often occupies distinct niches in terms of their diet and antipredator behaviour. For example, 16 species coexist alongside each other in the Serengeti-Mara ecosystem. Throughout Africa and Asia, antelopes often dominate the community of larger herbivores in undisturbed wilderness areas. Their numerical abundance – at least historically – combined with their long period of coevolution with plants and predators means that they are intrinsically linked to the function of the ecosystems they inhabit. Some of their ecological roles are fairly obvious whereas other important links are more subtle and indirect and some dynamics undoubtedly still await discovery.

Antelopes have a major impact on both the structure and function of the plant community. In some cases, the loss of antelope populations may even cause wilderness areas to switch from one biome to another. For example, the grazing pressure from the great migration of wildebeest in Serengeti-Mara is crucial for maintaining the open landscape to which the wider savanna community is adapted. In the absence of wildebeest, thickets proliferate, and the whole system could eventually reach an ecological tipping point where the habitat becomes unfavourable for today's rich community of grazers and gravitates towards an alternative, more wooded state (Sinclair *et al.*, 2007). Antelopes may also have important effects on the vegetation that are less conspicuous. For example, impala distribute themselves in a 'landscape of fear' as they avoid areas of thick cover due to high predation risk from leopards and hunting dogs (Ford *et al.*, 2014). As a consequence, impala browsing pressure on acacia is highest in open habitats, and this gives acacia species protected by thorns a competitive advantage in such areas. In this way, browsing by impala has been shown to shape the spatial structure of the woody community of African savannas (Ford *et al.*, 2014).

Antelopes can also have a profound effect on the vegetation by acting as seed dispersers. Frugivores in forest habitats, such as the duikers, are highly important in this regard (Jordano, 2013). They act as vectors of seeds, and seed germination may even depend on being passed through the gut of an antelope consumer. In tropical forests, many of the most carbon-rich hardwood trees rely on animals such as forest antelopes for their dispersal, and loss of seed-dispersers through bushmeat hunting has been linked to a reduction in hardwoods (Brodie & Gibbs, 2009). Because hardwoods are particularly important in sequestering CO_2, this could compromise the role of the forest as a carbon sink, which in turn reduces its potential to mitigate the adverse effects of climate change.

Antelopes are of crucial importance also as a prey base for larger predators: without thriving antelope populations, efforts to preserve carnivores will often make little sense. From a management perspective, it is important to recognize the intricate relationships between predators and their prey. Predator species show marked differences in their prey preference profiles. For instance, lions (*Panthera leo*) prefer large, relatively slow prey species that are not suitable prey for smaller predators (Sinclair *et al.*, 2003). In turn, cheetahs (*Acinonyx jubatus*) prefer smaller, but fast prey species that are less preferred by lions (Hayward *et al.*, 2006b), while leopards (*Panthera pardus*), ambush predators, also prefer smaller, but slower prey (Hayward *et al.*, 2006a). Such relationships are the result of long-term coevolutionary processes (Bro-Jørgensen, 2013), and it is unreasonable to expect that different prey species can readily substitute for each other. A decline in the population size of one species can have knock-on effects on others, and to maintain natural ecosystem dynamics the full breadth of species diversity within both predator and prey communities requires conservation.

Threats facing antelopes today

As a key component of natural ecosystems, antelopes are an integral part of global life support systems. In areas of poverty, they can directly benefit human livelihoods as sources of food for subsistence or sale and through other income-generating activities such as ecotourism and trophy hunting. The physiological efficiency and high productivity of bovids is shown by the fact that the taxon includes the ancestors of the most important domesticated livestock: that is, cattle, sheep and goats. Yet, the evolutionary potential of antelopes and the ecosystem services they provide are usually grossly undervalued in the formal economy, and human development therefore takes place without the relevant costs from squandering areas of wilderness being integrated into land use planning.

Consequentially, human activities are rapidly decimating many of the remaining antelope populations: 31% (27/88) of the extant antelope species assessed by the IUCN Red List are now formally categorized as threatened (including 64% [9/14] of the Asian species) and a further 9% (8/88) as near-threatened (IUCN 2015). The extinction in the wild of the scimitar-horned oryx (*Oryx dammah*) in year 2000, and the global extinction of the bluebuck (*Hippotragus leucophaeus*) in 1800, and probably also the kouprey (*Bos sauveli*) in recent years, clearly point to the serious danger that further bovid extinctions are imminent. Particular hot spots of highly threatened species include the desert regions of North Africa, the horn of Africa, the West African rainforests and the Asian steppes. Taxonomically, species with high threat status are dispersed throughout the phylogeny. Conservation concerns are not limited to red-listed species: the population trend is decreasing for 64% (54/84) of all the species assessed, stable for 33% (28/84) and increasing for only 2% (2/84) (i.e., the springbok *Antidorcas marsupialis* and black wildebeest *Connochaetes gnou* in Southern Africa). As many as 76% (67/88) of all species are threatened by exploitation through hunting and trapping primarily for meat, but also for horns (used predominantly as trophies and in traditional medicine), hides and – specifically in the Tibetan antelope – underfur ('shahtoosh') used for shawls. Various human land-use changes affect 69% (61/88) of species, practically all of which are simultaneously affected by exploitation; specifically, 45% (40/88) are affected by livestock farming and ranching, and 48% (42/88) are affected by encroaching human settlements. In addition, 13% (11/88) of species are threatened by war or other civil unrest; half of these are in the Horn of Africa and also the Sudano-Sahelian savannas belt is severely affected. Currently, 18% (16/88) of species are referred to as affected by climate change, but our knowledge in this area is still limited, and the figure may rise as more information becomes available (Akçakaya *et al.*, 2014; Payne & Bro-Jørgensen, 2016).

Outline of this book

In summary:

- Antelopes are a high conservation priority of significant ecological importance
- Multiple threats face this ecologically diverse set of species
- Conservation generally takes place in developing economies with growing human populations so social sustainability of any conservation action is a priority

Given these conditions, which approaches can most effectively secure antelope populations into the future? The chapters in this book seek a deeper understanding of the key threat processes facing antelopes today and critically evaluate the various options for action. Whereas a broad consensus emerges on several issues, a diversity of opinion also manifests itself on certain points, reflecting the varied experience of the authors. To begin with, Chapter 2 provides an overview of ecosystem functioning and conservation challenges pertaining to savannas, a habitat of vital importance for antelope biodiversity. Chapter 3 goes on to present a conceptual framework for understanding what regulates antelope populations in natural ecosystems and uses this insight to explore the potential impact of climate change alongside other threat drivers. Following on from this, Chapter 4 focuses specifically on interspecific interactions over resources and provides a critical review of the current evidence that competition and facilitation significantly affect antelope population performance. Chapter 5 reviews the role of disease in antelope ecology, both as part of natural systems and as a threat associated with human activities.

In Chapter 6, attention turns to human exploitation of antelope populations with a review of the conservation impact of subsistence hunting of antelopes for meat, emphasising forest systems. Next, Chapter 7 examines the potential of trophy hunting to contribute to antelope conservation. Considering a broader set of management interventions, Chapter 8 takes its outset in the South African context and discusses the usefulness of a range of options to promote antelope conservation. Chapter 9 in turn outlines ways in which molecular techniques can be applied to inform antelope conservation; and Chapter 10 focuses specifically on the application of landscape genetics as a tool in conservation. Chapter 11 introduces another novel conservation technique, the use of camera-trapping in population monitoring. Chapter 12 provides a review of the use of reintroduction in antelope conservation, and Chapters 13 and 14, by concentrating on the critical conservation status of Sahelo-Saharan desert antelopes, stresses the urgent need for action to preserve the most threatened antelopes. Rounding off, Chapter 15 reflects, based on experience from saiga (*Saiga tatarica*) conservation, on the factors that can create opportunities and present obstacles when it comes to safeguarding antelope populations in practice. Finally in Chapter 16, key challenges facing antelope conservation over the next century are summarized in a synthesis.

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2

Conservation Challenges Facing African Savanna Ecosystems

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People evolved in African savannas and rapidly spread across the rest of the globe, assuming a defining role in the acquisition of space, energy, and other resources. Despite an epoch of co-existence with wildlife, the tides are shifting towards an increasingly troubled future for antelope in these ancient landscapes. In this chapter, we review the biophysical characteristics of savannas, some of the key interactions that define how savannas function, and how people are changing this functionality. We end by highlighting conservation efforts that can help maintain ecosystem function in an increasingly human-dominated world. Within this context, we focus on issues relating to large herbivores in general and in particular the antelopes that often dominate the ecology of many savannas.

Key characteristics of savanna systems

At the global scale, savannas occur between grasslands and forests, typically where rainfall ranges between 50 and 130 cm per year and where average temperatures rarely fall below 20°C (Sankaran *et al.*, 2005; Lehmann *et al.*, 2014). At the landscape scale, savannas are defined by pronounced heterogeneity in vegetation cover, manifesting itself as a discontinuous overstory of woody cover, interspersed with herbaceous understorey and bare ground. Indeed, it is the co-domination of trees and grasses that most clearly distinguishes a savanna

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ecosystem from that of forest or grasslands. Over time, the relative composition of tree and grass cover changes in a shifting mosaic largely determined by the interaction of bottom-up factors – rainfall, fire, soil nutrients – and top-down factors – herbivory and, indirectly, via predation and pathogens.

The temporal pattern of rainfall underlies ecological interactions in savannas. Savanna ecosystems typically experience a period of four or more months of very low rainfall, coupled with one or more periods of high rainfall. Marked seasonality results in dramatic pulses in vegetation growth in both understorey and overstory plants. In these low rainfall environments, soil moisture is often the major limiting factor for plant growth (Breman & de Wit, 1983; McNaughton, 1985). As such, when sufficient rainfall occurs, a carpet of nutritious new grass-shoots rapidly emerge, either from the seed bank in the case of annuals or from root or crown reserves in the case of perennial grasses.

As with rainfall, both the frequency and intensity of fire affects the composition and spatial patterning of tree-grass cover in savannas. In landscapes where fires are frequent, fires tend to be less severe, and cover tends to be dominated by grasses. Within days (Green *et al.*, 2015) to years (Sensenig, Demment *et al.*, 2010) after a fire, nutrient release increases the quality of forage, which then attracts smaller and medium-sized ungulates. Fire also reduces the accumulation of plant biomass and increases visibility, thereby enhancing the ability of medium and larger-sized antelope to detect and avoid their predators. Thus, recently burned areas may offer both forage and antipredator benefits to antelope.

The biomass potential of vegetation communities in African savannas is also underlain by soil fertility. Concentrations of key nutrients for plant growth depend on geological materials and the degree of weathering, erosion, and leaching that has taken place (Hopcraft *et al.*, 2010). Over time, soils may become weathered and consequently low in crucial minerals. In other places, volcanism, such as that associated with the African rift, is responsible for deposition of nutrient-rich ash that can be highly productive. The distribution of nutrient-rich and poor soils can be highly patchy relative to the movements of large mammalian herbivores (Goheen & Palmer, 2010), further adding to the spatial heterogeneity of savanna vegetation. At the patch scale, 'hotspots' of nutrients provide access to high-quality forage, attract grazers, and keep grasses in a state of high productivity (Anderson *et al.*, 2010). These hotspots can be derived through natural variation in nutrient availability or through human sources, such as abandoned cattle corrals (Augustine, 2003; Augustine *et al.*, 2003; Augustine, 2004).

One of the most conspicuous top-down forces in African savannas is herbivory by the species-rich and abundant populations of ungulates. For example, the biomass of large herbivores in Laikipia, Kenya, is 1.74 t/km^2 among 9 species (Georgiadis *et al.*, 2007), and 0.94 t/km^2 among 31 species in the Serengeti-Mara ecosystem (Frank *et al.*, 1998). Conversely, in temperate systems, such as Yellowstone National Park in the United States, there are