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Our Antelope Heritage – Why the Fuss?

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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 tenfold in size and are found from dense forests (bongo *Tragelaphus eurycerus*, saola) to semi-deserts (common eland *Tragelaphus oryx*), and from swamps

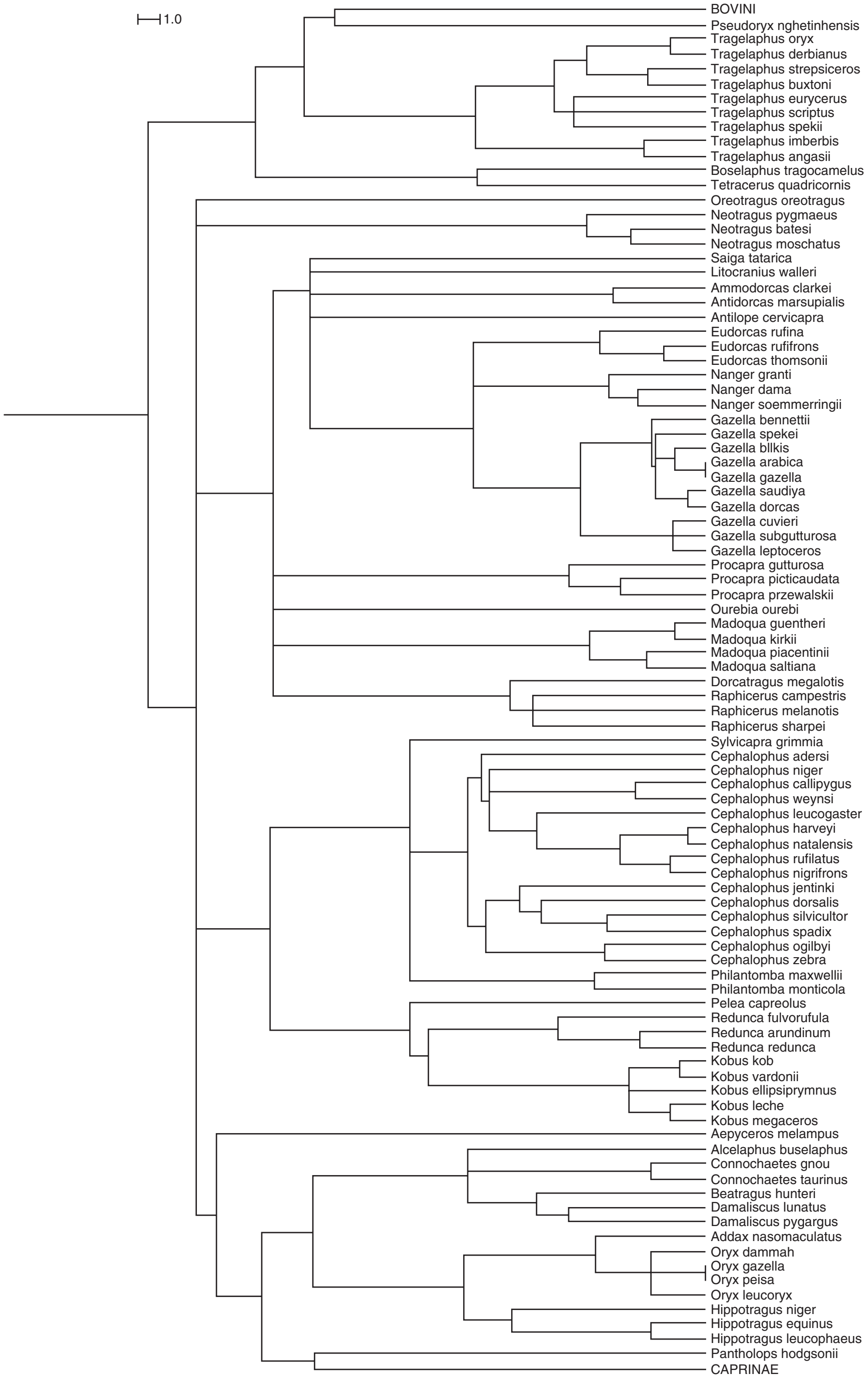

Figure 2 **The evolution within Bovidae since the divergence from deer 32 million years ago (for common names, see the Appendix). Bar indicates one million years. Based on Fernández & Vrba 2005; drawn in Dendroscope, Huson & Scornavacca 2012.**

(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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