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## **Ecology and behaviour of ungulates in African savanna ecosystem**

Ekologie a chování velkých přežvýkavců v ekosystému afrických savan

Ph.D. thesis

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## **DECLARATION**

I hereby declare that this submitted thesis, „Ecology and behaviour of ungulates in African savanna ecosystem“, is my own work, all co-authors of the manuscripts are properly listed, and only sources listed in the reference lists were used.

Pavla Jůnková Vymyslická

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## CONTENT

Declaration.....	4
Acknowledgement .....	5
Content.....	7
1. Introduction.....	8
2. Literature overview .....	9
2.1. Savanna .....	9
2.2. African savanna and ungulates .....	9
2.3. Animal behaviour and conservation .....	11
2.3.1. Small populations.....	12
2.3.2. Activity pattern .....	13
2.3.3. Feeding behaviour.....	14
2.3.4. Dominance hierarchies.....	15
2.3.5. Mother-offspring interactions .....	16
2.4. Investigated species.....	18
2.4.1. Swayne’s hartebeest .....	18
2.4.1.1. Taxonomy .....	19
2.4.1.2. Morphology.....	20
2.4.1.3. Ecology .....	20
2.4.2. Western Derby eland .....	21
2.4.2.1. Taxonomy .....	22
2.4.2.2. Morphology.....	22
2.4.2.3. Ecology .....	23
3. Aim of the thesis .....	24
4. Conducted studies .....	26
4.1. Daily activity pattern of the endangered Swayne’s Hartebeest ( <i>Alcelaphus buselaphus swaynei</i> Sclater, 1892) in the Nech Sar National Park, Ethiopia.....	26
4.2. Does supplemental feeding affect behaviour and foraging pattern of critically endangered Western Derby eland in an ex situ conservation site? .....	31
4.3. Do high ranking mothers produce high ranking babies? Study of dominance hierarchy in the Western Derby eland ( <i>Taurotragus derbianus derbianus</i> ) .....	47
4.4. Suckling behaviour of eland antelopes ( <i>Taurotragus</i> spp.) under semi-captive and farm conditions.....	68
5. Conclusions and recommendations.....	77
6. References .....	79

## 1. INTRODUCTION

Savannas cover approximately half of the African land surface and one fifth of the land surface of the world. They are one of the most important, but least understood terrestrial ecosystems (Scholer et Walker 2004).

Savannas lie between the equatorial rain forests and the semi-deserts of the southern continents. Their environment is characterized by a mixture of herbaceous and woody vegetation, varying in quantity and growth stage according to the seasonal cycle of rainfall (Illius 1997).

The African savanna biome supports a higher diversity of ungulate species than is found in any other biome or continent. This exceptional faunal diversity and herbivore biomass density is directly linked to the high spatial heterogeneity of African savanna ecosystems. But livestock now dominates the ungulate biomass of Africa, with indigenous ungulates presently contributing less than 10% of the standing crop (Cumming 1982, du Toit et Cumming 1999).

Conservation biology, a stage in the application of science to conservation problems, addresses the biology of species, communities, and ecosystems that are perturbed, either directly or indirectly, by human activities or other agents. Its goal is to provide principles and tools for preserving biological diversity (Soulé 1985).

Researchers studying animal behaviour play an important role in conservation biology (McNaughton et Georgidis 1986, Sutherland 1998). The obvious implication of animal behaviour research is that it may be possible to find ways of reducing extinction risk and to identify the risk of allowing population to become small. Conservationists need far more information on the habitat requirements of species of conservation concern; much of this is behavioural in term of diet choice, home range, social system and breeding behaviour. (Sutherland 1998).

Although the title of the thesis is so comprehensive, it is focused on selected behaviour (daily activity pattern, feeding behaviour, dominance hierarchies, mother-offspring interactions) of endangered species of antelopes (Swayne's hartebeest, *Alcelaphus buselaphus swaynei* and Western Derby eland, *Taurotragus derbianus derbianus*) originally inhabiting in large numbers extensive areas of African savanna ecosystem, but nowadays being forced by human activity to live in small populations in fragmented areas of protected landscapes.



## **2. LITERATURE OVERVIEW**

### **2.1. SAVANNA**

Savanna vegetation consists of a continuous layer of grass interspersed with scattered trees or shrubs, and covers approximately 10 million square kilometres of tropical Africa (Cahoon et al. 1992).

The savanna ecosystems play major role in the configuration of the natural landscapes. In some countries these grass-dominated ecosystems are the principal biotic resource. Tropical savanna can be characterised as a type of ecosystem of the warm (lowland) tropics dominated by herbaceous cover consisting mostly of bunch grasses and sedges that are more than 30 cm in height at the time of maximum activity. The herbaceous cover shows a clear seasonality in its development, with a period of low activity related to water stress. The savanna may include woody species (shrubs, trees, palm trees), but they never form a continuous cover that parallels the grassy one (Sarmiento 1984).

The climate associated with savanna lands is always seasonal with wet, warm to hot period alternating with more or less dry, warm to cool season. These lands represent the grazing lands of the tropics and subtropics. The core savanna lands of the world are dominated by Andropogonoid grasses and occupy most sites in the seasonally wet tropics receiving 750-1500 mm annual rainfall. Wet savannas dominated by Panicoid and Andropogonoid grasses occur in areas receiving more than 1500 mm where sites have impeded drainage and water logging and flooding occur annually for extended periods. With decreasing rainfall, dry savannas characterized by Aristidoid and Eragrostoid grasses appear initially on sandy and skeletal soils and at about 500 mm annual rainfall are found on most sites (Johnson et Tothill 1981).

### **2.2. AFRICAN SAVANNA AND UNGULATES**

The African savanna biome carries the earth's greatest diversity of ungulates and has sustained multispecies animal production systems for millennia. By contrast, modern attempts to impose single species systems, or monocultures of animal production, have been unsuccessful as development initiatives within the biome (e.g. Dyson-Hudson 1985). The African savanna biome includes those tropical ecosystems that are characterized by a continuous grass layer occurring together with trees under a climatic regime of distinct wet

and dry seasons (Walker et Noy Meir 1982, Justice et Frost 1994). These diverse ecosystems, which together cover about half of sub-Saharan Africa, are broadly grouped into two categories called either moist-dystrophic and arid-eutrophic savannas (Huntley 1982) or broad-leafed and fine-leafed savannas (Justice et Frost 1994) respectively. The moist-dystrophic/broad-leafed savannas occur on the African plateaux where the soils, derived mainly from igneous rocks of the basement complex, are relatively infertile and leached under annual rainfall regimes above 600 mm. The arid-eutrophic/fine-leafed savannas occur in lower-lying areas on heavier-textured nutrient rich soils, under an annual rainfall regime of 400–800 mm. The broad-leafed savannas in southern/central Africa are typified by *Brachystegia/Julbernardia* woodland interspersed with grassland along drainage lines, i.e. miombo woodland. The fine-leafed savannas are typified by the drier *Acacia* studded plains that merge into the steppes of the Sahel in the north and Karoo and Kalahari in the south. The African savanna environment is where *Homo sapiens* evolved as a generalist predator/scavenger and gatherer of fruits, seeds and tubers. Human populations in Africa sustained themselves exclusively in this way until the introduction of livestock and cropping from the Arabian Peninsula some 7000–8000 years ago. Livestock then spread across the Sahelian zone into West Africa about 6000 years ago, and into southern Africa about 2000 years ago (Cumming 1982, Denbow et Wilmsen 1986). A particularly high diversity of indigenous large mammals (>5 kg) is a natural feature of African savannas (Bourliere et Hadley 1970, Huntley 1982). While large mammal biomass varies considerably across the biome, largely in response to variations in mean annual rainfall and soil nutrient status (Coe et al. 1976, Bell 1982, East 1984), the biomass densities of herbivores in certain protected savanna ecosystems account for some of the highest levels of herbivory ever quantified in terrestrial ecosystems (McNaughton et Georgiadis 1986).

Extant ungulates endemic to the savanna biome of Africa number some 46 species, of which about 80% belong to one family along, the Bovids. This diversity of ungulates exceeds that of any other continent, even if for Eurasia and the Americas we include those species that went extinct in the late Pleistocene (Delany et Happold 1979). On the other hand, livestock dominates the ungulate biomass of Africa, with indigenous ungulates presently contributing less than 10% of the standing crop (Cumming 1982).

### **2.3. ANIMAL BEHAVIOUR AND CONSERVATION**

Many of the species with whom we share our planet are going to extinct because we overexploit them or destroy their habitat (Ehrlich et Wilson 1991, Coughley 1994, Hanks 2001). Species extinction and habitat destruction due to agricultural development, human settlement to accommodate rapidly growing populations, and global warming have an immediate impact upon many economic and social activities because various uses of wildlife provide socio-cultural, scientific, economic and nutritional values for millions of people (Hanks 2001, Chardonnet et al. 2002). It is therefore not surprising that interest in the conservation of biodiversity is increasing among general public as well as among behavioural ecologist who study wild animal and their environment (Festa-Bianchet et Apollonio 2003). The majority of current extinctions appear to be caused either directly or indirectly by human activities and a lot of species are threatened accordingly.

Two related disciplines, wildlife conservation and wildlife management, use ethological knowledge to limit the impact of humans on ecosystems. Wildlife management seeks sustainable strategies to exploit wild species while ensuring their persistence and availability for future use. Wildlife conservation is concerned with preservation of species and their habitat in the face of threats from human development (Festa-Bianchet et Apollonio 2003).

Some authors (Sutherland 1998, Sutherland et Gossling 2000, Caro 2007, Angeloni 2008) have pointed out that research of animal behaviour has little impact on conservation biology, because of missing overlap of these two disciplines. Animal behaviour and behavioural ecology can certainly provide important guidance to conservation biology by contributing valuable theories, approaches, data and scientific expertise to biodiversity conservation efforts. Behavioural research involving captive breeding, cultural evolution and learning, communication, foraging, predation, movement and dispersal, spread of invasive species, endocrinology and stress, social behaviour and mating systems all may contribute to a greater understanding of conservation problems (Angeloni et al. 2008)

Numerous studies demonstrated that behaviour is relevant to conservation biology and that conservation behaviour can be applied successfully to assist conservation efforts (e.g. Grant et al. 2002, Shier 2006; Moore et al. 2008). Furthermore, many conservation projects are failing because of ignorance about the behaviour of endangered species (Knight 2001).

The key element of behavioural ecology is the adaptive nature of behaviour (Berger-Tal et al. 2011) Behavioural strategies in a population are the outcome of evolutionary processes that depend on the fitness of particular strategies under prevailing environmental conditions

(Norris 2004). Behaviours should evolve to maximize the fitness of the individuals showing those behaviours in term of evolutionarily stable strategies (Sutherland et Norris 2002, Owens 2006, Berger-Tal et al. 2011).

Caro (2007) shows that theoretical understanding of animal behaviour has small influence on biodiversity conservation and emphasizes the importance of practical research based on seven steps that make behavioural research contribute better to conservation. As first and most important Caro (2007) as well as Angeloni (2008) suggests determination of specific conservation concern through discussion with managers or responsible authorities. Second, as a study area should be chosen threatened habitat, this shows the responses of animals to threat. Further he recommends working on several taxa simultaneously; working on threatened or endangered populations of species of conservation concern and avoid using surrogate species. Results from common species might not generalize, rare species are difficult to locate and inevitably result in small sample size (Caro 2007). The by-product of such studies is gaining the valuable knowledge of the habitat requirements, ecology and status of a species and ecology and changes in the land use of an area (Sutherland 1998, Berger-Tal et al. 2011). In the last two steps Caro (2007) urges in the same way as Sutherland (1998) or Angeloni (2008) to rapid publication and popularization of the research and results to managers and through popular writing to the public as well.

Management plays a crucial role in the success of conservation efforts for endangered animals (Carlstead et Shepherdson 1994, Balou et Foose 1996, Munson et al. 2005, Cabezas et Moreno 2007, Peignot et al. 2008). *Ex-situ* conservation breeding represents, for some species, the only way to ensure their survival and maintenance of their genetic resources (Ebenhard 1995, Hanks 2001, Koláčková et al. 2011a). Captive breeding often fails as a result of behavioural problems and behavioural issues are accepted as important in the management of captive species (Sutherland 1998). In particular, rare and endangered species are vulnerable to management decisions because we lack adequate knowledge of their ecology and behaviour (Seddon et al. 2007, Grey-Ross et al. 2009).

### **2.3.1. Small populations**

Populations of conservation concern are small, or declining (Sutherland 1998, Caro 2007). Human activities through habitat destruction and fragmentation, the introduction of exotic species and over-exploitation reduce population sizes, fractionate populations or can drive some species to extinction (Hudson et al. 2000, Frankham et al. 2003).

Habitat fragmentation reduces population sizes and increases isolation of population fragments (Frankham et al. 2003). Small populations are more susceptible to extinction than larger populations due to a variety of factors that directly influence the rates of survival and birth. If only a few individuals make up the population, the fate of each individual can be crucial to the survival of the population. The consequence of low numbers of individuals in the population could be breakdown of social structure, reduced genetic diversity, limited choice of mates or inbreeding (Frankham 1995, Sutherland 1998, Hudson et al. 2000, Smith et Smith 2006). Inbreeding is of profound importance in conservation biology as it leads to reductions in heterozygosity, to reduced reproduction and survival (inbreeding depression) and to increased risk of extinction (Hudson et al. 2000, Frankham et al. 2003).

The obvious implication of small population research is that it may be possible to find ways of reducing extinction risk and to identify the risks of allowing a population to become small (Sutherland 1998).

### **2.3.2. Activity pattern**

Observing animal behaviour in their natural habitat can provide information, which can directly affect management of the population by enabling understanding the animal's needs. Animals use their freedom to move and interact, both with their environment and with one another, as one of the most important ways in which they adapt themselves to the conditions in which they live. Even though much is already known about such adaptations a great deal remains to be discovered about the diversity and functions of behaviour (Martin et Bateson 1993).

The pattern of an animal's behaviour may be driven by a variety of external factors such as forage availability (Hejcmanová et al. 2009), environmental conditions (Brashares et Arcese, 2002) or living in a group (Shrader et al. 2007). Animal behaviour may thus reflect the various trade-offs that animals face and which may affect an individual's fitness.

Mammalian herbivores spend the majority of their time feeding (horses spend more than 70 % of their time grazing and cattle, 50–60 %). Ruminant ungulates must additionally allocate time to ruminating and resting. In savanna ecosystems, ruminants must not only obtain sufficient quality and quantity of food, but may also need to adjust their activity budget as seasonal changes constrain when the activity can take place in a 24-hour period (Ryan et Jordaan 2005).

In temperate regions, herbivores can increase time allocated to foraging during summer to improve forage intake (Shiple et al. 1994), which can lead to greater body condition and eventually higher overwinter survival. However, time is limited; individuals spending more time in a specific activity will inevitably do so at the expense of time spent in another activity. Animals therefore face daily compromises as to how much time should be spent in each activity, and they should adjust their activity budget according to their individual requirements (Illius et al. 2002). The extent of these compromises, therefore, should vary according to intrinsic factors such as reproductive status, age, mass and social rank, as well as extrinsic factors such as group size and forage availability and quality (Hamel 2008). Descriptive behaviour studies provide information about either animals under natural conditions (Taylor et al. 2006) or how animals cope with the disturbances caused for instance by resource partitioning with cattle (Voeten et Prins 1999) or how they respond to particular conservation actions (Tear et Ables 1999). Animal behaviour has the potential to indicate population viability (Anthony et Blumstein 2000), and its understanding may therefore play a crucial role in the management of animal populations, particularly in endangered species (Caro 2007).

### **2.3.3. Feeding behaviour**

One of the central issues for successful conservation and endangered species management is appropriate food resources for the species. Fluctuations in food supply or in particular nutrients influence breeding patterns (Sadler 1969, Persson 2005, Bishop et al. 2009). Scarce food resources may severely affect survival and/or breeding rates (Mysterud et al. 2007). In food-limited populations, supplemental feeding as a conservation measure has the potential to produce positive effects on fitness components, namely reproductive success, and on population parameters (survival, recruitment, carrying capacity) (Boutin 1990, Dorgeloh et al. 1996, Treydte et al. 2001). On the other hand, inappropriate provisioning of food may change the behaviour of animals, for instance their spatial distribution (Cooper et al. 2006), or vigilance, through habituation to a human presence (Recarte et al. 1998, Manor et Saltz 2003); this may have unexpected consequences on eventual reintroductions. The effects of supplemental feeding have been widely investigated for large herbivores in temperate zones, which were fed during winter periods (Schmitz 1990, Doenier et al. 1997, Schmidt et Hoi 2002). There is a lack of experimental studies in tropical environments.

The foraging decisions and processes of large herbivores operate in different spatial (and temporal) scales from the selection of plant parts or particular plant species at the landscape level (Senft et al. 1987, Prins et van Langevalde 2008). In response to increased availability of food resources, animals feed more selectively (Westoby 1974, Stephens et Krebs 1986) or shorten their foraging time (Owen-Smith 1994). If animals are offered a food supplement, they use it first, and then continue to forage native vegetation (Doenier et al. 1997, Cooper et al. 2006). They increase, however, their selectivity for higher quality forage species (Murden et Risenhover 1993, van der Waal 2005). Improving forage availability decreases foraging pressure on natural food resources, and induces changes in the behavioural patterns of animals. For instance, the total time devoted to foraging, or biting rate, as indicators of forage intake (Hodgson 1985), may decrease; animals may invest more time in activities to increase the individual's fitness, such as reproduction, anti-predator behaviour, resting, or social interactions (Hejcmanová et al. 2009). Very little information exists regarding how animal behavioural patterns may be changed, and what may be the ultimate consequences for conservation management (Caro 2007).

#### **2.3.4. Dominance hierarchies**

There are many studies detecting the social rank of individuals and the dominance relationship of ungulates, but they often differ more or less in methodology and working concepts. Kaufmann 1983 defined the dominance/subordination behaviour as a relationship between two individuals in which one the subordinate defers to the other the dominant in contest situations. This relationship is often determined by a mutual assessment, which may range from simple recognition to ritualized displays or serious fights. The concept of dominance has been continuously debated (e.g. Craig 1986, Cransac and Aulagnier 1996, Wirtu et al. 2004).

Social organization of ungulates is generally correlated by diet and body size (Davies et al. 2012). Small species have a higher metabolic requirement per unit weight and need to select high quality food. These tend to occur in the forest and are scattered in distribution, so the small species are forced to live a solitary existence. On the other side the large species eat poor quality food, graze less selectively than small species and occupy plains (Jarman 1974). These species stay in herds where is potential for the strongest males to monopolize several females by defence of a harem or a dominance hierarchy of mating rights (Davies et al. 2012).



Gregarious animals engage in social interactions that lead to the establishment of dominance hierarchies (Wirtu et al. 2004). These social hierarchies permit successful coexistence in social communities and have two major functions. It may reduce the level of aggression in a group that may benefit individual animals because they will avoid potentially costly interactions with conspecifics, whether dominant or subordinate (Fourier & Festa-Bianchet 1995; Côté 2000, Pelletier & Festa-Bianchet 2006), and it may determine the animals' access to resources such as space, food, resting places and mating opportunities, where higher animals in a dominance order generally have priority access to limited resources (Bouissou 1980; Alados and Escos 1992, Barroso et al. 2000). An understanding of the pattern of dominance behaviour in ungulates and its effect could be helpful to management systems, predominantly when manipulation is needed or for oral treatment of animals (Wirtu et al. 2004).

### **2.3.5. Mother-offspring interactions**

Mother-offspring interactions soon after parturition play a key role in the survival of mammals. Maternal behaviour in ungulates, manifested particularly during suckling, is generally intensive after birth and declines with the age of the calves (Rubin and Michelson 1994, Sarno and Franklin 1999, Cassinello 2001). In ungulate species, multiparous and older mothers generally display a higher level of maternal care than primiparous or younger ones, and this is because of their greater level of experience (Ozoga and Verme 1986, Green 1990, Cameron et al. 2000) or is the effect of residual reproductive value (Clutton-Brock 1991). On the other hand, because ungulates are highly susceptible to predation during the initial weeks and months of life, their mother-offspring interactions are variable within and across species and reflect the strategy adopted in the tradeoff between nursing and vigilance (Rachlow and Bowyer 1998, Toïgo 1999, Hamel and Côté 2008). The protection of offspring and the resulting anti-predator behaviour is one of the most conspicuous features of maternal care. Besides the general "follower" and "hider" strategies (Lent 1974, Leuthold 1977, Ralls et al. 1986), mothers naturally adopt an anti-predator pattern that is specific for the conditions and environment they experience (Braza et al. 2000, White and Berger 2001, Ciuti et al. 2006). In ungulate hider species, mothers may move directly towards neonates at very close distance or they may use other maternal behavioural tactics to stay at a distance of several meters and wait for the calf to approach (Hnida 1985, Thompson 1996, Wronski et al. 2006). Maternal females do trade off between the distance from a hiding place and the detectability



of the offspring and thereby balance the risk of neonate predation (Byers and Byers 1983, Bongi et al. 2008, Panzacchi et al. 2009). The success of the adopted anti-predator strategy is thus inevitably related to the type of habitat (Jarnemo 2004, Bongi et al. 2008). Mechanisms acting in maternal care appear conservative among and within species but, despite this, wild and captive populations may exhibit different attitudes in the care of their offspring. In the wild, vigilance against predators brings constraints to females with offspring in terms of the time devoted to foraging (Bowyer et al. 1999) and satisfying the higher nutritional requirements arising from energetically costly lactation (Oftedal 1985).

Consequently, the time intended for maternal care is highly limited and females facing these constraints may allocate energy to their own maintenance and/or survival and postpone reproductive success (Festa-Bianchet and Jorgenson 1998, Gaillard et al. 2000, Therrien et al. 2007). Captivity, which offers an environment without predators, may have a crucial impact on maternal expenditure and nursing behaviour. Indeed, the permanent availability of food resources may increase reproductive success (Andersen et al. 2000). The small area and the lack of predators enable more frequent visual contact between the mother and her offspring and, consequently, a different approach to a hidden calf, the reuse of hiding places (Murdock et al. 1983, Thompson 1996), or a higher suckling rate (Manski 1991, Rubin and Michelson 1994). However, both in captivity and in the wild the mothers contact the offspring before and during suckling for mutual identification to prevent the loss of invested energy, for instance by allosuckling (Roulin 2002, Zapata et al. 2009).

## **2.4. INVESTIGATED SPECIES**

This thesis is focused on behaviour of Swayne's hartebeest (*Alcelaphus buselaphus swaynei*) and Western Derby eland (*Taurotragus derbianus derbianus*), large polygynous subspecies of antelopes that belong to the Family *Bovidae*. Although both subspecies used to inhabit African savanna plains in large numbers, nowadays they are considered to be endangered, resp. critically endangered by IUCN (2008).

Study on Swayne's hartebeest was conducted in 2007 and was expected to continue in form of long-term project. Unfortunately the cooperation was quitted due to political reasons, thus it was not possible to continue with the research.

Other option became with the technically feasible and exclusive access to conservation programme of Western Derby eland in Senegal, where research of selected behaviours still continues.

### **2.4.1. Swayne's hartebeest**

Swayne's hartebeest (*Alcelaphus buselaphus swaynei*, P.L. Sclater, 1892) nowadays occurs in small numbers in only a few areas of southern Ethiopia. Until the early 1890's, *A. b. swaynei* was wide spread throughout Ethiopia and Somalia (Demeke 1997). Herds of thousand individuals were observed by brigadier-general Swayne, who discovered the hartebeest in 1891-92 south of the Golis range in Somalia, about 200 km from the coast. Within fifteen years these thousands seen by brigadier Swayne was dwindled to an extent that only about 800 were estimated to have remained (Girma 2002). The rapid decline was due to the rinderpest that swept Africa at the end of the 19<sup>th</sup> century. However up to 1940's a large number of Swayne's hartebeest was present in the Awash area of Ethiopia (Gebre 2000). Once abundant, has been greatly reduced in numbers through direct killing and habitat modification by people (Nowak 1999, Nishizaki, 2004; Kumssa et Bekele, 2008). Kingdon (1982) noted that it probably has suffered the greatest contraction in range of all African ruminant, primarily because it must compete for forage with domestic cattle and also because it is easy to hunt. By the early 60's, the only sizable population of Swayne's hartebeest was located in the Senkele and Siraro Plains, west of lake Awassa, Ethiopia (Bolton 1971, Gebre 2000).

At present they are restricted to the Ethiopian Rift Valley only, in small fragmented conservation areas, namely Senkelle Swayne's Hartebeest Sanctuary, Mazie National Park

and Nech Sar National Park (Antonínová et al. 2008b). In other areas such as Awash National Park and Yavello Sanctuary they have been extinct (East 1998).

By IUCN (2008) is Swayne's hartebeest listed as Endangered as the total population is estimated at 600 individuals (with the majority of the population confined to the Senkelle Wildlife Sanctuary and Mazie N.P. in Ethiopia); no subpopulation numbers more than 250 mature individuals. The small size of the population (c. 300 mature individuals) makes it close to qualifying as Critically Endangered.



Photo by author

#### **2.4.1.1. Taxonomy**

Swayne's hartebeest used to be recently considered as one of 6 subspecies of *Alcelaphus buselaphus* (Wilson et Reeder 2005, IUCN 2008). Very recent publications however indicate the Swayne's hartebeest to be one of 7 species of genus *Alcelaphus* (Groves et Grubb 2011, Wilson et Mittermeier 2011).

For the purpose of this thesis we remain by the taxonomy, where Swayne's hartebeest is the subspecies *Alcelaphus buselaphus swaynei*, because the study was conducted in the year 2007, when this taxonomy was still acknowledged.

#### **2.4.1.2. Morphology**

Swayne's hartebeests are long faced animals with high withers and sloping hindquarters (Girma 2002). They are medium to large sized antelopes in which breeding males weight between 150 and 180 kg while females weigh an average 120 kg (Stuart et Stuart 2006). Ringed and recurved horns are present in both sexes although they are more massive in males. Horns shape are fully expanded outwards from the pedicle the upwards with tips usually hooked backwards. Body colour is variable ranging from fawn to dark brown. Conspicuous black markings are distributed over shoulders, legs, face and flanks. Tail is long and following horselike. In general, they are with high forequarters and sloping backs. They show less sexual dimorphism (Estes 1992).

#### **2.4.1.3. Ecology**

Swayne's hartebeests inhabit dry savannas and grasslands and are largely grazers with occasional browsing (Nowak 1999). Herds are composed of females and their young. Females form temporary hierarchies in which threatening gestures with horns are noticeable (Kingdon 2003). Most commonly herds may comprise 20 to 50 animals (Lewis et Wilson 1979), but up to several hundred and even thousands may gather. These larger groupings are normally associated with onset of the rainy season and in arid areas they will travel great distances in search of fresh grass (Stuart et Stuart 2006). Males are territorial particularly in the mating season (Kingdon 2003). Bachelor herds occupy the areas around territories (Stuart et Stuart 2006). Swayne's hartebeests go to water regularly, but territorial males go without water for quite long periods (Kingdon 2003). Most activity takes place during the day but nocturnal feeding also takes place (Stuart et Stuart 2006).



#### 2.4.2. WESTERN DERBY ELAND

The Derby eland (*Taurotragus derbianus*) was first mentioned in the 1840s. Dr. Gray described this animal on the basis of two frontlets with horns together with a single horn of a younger bull from Senegambia shot by collector T. Whitfield in 1842, who was working for the thirteenth Earl of Derby, and by two later skins from a cow and a bull. In 1862, after visiting Senegambia, Reade (1863) informs about the existence of an enormous antelope, double the size of the Senegal bullock, with the horns lying backwards, a black mane, and white stripes on its sides and describes the occurrence of these animals in the shrubby and impenetrable landscape (Koláčková et al. 2010).

The only confirmed wild population of *T. d. derbianus* occurs in Niokolo Koba National Park in eastern Senegal, Africa (Nežerková et al. 2004), and it is estimated at less than 200 individuals (Renaud et al. 2006). Other 75 animals are bred in captivity under the Czech-Senegalese management of civic society Derbianus Czech Society for African Wildlife and Society for the protection of the Environment and Wildlife in Senegal (Koláčková et al. 2011b). This low population count, which is a result of overharvesting for meat and habitat destruction caused by the expansion of human and livestock populations, prompted the classification of the Western subspecies as Critically Endangered (IUCN 2010).



Photo by Tom Junek

#### **2.4.2.1. Taxonomy**

Although Derby eland is assigned by some authors to the genus *Tragelaphus* (Baillie and Groombridge, 1996, East 1998), according to Wilson and Reeder (2005) it belongs to the genus *Taurotragus* together with *Taurotragus oryx*, both regarded as full distinct species,. Two subspecies are commonly recognized: *Taurotragus derbianus gigas* (Eastern Derby eland) and *Taurotragus derbianus derbianus* (Western Derby eland) (Kingdon 1982, Koláčková et al. 2011a), although Groves et Grubb (2011) and Wilson et Mittermeier (2011) consider *Taurotragus derbianus* as monotypic species.

#### **2.4.2.2. Morphology**

The Derby eland is gregarious, polygynous, massive antelope with body length of 290 cm in the bulls, 220 cm in the cows, and its height at the withers is between 150 and 176 cm in the bulls, 150 cm in the cows. Males can reach weights of 450-907 kg, females 440 kg. Horn length ranges from 80 to 123 cm (Kingdon 1982, 1997, Stuart et Stuart 2006).

Its overall colour is ruddy fawn or chestnut, sometimes with a tint of bluish grey in adult bulls. It has roughly nine to seventeen white stripes on its flanks. The adult bulls grow a knot of brown hairs on the forehead. It has a black mane on its neck from which a black stripe continues along the entire length of the back. From the chin to the chest there hangs an enormous black and white dewlap. Two white cheek spots and a white stripe in front of the eye are present on each side. The ears are broad, rounded and prominently marked, as are the hocks (white and black). The dark tufted bovine tail measure 55 to 78 cm. Both sexes have large and massive horns, especially the bulls. They curve in a spiral and can reach lengths of up to 80 to 123 cm; those of the males are longer and more widely splayed. They are a greatly prized hunting trophy (Dorst et Dandelot 1970, Kingdon 1982, 1997, Koláčková et al. 2010) although they are alert, keen of sense, and thus difficult to approach with reported maximum speed to be at least 70km/h (Nowak 1999).

The Giant eland has two sub-species. The difference between the subspecies has, until now, only been determined on the basis of the morphological description. The western subspecies *Taurotragus derbianus derbianus* (Gray 1847) is characterised by smaller size, bright rufous ground colour and about fifteen body stripes. The eastern subspecies *Taurotragus derbianus gigas* (Heuglin 1863) is characterised by larger body size, sandy ground colour and around

twelve body stripes (Dorst et Dandelot 1970, Kingdon 1982, 1997, Ruggiero 1990, Koláčková et al. 2010).

#### **2.4.2.3. Ecology**

The preferred habitat of Derby eland is plains or moderately rolling country with brush and scattered trees (Nowak 1999) without venturing into the desert and avoiding dense forest (Estes 1992). The Derby eland is predominantly a browser. The three major components of its diet are leaves, shoots, and fruits of woody plants. Twenty-eight woody species were recorded as part of the diet of the antelope in the Niokolo Koba National Park, for instance *Boscia angustifolia*, *Grewia bicolor*, *Hymenocardia acida* or *Ziziphus mauritiana*, and fruits of *Acacia* spp. and *Strychnos spinosa*. In addition, clear browse marks were found on the species *Feretia apodanthera*, *Gardenia* sp., *Grewia flavescens*, *Hexalobus monopetalus*, *Mitragyna inermis*, and *Pterocarpus erinaceus* (Hejcmanová et al. 2010b).

### **3. AIM OF THE THESIS**

The aim of the thesis was to investigate selected behaviour (daily activity pattern; mother-offspring interactions, dominance hierarchies, and feeding behaviour) directly related to population management of critically endangered large antelopes in order to contribute to conservation efforts of managers or authorities responsible for protected areas. Two animal species were investigated: Western Derby eland (*Taurotragus derbianus derbianus*) bred in *ex-situ* conservation program in Senegal, and Swayne's hartebeest (*Alcelaphus buselaphus swaynei*) inhabiting plains of Nech Sar National Park in Ethiopia, habitat strongly influenced by human activities.

All submitted studies were carried out on the initiative from conservation managers or authorities responsible for management of the populations.

#### **STUDY I: Daily activity pattern of the endangered Swayne's Hartebeest (*Alcelaphus buselaphus swaynei* Sclater, 1892) in the Nech Sar National Park, Ethiopia**

In the first study concerning daily activity pattern of Swayne's hartebeest we aimed to determine whether the diurnal activity pattern of Swayne's hartebeests differed (i) according to the time of day; (ii) as the dry season progresses and / or (iii) among different social structures.

#### **STUDY II: Does supplemental feeding affect behaviour and foraging pattern of critically endangered Western Derby eland in an ex situ conservation site?**

Feeding behaviour was subject of investigation in the second study. Using the experiment, we tested the hypotheses whether supplementary feeding affects general behavioural pattern of Western Derby eland and whether supplementary feeding affects browsing pattern and selectivity for browsed plant species. We also hypothesized that change in behaviour due to supplementary food will not display if animals are not accustomed to it for a long period.



**STUDY III: Do high ranking mothers produce high ranking babies? Study of dominance hierarchy in the Western Derby eland (*Taurotragus derbianus derbianus*)**

In our research of social hierarchy in Western Derby eland we investigated whether (i) a linear or complex hierarchical order exist in the herd; (ii) adult individuals have higher rank positions than subadult animals and juveniles. Because of the visible differences between sexes we expected that (iii) males have higher rank positions than females in respective age classes. Finally we presumed that (iv) the rank of juveniles corresponds with the rank of their mothers.

**STUDY IV: Suckling behaviour of eland antelopes (*Taurotragus* spp.) under semi-captive and farm conditions**

Fourth study focused on differences in the basic suckling pattern of the two species of elands (*Taurotragus derbianus derbianus* and *Taurotragus oryx*) via the suckling bout duration. We predicted that the antelope calves would have larger suckling bouts after birth and that these would become shorter with age, and that multiparous mothers would have longer suckling bouts than primiparous ones. We predicted that the mother–offspring contact interaction before and during suckling would differ between species, as a response to the different breeding systems and the environment, namely vegetation cover.

## 4. CONDUCTED STUDIES

### 4.1. DAILY ACTIVITY PATTERN OF THE ENDANGERED SWAYNE'S HARTEBEEST (ALCELAPHUS BUSELAPHUS SWAYNEI SCLATER, 1892) IN THE NECH SAR NATIONAL PARK, ETHIOPIA

Vymyslická P., Hejzmanová P., Antonínová M., Stejskalová M., Svitálek J. 2011. Daily activity pattern of the endangered Swayne's Hartebeest (*Alcelaphus buselaphus swaynei* Sclater, 1892) in the Nechisar National Park, Ethiopia. *African Journal of Ecology*, 49, 246-249.

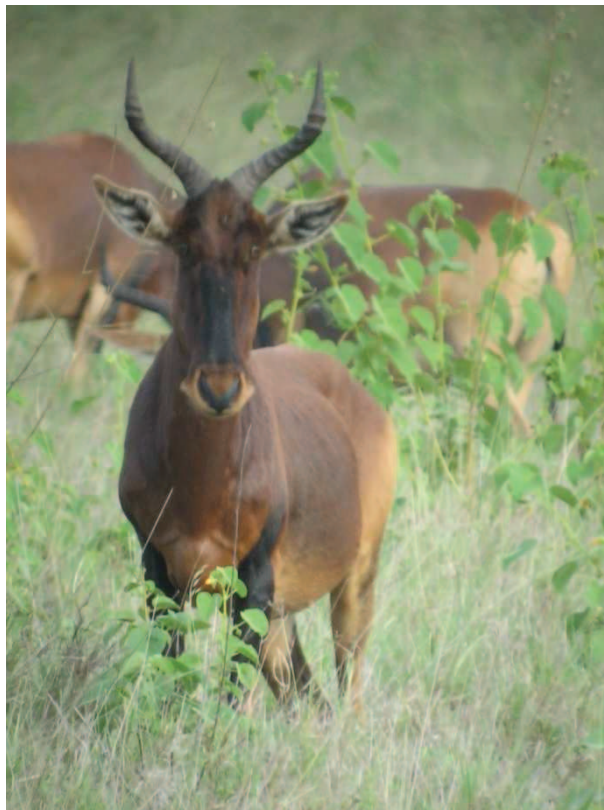


Photo by author

## Notes and records

Daily activity pattern of the endangered Swayne's Hartebeest (*Alcelaphus buselaphus swaynei* Sclater, 1892) in the Nechisar National Park, Ethiopia

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### Introduction

The pattern of an animal's behaviour may be driven by a variety of external factors such as forage availability (Hejmanová *et al.*, 2009), environmental conditions (Brashares & Arcese, 2002) or living in a group (Shrader *et al.*, 2007). Animal behaviour may thus reflect the various trade-offs that animals face and which may affect an individual's fitness. Descriptive behaviour studies provide information about either animals under natural conditions (Taylor, Skinner & Kreeck, 2006) or how animals cope with the disturbances caused for instance by resource partitioning with cattle (Voeten & Prins, 1999) or how they respond to particular conservation actions (Tear & Ables, 1999). Animal behaviour has the potential to indicate population viability (Anthony & Blumstein, 2000), and its understanding may therefore play a significant role in the management of animal populations, particularly in endangered species (Caro, 2007).

The Swayne's hartebeest (*Alcelaphus buselaphus swaynei* Sclater, 1892) is an endangered endemic antelope with c. 600 individuals remaining in three localities in Ethiopia: Senkele Swayne's Hartebeest Sanctuary, Mazie National

Park and Nechisar National Park (NSNP) (IUCN, 2008). All populations are threatened by the loss of habitat resulting from expanding agriculture and settlement (Nishizaki, 2004; Kumssa & Bekele, 2008), and only premeditated conservation action may ensure the survival of Swayne's hartebeest (Flagstad *et al.*, 2000).

The population status of Swayne's hartebeest has recently been investigated (Flagstad *et al.*, 2000; Antonínová *et al.*, 2008; Kumssa & Bekele, 2008), but knowledge of its behaviour remains limited (Lewis & Wilson, 1979; Abaturov *et al.*, 1995). We therefore provide the first investigation of the diurnal activity pattern of Swayne's hartebeests (SH) in the NSNP in Ethiopia as baseline knowledge for future monitoring and conservation of the population. In our study, we investigated whether the diurnal activity pattern of Swayne's hartebeests differed (i) according to the time of day; (ii) as the dry season progresses and/or (iii) among different social structures.

### Materials and methods

The study was conducted from July to September 2007 in the NSNP (5°56'19.06"N, 37°39'58.61"E) in Ethiopia, 510 km south of Addis Ababa. The NSNP covers 514 km<sup>2</sup>, of which 85% is terrestrial and 15% consists of lakes and rivers; the altitude varies between 1108 and 1650 m a.s.l. The average annual rainfall is 880 mm, falling from March to May (long rainy season) and between September and November (short rainy season). The temperature ranges from 12.2 to 34.3°C (Duckworth *et al.*, 1992).

Within the NSNP, Swayne's hartebeests occur exclusively in the open short grass plain (20 000 ha) dominated by *Cenchrus ciliaris*, *Chloris roxburghiana*, *Chrysopogon aucheri* and *Ischaemum afrum* (Svitálek, 2008). Predators in the NSNP include the lion (*Panthera leo*), leopard (*Panthera pardus*) and spotted Hyaena (*Crocuta crocuta*) (Duckworth *et al.*, 1992). During the study, the SH population comprised 35 animals: 23 individuals in a reproductive herd (17 females, six males), three individuals in a temporary male bachelor group and nine solitary males (Antonínová *et al.*, 2008).

Over a total of 42 observation days, we collected behavioural data on the reproductive herd (16 days),

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bachelor group (8 days) and solitary males (18 days). Animals were observed from 07.00 until 19.00 hours using a Swarovski telescope or binoculars from elevated fixed points at 100–300 m. Data were collected using herd scan sampling for reproductive and bachelor herds and focal animal scan sampling for solitary males (Martin & Bateson, 1993), all at the intervals of 10 min. We recorded activities such as foraging (FOR: biting or chewing food), ruminating (RUM: chewing the cud), standing (STA: scanning surroundings in quiet position, head raised), lying (LIE: while resting) and moving (MOV: walking, galloping or jumping). Recordings when animals went out of the sight were omitted from the analyses. The day was divided into four observation sequences (morning: 07.00–10.00 hours, midday: 10.00–13.00 hours, afternoon: 13.00–16.00 hours and late afternoon: 16.00–19.00 hours). The season was divided into two periods: July (early dry season) and August (late dry season).

STATISTICA 8.0 software (STATSOFT, 1995) was used for statistical analyses. In all analyses, each activity was tested separately. We tested the effect of the time of day and social structure on hartebeest behaviour using Kruskal–Wallis nonparametric analysis of variance. Multiple comparisons of mean ranks for all groups were used for post hoc comparisons of significant differences at a 95% level of significance. The effect of the dry season period was analysed using a Mann–Whitney *U* test. The statistical units were observation sequences within the day. Given the limited number of animals in the population, repeat observations of the same animals occurred within the day and no replication of social structure was possible. The observations cannot be assumed to be independent and the study aims only to provide a reference for the current small population.

## Results and discussion

Swayne's hartebeest spent on average 24.6% of their time foraging, 14.3% ruminating, 26.4% standing, 15.6% lying and 7.1% moving. We revealed significant differences in the time allocated to all activities among the various parts of the day (FOR:  $H_{147,3} = 37.96$ ,  $P < 0.001$ ; RUM:  $H_{148,3} = 16.83$ ,  $P < 0.001$ ; STA:  $H_{148,3} = 22.56$ ,  $P < 0.001$ ; LIE:  $H_{148,3} = 28.01$ ,  $P < 0.001$ , MOV:  $H_{148,3} = 11.95$ ,  $P = 0.008$ ) (Fig. 1). The SH in the NSNP showed two foraging peaks and the period between them was devoted to other activities, which was similar to that in the Senkele area as shown by Lewis & Wilson (1979). The diurnal behavioural pattern followed diurnal variations in

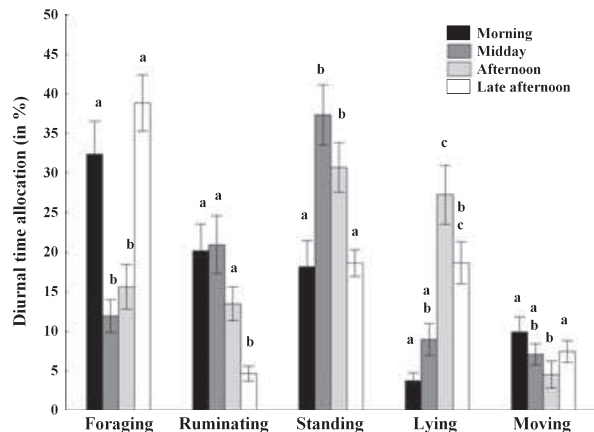


Fig 1 Daily activity patterns of Swayne's hartebeest in the Nechisar National Park in different diurnal periods. Columns with the same letter within each activity were not significantly different

ambient temperature similar to eland, buffalo (Lewis, 1977), wildebeest (Twine, 2002), impala (Du Toit & Yerman, 2005) and mountain reedbeest (Taylor, Skinner & Kreck, 2006). In the NSNP, Swayne's hartebeest spent significantly more time resting (LIE) between 10.00 and 16.00 hours, probably because of the need to minimize thermal stress during the hottest part of the day (Owen-Smith, 1998). The animals were more active in the early morning and late evening when seeking food, and thereby foraging was the most represented activity. Swayne's hartebeests ruminated after grazing periods mostly during the hotter part of the day. The pattern of ruminating is related to the periods of rest. The timing of daily activities is one behavioural mechanism that animals use to cope with high temperature and maintain their water balance (Cain *et al.*, 2006).

We revealed differences in the time spent foraging ( $U = 1268.5$ ,  $P < 0.001$ ,  $n_{July} = 63$ ,  $n_{Aug} = 84$ ) and standing ( $U = 1949$ ,  $P = 0.004$ ,  $n_{July} = 64$ ,  $n_{Aug} = 84$ ) between July and August, whereas no differences were found for the other activities ( $P > 0.05$ ) (Fig. 2). The increased time spent grazing in the late dry season suggests a decreasing trend in forage quality or availability during the dry period (Beekman & Prins, 1989). The animals cope with restricted resources by searching for more food and increasing their grazing time (Underwood, 1983).

Among the social structures, there were differences in the time spent foraging ( $H_{147,2} = 10.33$ ,  $P = 0.005$ ), ruminating ( $H_{148,2} = 7.17$ ,  $P = 0.028$ ), standing ( $H_{148,2} = 11.26$ ,  $P = 0.003$ ) and moving ( $H_{148,2} = 7.66$ ,  $P = 0.022$ ), but no difference in the time spent lying

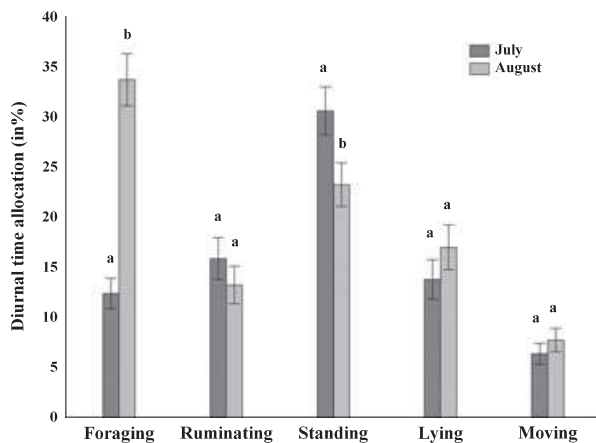


Fig 2 Daily activity patterns of Swayne's hartebeest in the Nechisar National Park in different months of the dry season. Columns with the same letter within each activity were not significantly different

( $H_{145,2} = 0.99, P = 0.61$ ) (Fig. 3). The higher time allocation of solitary males to foraging compared to animals in both herds is not consistent with the predictions of the group-size effect on anti-predator behaviour (Roberts, 1996; Beauchamp, 2003) or foraging (Underwood, 1982; Fortin *et al.*, 2004; Dalerum *et al.*, 2008). This could be explained by the benefits that accrue from the absence of interactions from conspecifics and the consequent maximizing of forage intake (Shrader *et al.*, 2007). Surprisingly, solitary males spent less time standing in a vigilant position and they moved more than males in the bachelor herd. In turn, males in the bachelor herd spent most of their time standing, partly probably as interruptions to

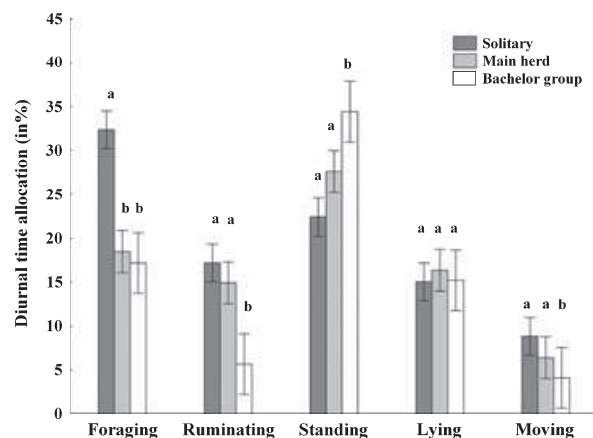


Fig 3 Daily activity patterns of the different social structures of Swayne's hartebeest in the Nechisar National Park. Columns with the same letter within each activity were not significantly different

rumination while scanning their surroundings. The allocation of time either to foraging or to vigilant behaviour is not always related to group size or the type of social structure (Shorrocks & Cockayne, 2005; Smith & Cain, 2008). Therefore, a longer-term study including seasonal variations in foraging efficiency, changes in social structure and the dynamics of potential predators is required for a better understanding of the time-investing strategy of the endangered Swayne's hartebeest. We can, however, conclude that the SH's general behaviour patterns do not markedly differ from similar large herbivore species, and it appears possible to use the experience from these species for the management and conservation of Swayne's hartebeests in Ethiopia.

### Acknowledgements

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#### **4.2. DOES SUPPLEMENTAL FEEDING AFFECT BEHAVIOUR AND FORAGING PATTERN OF CRITICALLY ENDANGERED WESTERN DERBY ELAND IN AN EX SITU CONSERVATION SITE?**

Hejzmanová P., Vymyslická P., Žáčková M., Hejzman M. 2012. Does supplemental feeding affect behaviour and foraging pattern of critically endangered Western Derby eland in an ex situ conservation site? Submitted paper.



Photo by Tom Junek

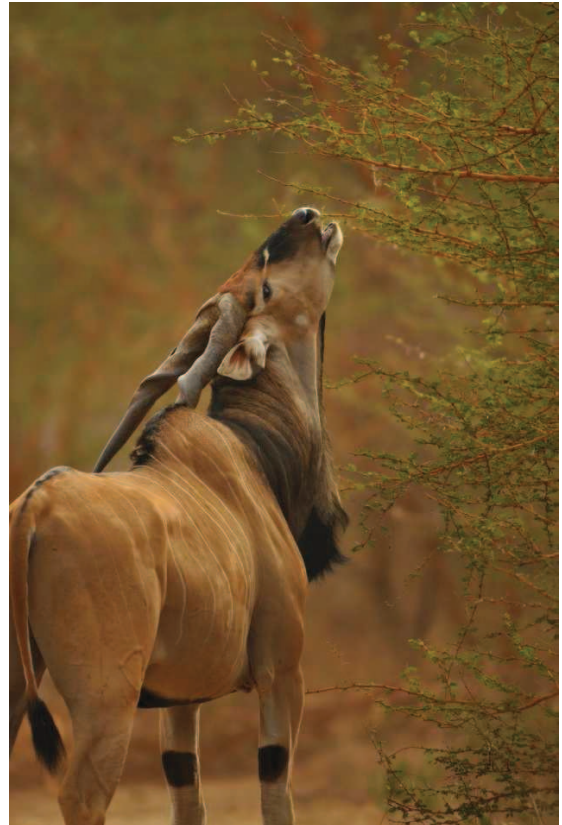


Photo by Tom Junek

# Does supplemental feeding affect behaviour and foraging pattern of critically endangered Western Derby eland in an *ex situ* conservation site?

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## ABSTRACT

Western Derby eland (*Taurotragus derbianus derbianus*) in the world-unique conservation breeding programme needs appropriate management for its survival. We conducted an experiment on a herd of six animals in the Fathala Reserve (Senegal) to reveal effects of supplemental food on activity time budgets and browsing patterns during seasons of scarce natural food resources in 2008 and 2009. In response to high-quality supplemental pods of *Acacia albida*, animals shortened their time invested in foraging in 2008 and allocated it to resting. This pattern corresponds to animals' behaviour in captivity without foraging *versus* vigilance trade-offs and with access to food provisions predictable in time and space. In 2009, supplemental feeding had no effect on behaviour and was associated with higher foraging and ruminating times than in 2008 indicating thus more limited natural food resources in 2009. We documented high species diversity in the animals' natural diet. Supplemental food did not induce changes in browsing pattern at the plant species level, probably due to small individual effect on total nutrient and energy intake. Food supplementation, however, facilitates the animals to surpass unfavourable conditions or alleviate stress with additional rest, and could therefore serve in special conservation situations in order to enhance animals' fitness.

**Keywords:** diet composition, large herbivore, *Taurotragus derbianus*, West Africa, wildlife management



## INTRODUCTION

Management plays a crucial role in the success of conservation efforts for endangered animals (Balou & Foose 1996; Peignot *et al.* 2008). *Ex situ* conservation breeding represents, for some species, the only way to ensure their survival and maintenance of their genetic resources (Ebenhard 1995). In particular, rare and endangered species are vulnerable to management decisions taken without adequate knowledge of their ecology and behaviour (Grey-Ross *et al.* 2009).

One of the central issues for successful conservation and endangered species management is appropriate food resources for the species. Fluctuations in food supply or in particular nutrients influence breeding patterns (Sadlier 1969; Bishop *et al.* 2009). Scarce food resources may severely affect survival and/or breeding rates (Myserud *et al.* 2007). In food-limited populations, supplemental feeding as a conservation measure has the potential to produce positive effects on fitness components, namely reproductive success, and on population parameters such as survival, recruitment and carrying capacity (Dorgeloh *et al.* 1996; Treydte *et al.* 2001). On the other hand, inappropriate provisioning of food may change the behaviour of animals, for instance their spatial distribution (Cooper *et al.* 2006), or vigilance, through habituation to human presence (Manor & Saltz 2003), which may have unexpected consequences on eventual reintroductions. The effects of supplemental feeding have been widely investigated for large herbivores in temperate zones, which were fed during winter periods (Schmitz 1990; Doenier *et al.* 1997; Schmidt & Hoi 2002). There is a lack of experimental studies in tropical environments (Boutin 1990).

The foraging decisions and processes of large herbivores operate in different spatial (and temporal) scales from the selection of plant parts or particular plant species at the landscape level (Prins & van Langevalde 2008). In response to increased availability of food resources, animals feed more selectively (Stephens & Krebs 1986) or shorten their foraging time (Owen-Smith 1994). If animals are offered a food supplement, they use it first, and then continue to forage native vegetation (Doenier *et al.* 1997; Cooper *et al.* 2006). Improving forage availability, the animals increase their selectivity for higher quality forage species (van der Waal 2005). Artificially increasing forage availability or quality may decrease foraging pressure on natural food resources (Kowalczyk *et al.* 2011) and induce changes in the behaviour. For instance, the total time devoted to foraging, or biting rate, as indicators of forage intake (Hodgson 1985), may decrease, animals may invest more time in activities to increase the individual's fitness, such as reproduction, anti-predator behaviours, resting, or social interactions (Hejmanová *et al.* 2009). Very little information exists regarding how

animal behavioural patterns may be changed, and what may be the ultimate consequences for conservation management (Caro 2007).

We conducted a food supplementation experiment on a herd of Western Derby eland (*Taurotragus derbianus derbianus*, Gray 1847), a critically endangered antelope (IUCN SSC Antelope Specialist Group 2008) in the Sudanese savanna woodland, in the conservation enclosure in the Fathala Reserve in Senegal. These animals constitute one of four unique breeding herds of *ex situ* populations established in Senegal since 2000 (Nežerková *et al.* 2004, Koláčková *et al.* 2011) and are susceptible to management interventions. The objective of the study was to determine how supplementary feeding affects the foraging behaviour of the Western Derby eland under semi-captive conditions. In this experiment, we tested hypotheses regarding whether supplementary feeding affects activity time budgets, or whether it affects browsing patterns at the level of individual plants.

## MATERIALS AND METHODS

### *Study area*

The study was conducted in the Fathala Reserve, a part of the Delta du Saloum National Park in Western Senegal (13°39'N, 16°27'W). The climate has a seasonal character, with a warm, rainy season from June to October, and a dry season from November to May. The mean annual precipitation is 1022 mm, and the mean annual temperature is 26 °C (1951-2000, Banjul Yundum meteorological station). The area is situated at the interface of the Sudanese and Sudano-Guinean savannas. The major vegetation types are wooded grassland and woodland dominating by plant families *Caesalpiniaceae* (16.3%), *Combretaceae* (16.3%) and *Mimosaceae* (12.2%). The enclosure was dominated by *Acacia macrostachya* with several species of the *Combretum* genus, *Piliostigma thonningii*, *Prosopis africana*, *Pterocarpus erinaceus*, *Terminalia laxiflora*, and *T. macroptera* with scarce and senescent undergrowth formed mostly by *Andropogon gayanus* and *Schizachyrium sanguineum* and almost no forbs (Nežerková-Hejčmanová *et al.* 2005, Žáčková and Hejčmanová 2008, unpublished data).

The Fathala Reserve is a fenced area managed for tourist safari, covering 2000 ha and various indigenous as well as introduced wildlife species dwell there (Nežerková *et al.* 2004). Within the reserve a fenced enclosure (70ha) separated from all other animals by double fence and with access restrictions to the public was established there as an integral part of a conservation breeding program for the critically endangered Western Derby eland

(*T. d. derbianus*) (Koláčková *et al.* 2011). Animals within the conservation program were supplementary fed during each dry season, mostly from March to July. In 2008 and 2009 the herd in the Fathala reserve was made up of one male and five females, all of the age of two or three years and without calves in both years.

### ***Experimental design and data collection***

The data were collected in April and May 2008 (22 observation days) and April 2009 (12 observation days), during the hot dry season. We selected the peak of the dry season for the experiment because that is when food resources available for herbivores in the area are the most limiting. We expected the most pronounced changes in behavioural patterns to manifest under the harshest conditions. Another reason for the selection of hot dry season was stability of the weather in order to avoid phenological shifts in vegetation and water availability during data collection. Six Western Derby elands, trained for human presence, were observed in the 70 ha fenced enclosure directly, at a distance of 15 to 30 m, when necessary we identified browsed plant species using binoculars. Observations were made continuously during 10 hours of the daylight period (mostly from 7 a.m. till 5 p.m.) on a focal animal (Martin & Bateson 1993). Focal sampling was repeated at least three times for each animal. We recorded activities of the observed animals, all plant species (and plant parts such as leaves or fruits) browsed by the antelopes, the time spent browsing on particular individual plants, and the number of browsing bites on particular plants. Recorded activities were: 1) 'Foraging' defined as continuous intake of food resources, including walking between two successive individual plants. According to our field observations, animals were foraging while walking for up to several minutes from one plant to another, but when they walk longer than seven minutes, they have moved to another place (displacement); 2) 'Browsing' defined as biting and separation of leaves, fruits or terminal shoots from a single individual plant. This was an integral part of foraging, but did not include movements between individual plants; 3) 'Ruminating' – chewing the cud; 4) 'Resting' when animals were calm, laying on the ground or standing without any activity, nor in a vigilant posture; and 5) 'Displacement' when animals moved to another place without foraging. We calculated the following parameters from the observation records: total time spent on a particular activity during 10 hours of daylight, activity bouts, defined as a continuous sequence of a particular behaviour, and frequency of activity bouts per hour, in order to determine the behavioural rhythm (Martin & Bateson 1993). From the number of bites per plant, the biting rate per minute was calculated. Fresh biomass available to animals

(up to 2.5m of height) was assessed using estimation of leaf cover (in %) similarly as in Nežerková-Hejčmanová *et al.* 2005. We used plant species nomenclature according to Arbonnier (2002). There was an important population of *Daniellia oliveri* saplings (individuals less than 1m in height) in the enclosure, these were considered a separate food resource from full grown trees.

The animals were observed in two feeding situations: with and without supplementary food (20 kg of pods of *Acacia albida*) offered in the morning at a predetermined place in the enclosure. Both feeding situations were equally distributed, alternating them every three days over the course of the observation period. To evaluate the effect of habituation of the animals to supplementary food, we proceeded differently in each year. In 2008, we started to offer the food supplement to the animals two weeks before the start of observations, to get the animals accustomed to it. In 2009, we started to offer the animals the supplemental food at the same time we started the animal observations. The experimental design was limited due to subordination to conservation management restrictions and adopted according to the demand of managers for practical conservation purposes. A total of 194.5 hours of observation were carried out in 2008 (mean  $\pm$  SE observation time per animal was  $32.4 \pm 0.14$  hours), and 125.6 hours in 2009 (mean  $\pm$  SE observation time per animal was  $18 \pm 2$  hours).

### ***Data analyses***

All statistical treatments were performed using the STATISTICA 8.0 package (StatSoft, Tulsa, USA). All data were tested for normality by the Kolmogorov-Smirnov test before each analysis. The general activity time budget analyses were based on three basic activities: foraging, ruminating, and resting. For each of these activities, the total time, the bout lengths, and frequencies (per 1 hour) were tested separately as dependent variables for the effect of supplemental food, applying Student's t-tests. The variable "bout length" was square root transformed to meet the assumption of normality. Years 2008 and 2009 were tested separately. Student's t-test was also employed separately for comparisons between years 2008 and 2009 for total times spent foraging, ruminating, and resting.

The browsing pattern analyses were based on three dependent variables: browsing bout length (the time spent browsing on individual plants), biting rate (the number of bites per minute), and number of bites per individual plant. All three variables were log transformed to achieve a normal distribution of data. We tested these dependent variables separately using Student's t tests to estimate the effect of the food supplement. The relationship

between browsing bout length and number of bites per plant was tested by Pearson's correlation.

## RESULTS

### *Activity time budgets*

The antelopes spent on average 214 min (S.E.  $\pm$  12 min) foraging (36%), 164 min (S.E.  $\pm$  9 min) ruminating (27%), and 64 min (S.E.  $\pm$  9 min) resting (11%) over 10 hours during the day. These basic activities therefore took up 74 % of the time of their daylight hours. The remainder of their time was dedicated mainly to displacement, drinking, social interactions, and comfort behaviours.

In 2008, the antelopes spent significantly (20%) less time foraging when supplemental food was provided (167 min  $\pm$  13 min S.E.), compared with days when it was not provided (210 min  $\pm$  16 min S.E.) ( $t_{(20, 18)} = -1.96$ ,  $P = 0.049$ ). At the same time, there was no significant difference in the time spent resting ( $t_{(19, 17)} = 1.87$ ,  $P = 0.078$ ), nevertheless animals tended to spend less time resting in cases without food supplement (30 min  $\pm$  16 min S.E.) than when they received it (80 min  $\pm$  17 min S.E.) (Fig. 1a). The length of the foraging bouts was also significantly longer when no supplemental food was offered to animals than in the opposite situation ( $t_{(225, 223)} = -2.62$ ,  $P = 0.009$ ), while other basic activities were not affected by food supplementation (ruminating:  $t_{(108, 106)} = -1.61$ ,  $P = 0.11$ , resting:  $t_{(77, 75)} = 1.54$ ,  $P = 0.13$ ) (Fig. 1b). The frequency of foraging bouts was no different when the animals received the food supplement ( $t_{(20, 18)} = 1.90$ ,  $P = 0.073$ ). The bout frequency of two other basic activities also did not significantly differ between the two situations (ruminating:  $t_{(20, 18)} = 1.04$ ,  $P = 0.31$ , resting:  $t_{(20, 18)} = 1.43$ ,  $P = 0.17$ ) (Fig. 1c).

In 2009, total foraging and ruminating times were 50% and 56% higher than in 2008, while total resting time was similar (foraging:  $t_{(20, 12)} = -5.06$ ,  $P < 0.001$ , ruminating:  $t_{(19, 12)} = -5.83$ ,  $P < 0.001$ , resting:  $t_{(19, 12)} = 0.11$ ,  $P = 0.91$ ), in summation, the antelopes spent on average 271 min  $\pm$  15 min S.E. foraging, 210 min  $\pm$  5 min S.E. ruminating, and 62 min  $\pm$  8 min S.E. resting. There were no differences in the total time spent on particular activities during the day, either with or without supplemental food (foraging:  $t_{(12, 10)} = -0.18$ ,  $P = 0.85$ , ruminating:  $t_{(12, 10)} = -1.40$ ,  $P = 0.19$ , resting:  $t_{(12, 10)} = 0.31$ ,  $P = 0.76$ ) (Fig. 1d). Neither mean bout length (all activities:  $P > 0.05$ ) (Fig. 1e), nor bout frequencies of all basic activities (all activities:  $n = 12$ ,  $P > 0.05$ ) (Fig. 1f) were affected by supplemental food.

### ***Diet composition and browsing pattern***

The Western Derby eland diet was composed of woody plant species only, no foraging on forbs or grasses was recorded. A total of 32 out of 36 woody plant species available in the enclosure were determined to be a natural part of the diet of the Western Derby eland in the Fathala Reserve. The animals browsed mostly on leaves, however pods of *Piliostigma thonningii* also represented a substantial part of forage (Table 1). The mean browsing bout length per plant was  $95 \pm \text{S.E. } 3$  seconds, with a mean number of bites of  $11.2 \pm \text{S.E. } 0.5$  per plant, and a mean biting rate of  $10.7 \pm \text{S.E. } 0.2$  bites per minute. The animals spent the longest time foraging on supplemental pods of *Acacia albida* when offered, namely  $848 \pm \text{S.E. } 162$  seconds, on average. Among native plant species, the longest mean browsing bout was recorded on *Prosopis africana* and the shortest on *Icacina senegalensis*. The highest browsing rate was recorded on *Daniellia oliveri* saplings and the lowest on *Piliostigma thonningii* pods. The highest number of bites was recorded on *Saba senegalensis* and the lowest on *Icacina senegalensis*. Detailed results for the most browsed plant species are given in Table 1. The browsing bout length per plant was positively correlated with the number of bites per plant ( $r = 0.845$ ,  $P < 0.001$ ,  $n = 2191$ ). There was no general effect of supplemental food on the browsing bout length per plant, the number of bites per plant, or the biting rate (all analyses  $P > 0.05$ ).

### **DISCUSSION**

The activity time budgets of Western Derby eland in the Fathala Reserve enclosure, namely, time allocated to foraging within the daylight period, were similar to time budgets reported for other free ranging African ruminants (Owen-Smith 1994; Twine 2002; Du Toit & Yetman 2005; Taylor *et al.* 2006, Vymyslická *et al.* 2011). Our results therefore indicate that the animals under semi-captive conditions still maintain their natural behaviour, without any dramatic changes caused by breeding in an enclosed area, and support our previous findings on maternal behaviour (Hejcmanová *et al.* 2011). The dietary composition of Western Derby elands in *ex situ* breeding enclosures was also similar to in the wild (Hejcmanová *et al.* 2010). On the other hand, we revealed functional responses of activity time budgets to increased food abundance by supplementation, particularly in 2008. If offered supplemental food, the animals shortened their total foraging time as well as the length of their foraging bouts, similarly as reported for kudu (*Tragelaphus strepsiceros*) by Owen-Smith (1994). The shorter time allocated to foraging suggests that the Western Derby elands fed without constraints to satiation (Jeschke & Tollrian 2005), and may indicate either a time minimizing



strategy (Bergman *et al.* 2001), or a preference for fulfilling energy requirements with the least overall cost (Owen-Smith 1994). The surplus available time was apparently allocated to resting, considering that the animals do not face foraging *versus* vigilance trade-offs as do free-ranging animals (White & Berger 2001; Ruckstuhl *et al.* 2003). This daily activity pattern is typical for species in captivity without predators or competitors, and with a predictable provision of food in time as well as space (Bowman & Plowman 2002). The animals habituated to supplementing spent mornings in the area closest to the feeding site, apparently awaiting feeding with the supplemental *Acacia* pods. Consequently, the animals reduced their displacement over the enclosure, and spent the most of their time in the environs of the feeding site, similar to other supplemented animal species (Cooper *et al.* 2006; Lopez-Bao *et al.* 2010). In 2009, there were no differences in activity time budgets between situations with and without supplemental food. This absence of supplemental food being associated with substantially higher foraging and ruminating times, in comparison with 2008, indicates that in 2009 the natural food resources in the enclosure were limited. In addition, the animals were not habituated to food supplementation on the long-term prior to the start of observation, and they maintained their well-established spatial pattern over the whole enclosure, similar to what they did without food supplement (Lopez-Bao *et al.* 2008). The Western Derby elands' diet during the dry season in the Fathala reserve was composed exclusively of trees and shrubs. They browsed a large variety of plant species, generally leaves and some types of fruits, namely pods, this continued even if they were given supplementary food. Western Derby elands in the wild (Niokolo Koba National Park in Senegal) or in conservation breeding enclosures in the Bandia reserve (Senegal) feed, however, not only on woody plants, but partly also on forbs and grasses (Hejcmanová *et al.* 2010). The difference is probably due to different food resources available at each site, although all referring to the dry season. There was no fresh undergrowth vegetation in the Fathala enclosure in the dry season and different grass species in comparison to Bandia Reserve. Niokolo Koba National Park offers, on the other hand, many times larger area (913000 km<sup>2</sup>) implying higher landscape heterogeneity and richness of potential food resources in any period of the year than a fence-delimited enclosure. The animals browsed along their foraging path, spending a relatively short time, with only a few bites on each plant species (Table 1). This pattern designates a browser foraging strategy (Owen-Smith 1993; de Garine-Wichatitsky *et al.* 2004). The length of browsing bouts, as well as biting rates, was plant species specific. Although supplemental food affected the general foraging pattern, browsing bout length on particular plants, and biting rate per individual plant

remained unchanged, without any effect of the supplemental food. Considering the high diversity of plant species in the Western Derby eland diet, individual plants separately probably make a minimal contribution to total nutrient and energy intake.

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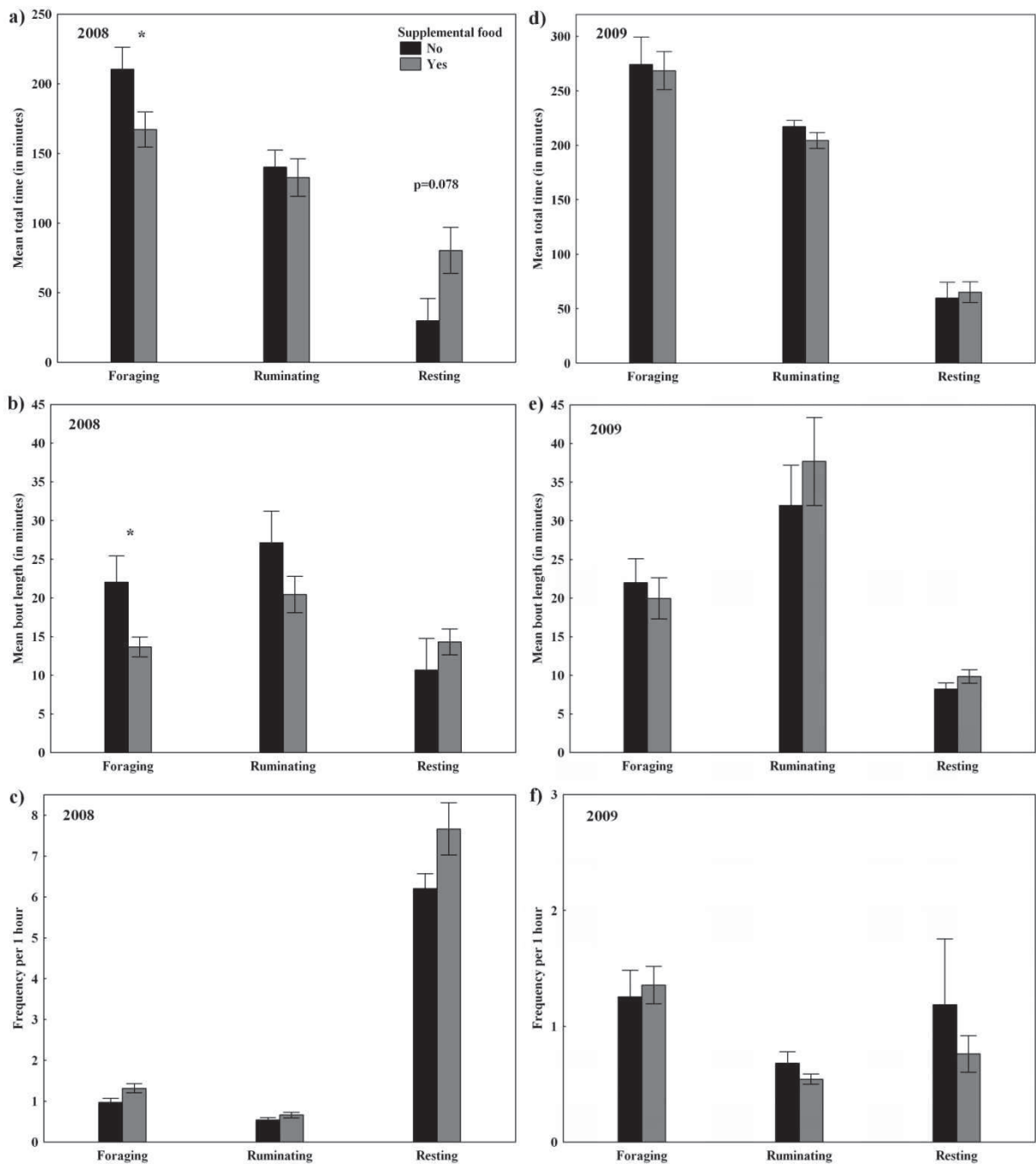
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## TABLES AND FIGURES

**Table 1** List of the most frequently browsed plant species by Western Derby eland in the conservation breeding enclosure in the Fathala reserve. Numbers of records are given separately for the browsing bout length per plant, and the number of bites per plant, together with biting rate. Leaf cover (in %) represents available fresh biomass in the enclosure.

Plant species	Family	Leaf cover (%)			Browsing bout per plant (s)			Number of bites per plant			Biting rate per minute		
		N	Mean	SE	N	Mean	SE	N	Mean	SE	Median	Mean	SE
<i>Acacia ataxacantha</i>	Mimosaceae	2.5	503	56.6	2.9	33	436	8.4	0.5	5	11.0	0.3	9.7
<i>Aphania senegalensis</i>	Sapindaceae	0.6	8	71.3	20.3	65	6	9.3	4.8	5	7.8	1.7	6.2
<i>Combretum glutinosum</i>	Combretaceae	7.0	192	128.0	13.3	56.5	148	17.6	2.4	6	10.8	0.6	9.3
<i>Combretum micranthum</i>	Combretaceae	0.7	40	174.5	51.2	64.5	20	7.8	2.8	3	5.9	0.9	4.9
<i>Combretum paniculatum</i>	Combretaceae	6.2	695	67.5	3.6	36	619	11.1	0.7	5	12.1	0.3	10.6
<i>Daniellia oliveri</i>	Caesalpiniaceae	7.4	119	50.5	9.2	21	101	7.0	1.3	3	13.4	0.9	10.9
<i>Daniellia oliveri</i> sapling	Caesalpiniaceae	8.0	199	54.3	7.1	19	117	4.6	0.5	3	14.0	1.0	11.2
<i>Icacina senegalensis</i>	Icacinaceae	9.8	74	32.6	3.2	24	65	3.6	0.5	3	9.7	1.1	7.5
<i>Lonchocarpus laxiflorus</i>	Fabaceae	0.6	7	96.1	28.8	60	5	15.8	7.1	13	10.2	1.8	12.0
<i>Maytenus senegalensis</i>	Celastraceae	0.2	9	95.8	23.3	95	6	14.5	4.7	12.5	8.9	2.3	7.1
<i>Ptilostigma thonningii</i> fruit	Caesalpiniaceae	-	224	149.1	12.4	73	138	8.7	1.0	4	5.2	0.4	3.6
<i>Ptilostigma thonningii</i> leaf	Caesalpiniaceae	0.1	5	99.0	55.6	31	4	3.5	0.6	3.5	6.6	2.0	5.9
<i>Prosopis africana</i>	Fabaceae	0.6	51	210.8	39.7	101	18	19.1	5.3	8.5	6.0	0.7	5.9
<i>Saba senegalensis</i>	Apocynaceae	2.6	172	179.9	24.3	95.5	131	28.2	5.3	11	11.1	0.6	9.9
<i>Strychnos spinosa</i>	Loganiaceae	0.1	18	102.0	30.6	52.5	16	9.2	4.6	4	8.3	1.6	6.2
<i>Terminalia laxiflora</i>	Combretaceae	3.0	273	82.1	6.7	47	208	10.5	1.2	5	9.9	0.5	8.0
<i>Terminalia macroptera</i>	Combretaceae	0.9	218	145.5	15.5	63	152	10.5	1.5	5	8.2	0.4	6.9

**Figure 1** Diurnal time budgets of Western Derby elands for basic activities without (No) and with (Yes) offered food supplementation in years 2008 and 2009: a) and d) total time, b) and e) the length of a behavioural bout, c) and f) the frequency of behavioural bouts within 10 hours of daylight. The error bars indicate S.E. The results of Students' t-test are defined as significant if  $P < 0.05$  and indicated by \*.





#### **4.3. DO HIGH RANKING MOTHERS PRODUCE HIGH RANKING BABIES? STUDY OF DOMINANCE HIERARCHY IN THE WESTERN DERBY ELAND (TAUROTRAGUS DERBIANUS DERBIANUS)**

Jůnková Vymyslická P., Brandlová K., Hejčmanová P., Žáčková M., Hozdecká K. 2012. Do high ranking mothers produce high ranking babies? Study of dominance hierarchy in the Western Derby eland (*Taurotragus derbianus derbianus*). Submitted paper.



Photo by Tom Junek



# Do high ranking mothers produce high ranking babies? Study of dominance hierarchy in the Western Derby eland (*Taurotragus derbianus derbianus*)

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## ABSTRACT

Adaptation of dominance hierarchies in social living ungulates permits successful coexistence and determine the animals' access to resources as well as reproductive success. Dominance hierarchies were well examined in female or male herds, studies about mixed herds are scarce. We examined the structure of social hierarchies in Western Derby eland in Bandia reserve, Senegal. We tested whether i) dominance hierarchies were linear or complex; ii) age and iii) sex influence the social rank of animals in mixed herds; iv) maternal rank inheritance appears in Derby eland offspring. Two herds (h1, h2) were observed in 2006, 2010, and 2011 ( $N_{h1/2006} = 24$ ,  $N_{h1/2010} = 22$ ,  $N_{h1/2011} = 22$ ,  $N_{h2/2011} = 13$ ). Total 615 and 198 dyadic interactions in h1 and in h2 were recorded, respectively. Frequency based dominance index revealed linear hierarchy in Derby eland ( $h_{h1/2006}=0.93$ ,  $h_{h1/2010}=0.68$ ,  $h_{h1/2011}=0.83$ ,  $h_{h2/2011}=0.89$ ). The dominance order was significantly influenced by age ( $r_s = -0.763$ ,  $N = 81$ ,  $P < 0.01$ ). Although the influence of sex on dominance order was significant ( $H_5 = 48.25$ ,  $P < 0.001$ ), we revealed no difference between males and females in respective age categories: juveniles – < 18 months, subadult animals – 18-42 months, adults - > 42 months. Relationship between mother's and offspring's rank did not occur ( $r_s = 0.05$ ,  $N = 13$ ,  $P = 0.873$ ) that may be caused by adapted nursery herd system.

**Keywords:** ungulate, social rank, mixed herd, dominance, antelope

## INTRODUCTION

Knowledge of mechanism of animal behaviour enables efficient management techniques development for optimum production as well as the animals' welfare (Bouissou 1980, Wirtu et al. 2004). Many studies detect the social rank of individuals and the dominance relationship of ungulates, but they often differ more or less in methodology and working concepts.

Social rank can alter behavioural, physiological, biochemical and anatomical parameters, and can affect overall health and reproductive performance in many mammals (Ellis 1995, Pedersen et al. 2003). Phillips and Rind (2002) have showed that separation of dominant from subordinate domestic cow increases time spent resting and improves herd productivity. Furthermore the knowledge of hierarchy in the herd can be used for manipulation/treatment of dominant animals though oral served medicaments without the need of anaesthesia (Wirtu et al. 2004).

Social organization within group can be relatively simple, i.e. linear or near linear, or highly complex (Craig 1985). Some authors indicate that small groups (less than 6 to 10 individuals) domestic animals of the same sex and about the same size frequently have linear or near-linear social organization, while larger groups tend to form a complex hierarchy (McCort & Graves 1982, Craig 1985). Favre et al. (2008) in his study of social dominance in bighorn ewes indicates that the linearity index is weakening with the increasing number of observed animals.

The influence of mother's position in the herd on the dominance rank of its offspring has been continuously discussed. Some authors admit the possibility of inheritance of dominance (Dewsberry 1990, Moore 1990), whereas Capitanio (1991, 1993) refuse it. Holekamp and Smale (1991) use the term maternal rank inheritance for the process when offspring gains dominance rank similar to its mother's rank. In some ungulates, this process is thought to be more important for daughters that remain with their natal herd longer than sons (Dušek et al. 2007). Significant influence of matrilineal genealogy on social rank of daughters was revealed in common eland *Taurotragus oryx* (Kiley-Worthington 1978, Cransac & Aulagnier 1996), red deer *Cervus elaphus* (Clutton-Brock et al. 1984), or American bison *Bison bison* (Green & Rothstein 1991).

Beyond the other factors the social hierarchy in the herd can be influenced also by sex. Craig (1985) suggests that among group living ungulate species in which polygyny and secondary sexual dimorphism occurs, males are dominating adult females and younger animals are on the bottom of the hierarchy. However, studies of social behaviour concerning dominance

hierarchies were predominantly conducted on females (e.g. Cassinello 1995, Holand et al. 2004), or males (e.g. McElligott et al. 2001; Pelletier & Festa-Bianchet 2006), studies on mixed herd of ungulates are scarce.

We investigated dominance hierarchy on mixed herds of the Western Derby eland (*Taurotragus derbianus derbianus*) large body-sized, gregarious polygynous antelope with visible differences between sexes in body mass and in robustness of horns.

We first examined the structure of social hierarchies in Western Derby eland in three years. We tested whether dominance hierarchies were linear or complex and we investigated whether age and sex influence the social rank of animals in mixed herds. Finally we aimed to reveal whether maternal rank inheritance appears in Derby eland offspring.

## **METHODS**

### ***Study site and investigated animals***

The study was conducted in Bandia reserve, 65 km east of Dakar (14°35'N, 17°00'W), Senegal. The reserve covers 3500 ha of natural Sahelian savanna vegetation with a high density of woody species (Hejcmanová et al. 2010). The climate is typical seasonal with dry and rainy season. Average annual precipitation is 484 mm and the average temperature is 25°C in January (middle dry season) and 30°C in September (high rainy season). We investigated Western Derby elands; critically endangered (IUCN 2008) western subspecies in ex-situ conservation programme (Koláčková et al. 2011). Investigated animals were in two breeding herds (herd 1, herd 2) in separated double-fenced enclosures within the Bandia reserve. Numbers of animals, sex and age structure of herds are given in the Table 1.

Herd 1 was observed in 2006 in the 60 ha enclosure. The animals were transferred to another enclosure in 2008, thus the observation in 2010 and 2011 were carried out on the same animals with their offspring in larger 250 ha enclosure. Herd 2 was observed in 2011 only in 100 ha enclosure. All breeding enclosures were restricted exclusively to Western Derby elands. All animals were individually recognized by distinctive physical appearances such as number and form of lateral body stripes and horn shapes (Koláčková et al. 2011). Enclosures were covered by native Sahelian vegetation providing forage for animals and were supplied by water. Animals were daily supplementary fed by peanut hay, commercial livestock granules and pods of *Acacia albida*.

### ***Data collection***

Data were collected in February 2006, in March and April 2010 and in February and March 2011 during the daylight, between 7am and 7pm. *Ad libitum* sampling (Altman 1974) of dyadic interactions was used, mainly during supplemental feeding by *Acacia albida* pods that were highly preferred forage for Western Derby elands, thus interactions were well visible. Records of interactions were based on dominance/submissive displays between two animals that are defined as all agonistic acts including different kinds of threats, bites, kicks, charges and avoidances. We considered namely following interactions: leaving of the animal from a heap of supplementary feeding based on coming of another animal without any aggression neither physical contact; runaway of the animal from a heap of supplementary feeding based on fast coming of another animal without any aggression neither physical contact; threat with horns of one animal that forces another animal to escape but without physical contact; physical threat of one animal using its horns to push away another animal. The matrix tabulation was used to record the outcomes of agonistic interactions between pairs. Information about winner's name, loser's name, their sex, age category, kinship in relation to other animals, namely sire and dam was recorded.

### ***Calculation of dominance indices***

For construction of social hierarchy in the herd, three indices of dominance were computed. David's score (DS) (David 1987) for each observed subject was calculated with the formula:  $DS = w + w_2 - l - l_2$ , where  $w$  is the sum of proportion of wins by the subject,  $w_2$  is sum of weighted proportion of wins of the individual against whom the subject has won,  $l$  is sum of proportion of losses by the subject,  $l_2$  is sum of weighted proportion of losses of the individuals against whom the subject has lost. To calculate  $w_2$  and  $l_2$ , weight is given by its multiplying an opponent's proportion of wins or losses by its respective  $w$  or  $l$  value.

Clutton-Brock index (CBI) (Clutton-Brock et al. 1979) was calculated for each observed animal as follows:  $CBI = (B + b + I) / (L + l + I)$ , where  $B$  is number of individuals whom the subject dominates,  $b$  is number of individuals who dominate the subject,  $L$  is number of individuals who dominate the subject and  $l$  is number of individuals who dominate those dominating the subject.

Frequency-based dominance index (FDI) (Premnath et al 1990) for each observed subject was calculated with the formula:  $FDI = \sum_{i=1}^n Bi + \sum_{i=1}^n \sum_{i=1}^m b_{ij} + I / \sum_{i=1}^p Li + \sum_{i=1}^p \sum_{i=1}^q l_{ij} + I$ , where  $\sum Bi$  represents the rate at which the subject shows dominance behaviour towards herd members and  $n$  is the number of individuals over which the subject shows

dominance.  $\sum b_{ij}$  is the sum of the rates at which all individuals dominated by the subject in turn shows dominance behaviour towards herd members and  $m$  for each summation is the number of individuals over which the observed animal shows dominance.  $\sum Li$  represents the rate at which the subject shows subordinate behaviour towards herd members and  $p$  is the number of individuals to which the subject shows subordinate behaviour.  $\sum l_{ij}$  is the sum of the rates at which those individuals toward whom the subject shows subordinate behaviour in turn show subordinate behaviour toward other herd members and  $q$  is the number of individuals to whom the observed animal shows subordinate behaviour. Using each of the indices, dominance hierarchies were constructed by arranging all individuals in order of their value of the index and assigning them ranks from 1 to  $n$ , where  $n$  is number of individuals in the herd.

According to de Vries (1998) Clutton-Brock index (CBI) does not take into account the total number, or win/loss asymmetry, of interactions recorded between different dyad member, therefore a relatively unsuccessful individual may have his index disproportionately raised because of a single win against a highly successful individual. Individual ranks calculated with David's score (DS) are not disproportionately weighted by minor deviations from the main dominance direction within dyads because win/loss asymmetries are taken into account by the use of dyadic dominance proportions in the calculations (Gammell et al. 2003). The most suitable index for hierarchy measuring was selected the FDI index, where the number of inconsistencies (the backward directed dominance) was the lowest. The animals standing on the top in the hierarchy have the rank one, the rank is increasing with lowering of the position in the herd.

### ***Data analyses***

To determine the linearity in the herd Landau's index of linearity ( $h$ ) was used. Landau's index provides a measure of the degree to which a dominance hierarchy is linear. The index is calculated as follows:  $h = 12 / (n^3 - n) * \sum (v_a - \frac{1}{2} (n-1))^2$ , where  $n$  is the number of animals in the group and  $v_a$  is the number of individuals whom individual  $a$  has dominated. The index ranges from zero to 1.0, with a value of 1.0 indicating perfect linearity. Values of  $h$  greater than 0.9 are generally taken to denote a strongly linear hierarchy.

Because the data did not have the normal distribution we used the nonparametric tests and analysed them in STATISTICA package (StatSoft, Inc. 2011). For testing whether the age affects rank position in the herd Spearman rank order correlation was used. We tested each herd and each year separately and then all individuals in all years together. The Kruskal-

Wallis ANOVA was used to find out the effect of age category on the dominance rank. For this purpose the animals were divided into age categories: juveniles under 18 months, subadult animals between 18 and 42 months, and adults over 42 months. Reproduction and parturition of Derby eland in Bandia reserve is naturally synchronized to the period between December and March (Koláčková et al. 2011). During this time the data were collected, thus the lower limit of 18 months was chosen to avoid the possibility of animals from the same cohort to be separated in different age categories.

The prediction that males have higher rank positions than females was tested by non-parametric Mann-Whitney U test. In order to avoid confounding effect of age and sex, we segregated all individuals in age-sex categories and Kruskal-Wallis ANOVA was used to test whether males are higher than females in the rank order.

Finally the relationship between the rank of offspring within respective age category and the rank of their mothers was tested by the Spearman rank order correlation. Thirteen mother-offspring pairs from 2011 are given in the Table 2.

## RESULTS

Altogether data were collected within 29 days and were recorded 615 and 198 dyadic interactions in herd 1 and herd 2, respectively.

For both herds of Western Derby eland in all observed years the hierarchical order based on David's score (DS), Clutton-Brock index (CBI) and frequency-based dominance index (FDI) was defined (supplemental data – Table 1). The hierarchy was strongly linear in the herd 1 in 2006 ( $h_{\text{herd1}/2006} = 0.93$ ), and near linear in herd 1 in other years ( $h_{\text{herd1}/2010} = 0.68$ ,  $h_{\text{herd1}/2011} = 0.83$ ) as well as in herd 2 in 2011 ( $h_{\text{herd2}/2011} = 0.89$ ).

The hierarchical rank was significantly related to age in both herds in all observed years ( $r_{s \text{ herd1}/2006} = -0.83$ ,  $N = 24$ ,  $P < 0.01$ ;  $r_{s \text{ herd1}/2010} = -0.86$ ,  $N = 22$ ,  $P < 0.01$ ;  $r_{s \text{ herd1}/2011} = -0.74$ ,  $N = 22$ ,  $P < 0.01$ ;  $r_{s \text{ herd2}/2011} = -0.8$ ,  $N = 13$ ,  $P < 0.01$ ). For all individuals in all years the rank was significantly influenced by age ( $r_{s \text{ all}} = -0.763$ ,  $N = 81$ ,  $P < 0.01$ ) (Figure 1). We revealed the same significant Similar results were gained while testing relationship between social rank and age categories. Generally younger animals have lower position in the hierarchy than adults (Figure 2).

No effect of sex on hierarchical order was revealed in the herd 1 in 2010 ( $U = 43$ ,  $N_{\text{males}} = 8$ ,  $N_{\text{females}} = 14$ ,  $P = 0.39$ ), and in 2011 ( $U = 52$ ,  $N_{\text{males}} = 10$ ,  $N_{\text{females}} = 12$ ,  $P = 0.62$ ) and in the herd 2 in 2011 ( $U = 19$ ,  $N_{\text{males}} = 5$ ,  $N_{\text{females}} = 8$ ,  $P = 0.94$ ). Some tendency of effect of sex on the rank was visible in herd 1 in the year 2006 ( $U = 38$ ,  $N_{\text{males}} = N_{\text{females}} = 12$ ,  $P = 0.053$ ).

Similar tendency of males having higher rank than females occurred when testing all animals in all years together ( $U = 603.5$ ,  $N_{\text{males}} = 35$ ,  $N_{\text{females}} = 46$ ,  $P = 0.055$ ). Influence of age-sex categories on the social rank was significant ( $H_5 = 48.25$ ,  $P < 0.001$ ), but no differences were revealed between males and female in respective age category (Figure 3, 4).

The Spearman rank order correlation did not prove the correlation between the rank of the offspring and the rank of its mother ( $r_s = 0.05$ ,  $N = 13$ ,  $P = 0.87$ ). The same results were gained while testing only offspring older than one year ( $r_s = -0.039$ ,  $N = 9$ ,  $P = 0.92$ ) as well as while testing only daughters ( $r_s = 0.013$ ,  $N = 8$ ,  $P = 0.98$ ).

## DISCUSSION

Our results indicate that a dominance hierarchy does exist in Western Derby eland. Furthermore, this hierarchy is linear, indicating minimum reversals of interactions. While Favre et al. (2008) showed decreasing level of linearity with increasing number of animals, in our study the linearity was not influenced by the number of animals in the herd. The strongest linearity was revealed within 24 animals, while the weakest linearity within 22 animals. In other observation within 22 and 13 animals remain in-between.

In mixed herd of Western Derby eland the social rank was influenced by age similarly as in studies of only males (Hass & Jenni 1991, Pelletier et al. 2003) or females (Thompson 1993, Côté 2000). Older individuals are typically larger and have larger weapons, but they could also be more experienced than younger animals, and experience could confer a competitive advantage during contest (Pelletier & Festa-Bianchet 2006). In our study the oldest animals were however not always on the top of the hierarchy. Two oldest females from the herd 1 were in the first year of observations in the third and ninth position, resp. second and seventh position in its sex category. In the year 2010 they moved to the second and sixth position, resp. first and fourth position. In the year 2011 the position of two oldest females was second and fifth, resp. first and third in their sex category. This indicates the progress of the rank with age. On the other hand males remained on the top position in all years in both herds, except of the herd 1 in 2011, where the top position was occupied by the second oldest male, while the oldest 12-years-old male was on the third, resp. second position. This situation was visible even in 2012 from personal observations. This is probably due to decreased influence of age on dominance rank with achievement of certain age level in males. By then the body mass becomes an increasingly important determinant of social rank (Pelletier & Festa-Bianchet 2006). Similar results gained Hass and Jenni (1991) on bighorn rams which after 10



years of age declined in condition, spent more time alone, and interacted less frequently with others.

In Derby eland males achieve the high and robustness of adult females in the age of approx. 2 years, therefore we expected that males are higher in the hierarchy than females. This prediction was not proved. The rank order was positively correlated by age, thus the older males were higher in the hierarchy than younger females, but the difference between the position of males and females in the respective age category was not significant. Schloeth's observations of feral cattle (Schloeth 1961 in Craig 1986) indicated that the dominance order, with all adult males in top positions, adult females in the middle, and younger animals at the bottom was present within a herd made up of both sexes and all age groups. Males began to work their way up through the adult female hierarchy at about 1.5 year of age and emerged at or near the top of the group at about 2.5 years. At that time they occupied the lowest positions of the adult male hierarchy. Craig (1986) expects this way of social hierarchy establishment in group-living species in which polygyny and secondary sexual dimorphism occur. Insignificant differences between males and females in our study can be caused by less sexual dimorphism in Derby eland. The most pronounced sign of sexual dimorphism in ungulates, the horns, is carried by both sexes, but there is visible difference in body mass between males and females.

In Derby eland the social rank of offspring was not related to the social rank of its mother, although according to Clutton-Brock et al. (1986), or Craig (1986) offspring of high-ranked mothers tend to achieve high social rank as adults. The mechanism for this is still debated. It may be that offspring learn agonistic behaviour by watching their mothers interact aggressively with other individuals (Mosley 1999). It may be that offspring inherit aggressive temperaments (Moore 1990), or it may be that the other individuals in the herd learned to avoid the offspring when it was near its high-ranked mother and the other animals continue to avoid it after weaning (Mosley 1999). In our study the missing relationship between mother's and offspring's rank could be explained by the short contact between mother and its young during its early ontogeny, when young prefer to stay in nursery herds, away from the adults and only rarely interact with them (Cransac and Aulagnier 1996).

Higher social rank determines priority access to limited resources (Clutton-Brock et al. 1984, Côté 2000) as well as reproductive success (Morell 1996, Mosley 1999, Wirtu et al. 2004). Reproductive success in males is predominantly limited by access to females in oestrus, in females this success is more often directly linked to resource availability (Holand et al. 2004). By contrast, higher foraging efficiency, but not reproductive success, has been shown

to be associated with dominance for several female ungulates, such as American bison *Bison bison* (Rutberg 1986). However a correlation between female dominance status and reproductive success has been shown for red deer *Cervus elaphus* (Clutton-Brock et al. 1986). Several studies of bighorn sheep, *Ovis canadensis*, have repeatedly failed to show any link between female dominance and reproductive success (Festa-Bianchet 1991, Hass 1991, Fourier & Festa-Bianchet 1995). Vaca et al. (1985) revealed in a group of cattle that oestrus expression can be reduced if the social structure of cows is disrupted. In our study we did not compare the reproductive success and dominance order in the herd, but it could be an requisite subject of consecutive study, because the composition of the herd was changed in the years 2008, 2009, and 2011, consequently the reproductive success could be influenced by transports of animals in Western Derby eland.

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## TABLES AND FIGURES

**Table 1** Number of animals, sex and age structure of herd 1 and herd 2 in particular years.

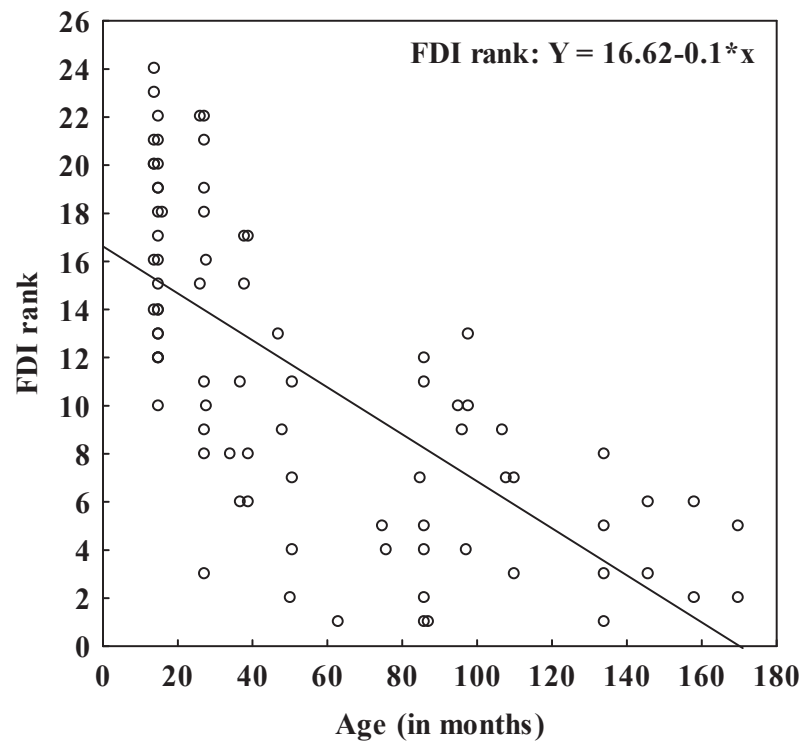
Year/herd	Total number	Males			Females		
		< 18 months	18 – 42 months	> 42 months	< 18 months	18 – 42 months	> 42 months
2006/herd1	24	5	6	1	2	3	7
2010/herd1	22	5	1	2	4	0	10
2011/herd1	22	3	4	3	2	2	8
2011/herd2	13	1	3	1	2	2	4

**Table 2** Mother-offspring pairs build from animals in both herds. Abbreviations: FDI – Frequency based dominance index, age-sex categories - 1F – females until the age of 18 months, 1M – males until the age of 18 months, 2F – females 19 to 42 months, 2M – males 19 to 42 month, 3F – females older than 43 months, 3M – males older than 43 months.

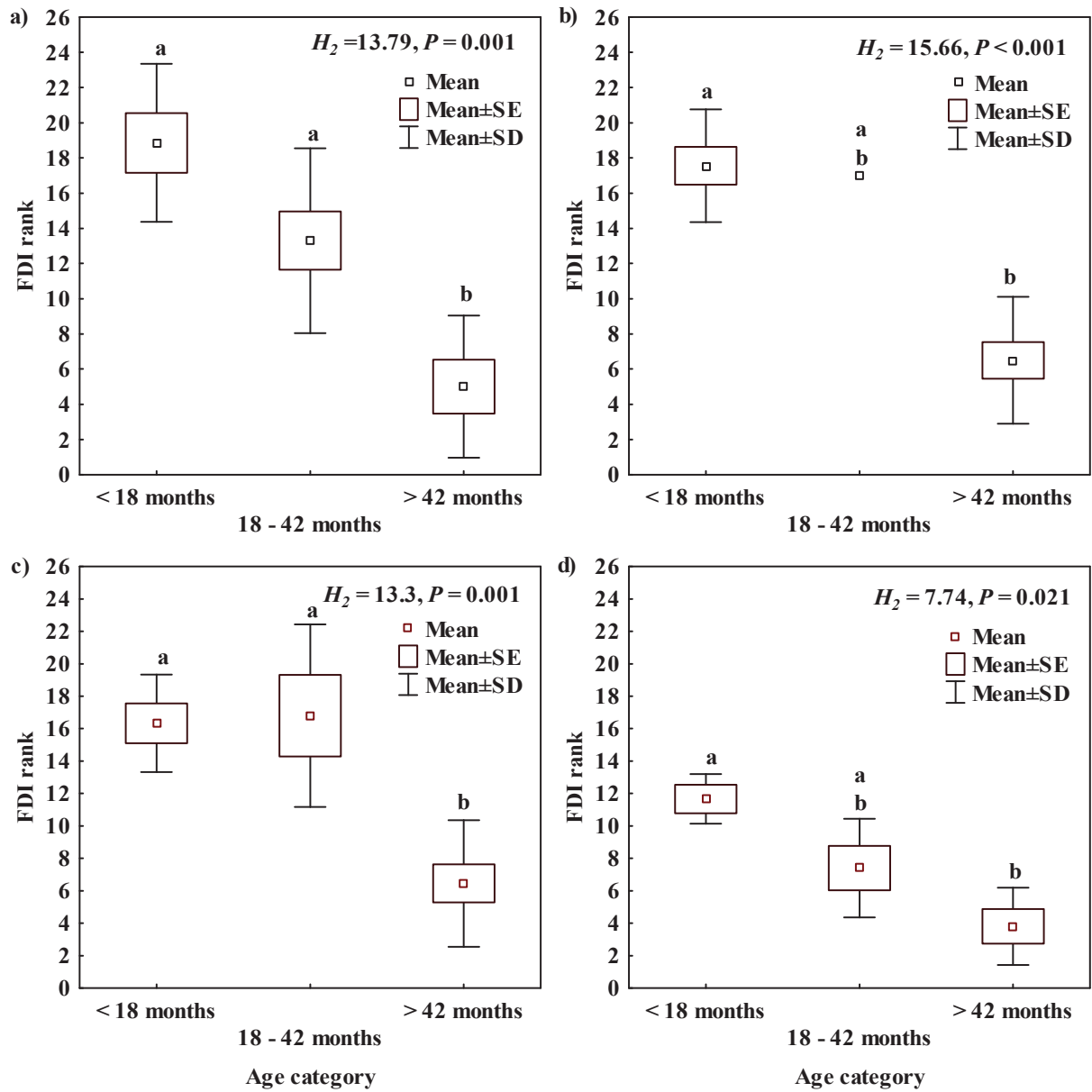
Name	Offspring			Mother					
	Age in months	Age- sex cat.	FDI	Rank within age cat.	Name	Age in months	Age- sex cat.	FDI	Rank within age cat.
Mirabelle	15	1F	0.05	3	Minna	75	3F	1.12	4
Soleil	27	2M	3.00	1	Salémata	170	3F	14.13	2
Dewene	50	3F	8.50	2	Dalaba	170	3F	8.00	5
Toko	27	2M	1.40	1	Thelma	107	3F	1.46	8
Sindia	76	3F	1.33	3	Salémata	170	3F	14.13	2
Didi	39	2F	0.96	1	Dalaba	170	3F	8.00	5
Dagou	51	3F	0.67	5	Dagana	108	3F	5.71	7
Bandiagara	39	2F	0.29	2	Bembou	146	3F	5.80	6
Sabar	27	2M	0.26	2	Sindia	76	3F	1.33	3
Salut	15	1M	0.23	1	Sindia	76	3F	1.33	3
Mango	27	2M	0.13	3	Minna	75	3F	1.12	4
Demba	15	1F	0.04	2	Dewene	50	3F	8.50	2
Mirabelle	15	1F	0.01	3	Minna	75	3F	1.12	4



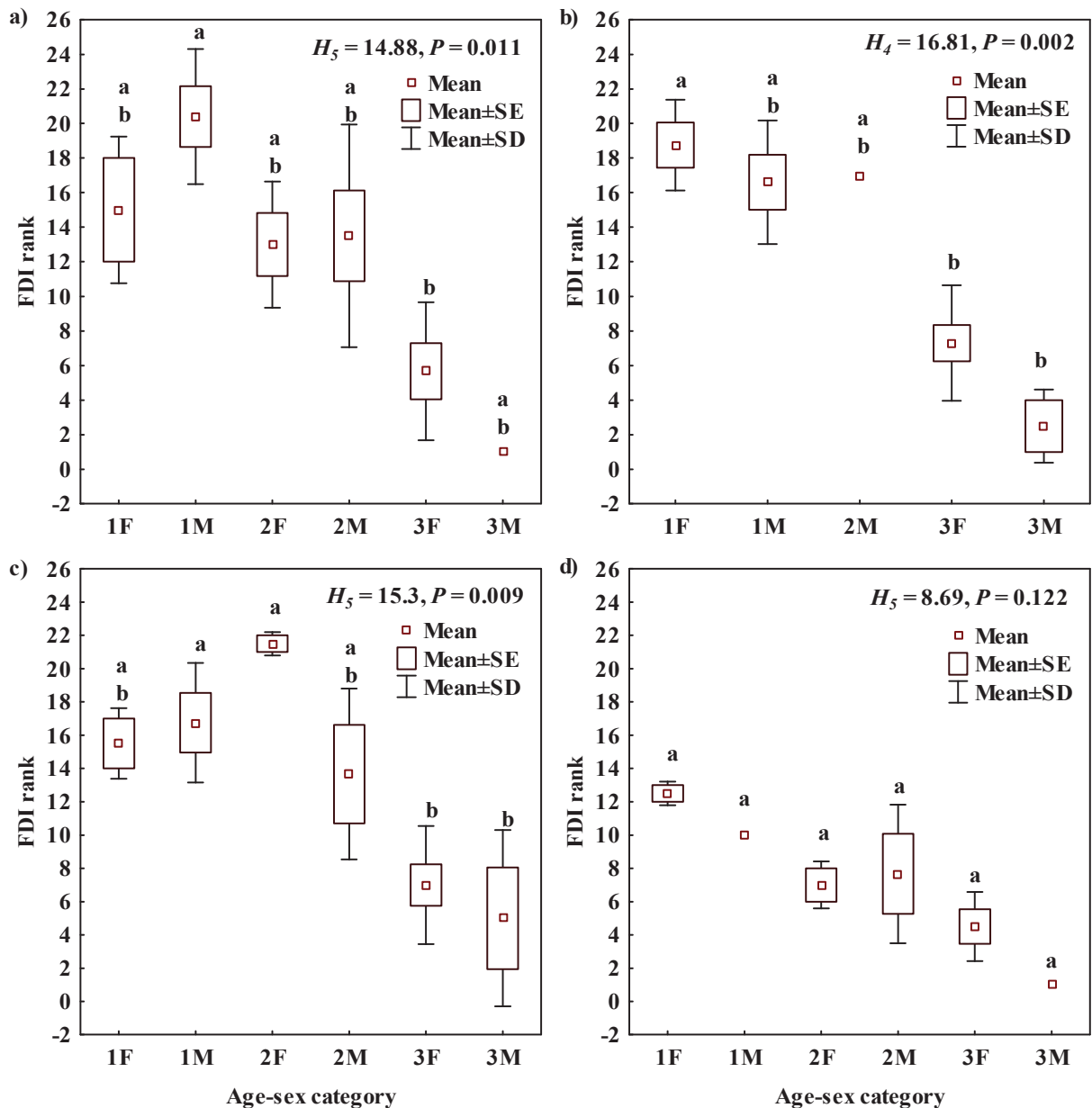
**Figure 1** Relationship between age and FDI rank for all individuals in all years (2006, 2010, and 2011).



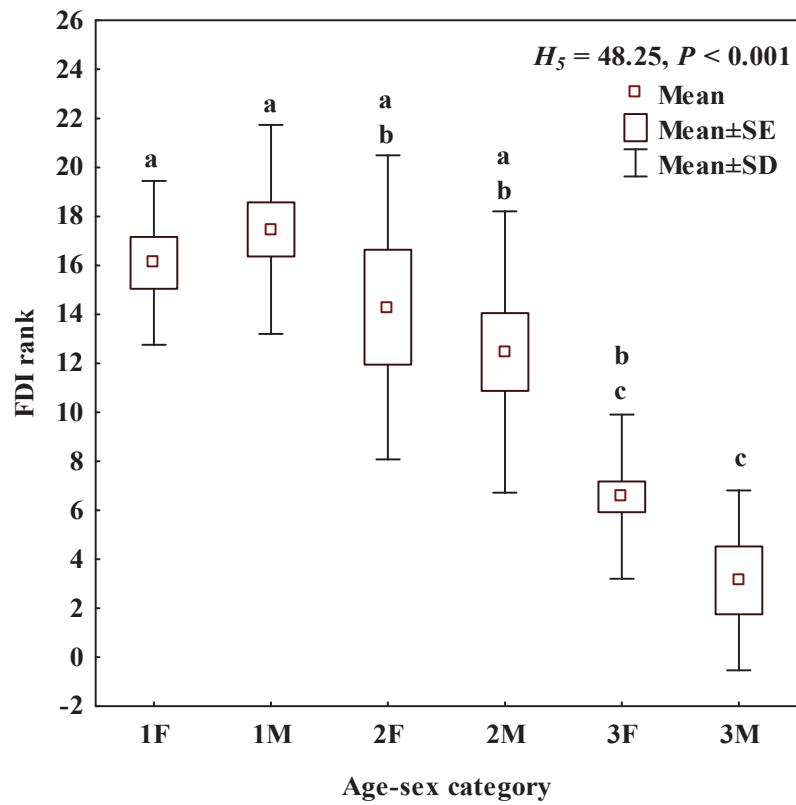
**Figure 2** Effect of age category on FDI rank: a) in the herd 1 in the year 2006, b) in the herd 1 in the year 2010, c) in the herd 1 in the year 2011, and d) in the herd 2 in the year 2011. Different letters indicate significant differences.



**Figure 3** Relationship between age-sex category and FDI rank: a) in the herd 1 in the year 2006, b) in the herd 1 in the year 2010, c) in the herd 1 in the year 2011, and d) in the herd 2 in the year 2011 (1F – females until the age of 18 months, 1M – males until the age of 18 months, 2F – females 19 to 42 months, 2M – males 19 to 42 month, 3F – females older than 43 months, 3M – males older than 43 months). Different letters indicate significant differences.



**Figure 4** Relationship between age-sex category and FDI rank in all years in both herds together (1F – females until age of 18 months, 1M – males until age of 18 months, 2F – females 19 to 42 months old, 2M – males 19 to 42 month old, 3F – females older than 43 months, 3M – males older than 43 months). Different letters indicate significant differences.



## SUPPLEMENTAL DATA

**Table 1** Hierarchical order of Western Derby eland observed in years 2006, 2010 and 2011 in Bandia reserve, Senegal, based on David's score (DS), Clutton-Brock index (CBI) and frequency-based dominance index (FDI) (age category 1: < 18 months, age category 2: of 18 – 42 months, age category 3: > 42 months of age; M – male, F – female)

Year	Name	Age (in months)	Age cat.	Sex	Age-sex cat.	DS	DS rank	CBI	CBI rank	FDI	FDI rank
2006/1	Niokolo	86	3	M	3M	40.00	1	46.00	1	73.00	1
2006/1	Tamba	86	3	F	3F	29.00	3	17.50	2	19.67	2
2006/1	Salémata	110	3	F	3F	35.50	2	11.75	3	12.50	3
2006/1	Bembou	86	3	F	3F	22.50	7	9.67	4	11.50	4
2006/1	Malapa	86	3	F	3F	26.50	5	5.57	6	6.70	5
2006/1	Popenguine	37	2	M	2M	27.50	4	7.80	5	6.09	6
2006/1	Dalaba	110	3	F	3F	24.00	6	3.73	7	3.55	7
2006/1	Karang	34	2	M	2M	2.50	10	2.00	8	2.67	8
2006/1	Dagana	48	3	F	3F	1.00	11	1.15	11	1.23	9
2006/1	Matam	28	2	M	2M	3.50	8.5	1.21	10	1.17	10
2006/1	Fathala	37	2	F	2F	3.50	8.5	1.31	9	1.10	11
2006/1	Minna	15	1	F	1F	-8.00	13	0.43	12	0.43	12
2006/1	Thelma	47	3	F	3F	-16.50	18	0.35	14	0.42	13
2006/1	Tuuti	15	1	M	1M	-13.00	15	0.22	16	0.35	14
2006/1	Ndiogoye	38	2	F	2F	-13.50	16	0.38	13	0.31	15
2006/1	Sokone	28	2	M	2M	-8.50	14	0.27	15	0.21	16
2006/1	Guddi	38	2	F	2F	-17.00	19.5	0.16	17	0.15	17
2006/1	Sindia	16	1	F	1F	-26.50	23	0.09	20	0.10	18
2006/1	Toubab	27	2	M	2M	-19.00	22	0.15	18	0.09	19
2006/1	Doole	14	1	M	1M	-4.50	12	0.14	19	0.08	20
2006/1	Bandia	15	1	M	1M	-15.00	17	0.06	21	0.04	21
2006/1	Bayane	27	2	M	2M	-17.00	19.5	0.05	22	0.03	22
2006/1	Gaaw	14	1	M	1M	-17.50	21	0.04	23	0.03	23
2006/1	Taiba	14	1	M	1M	-40.50	24	0.02	24	0.01	24
2010/1	Niokolo	134	3	M	3M	73.75	2	75.00	1	188.00	1
2010/1	Salémata	158	3	F	3F	105.00	1	22.60	2	28.40	2
2010/1	Tamba	134	3	F	3F	56.50	3	5.62	3	6.03	3
2010/1	Baax	51	3	M	3M	8.00	10	3.78	5	3.73	4
2010/1	Malapa	134	3	F	3F	46.00	6	4.14	4	3.25	5
2010/1	Dalaba	158	3	F	3F	52.75	4	2.91	8	2.73	6
2010/1	Fathala	85	3	F	3F	51.50	5	3.09	7	2.31	7
2010/1	Bembu	134	3	F	3F	42.00	7	3.31	6	2.16	8
2010/1	Dagana	96	3	F	3F	36.75	8	2.80	9	2.11	9
2010/1	Thelma	95	3	F	3F	14.00	9	1.06	10	0.68	10
2010/1	Guddi	86	3	F	3F	-16.00	12	0.43	11	0.37	11

2010/1	Ndiogoye	86	3	F	3F	-34.00	16	0.39	12	0.29	12
2010/1	Soleil	15	1	M	1M	-23.00	14	0.29	14	0.14	13
2010/1	Toko	15	1	M	1M	-42.25	17	0.17	15	0.12	14
2010/1	Dara	15	1	F	1F	-18.00	13	0.14	16.5	0.09	15
2010/1	Teranga	14	1	M	1M	-46.00	18	0.06	18	0.06	16
2010/1	Bonheur	39	2	M	2M	-0.25	11	0.14	16.5	0.05	17
2010/1	Bisaab	15	1	M	1M	-27.00	15	0.33	13	0.03	18
2010/1	Donma	15	1	F	1F	-60.50	20	0.03	19	0.02	19
2010/1	Mbalax	14	1	F	1F	-54.25	19	0.02	20	0.01	20
2010/1	Gaanga	14	1	F	1F	-80.75	22	0.01	21	0.01	21
2010/1	Nanuk	15	1	M	1M	-78.25	21	0.01	22	0.01	22
2011/1	Baax	63	3	M	3M	34.00	3	35.00	1	80.00	1
2011/1	Salémata	170	3	F	3F	39.00	1.5	10.75	2.5	14.13	2
2011/1	Niokolo	146	3	M	3M	6.00	8	7.00	4	14.00	3
2011/1	Fathala	97	3	F	3F	39.00	1.5	10.75	2.5	12.88	4
2011/1	Dalaba	170	3	F	3F	31.00	4	6.17	5	8.00	5
2011/1	Bembou	146	3	F	3F	8.00	6.5	3.00	7	5.80	6
2011/1	Dagana	108	3	F	3F	28.00	5	5.00	6	5.71	7
2011/1	Soleil	27	2	M	2M	1.00	9	2.00	8	3.00	8
2011/1	Thelma	107	3	F	3F	8.00	6.5	1.53	9	1.46	9
2011/1	Guddi	98	3	F	3F	-11.00	14	0.48	12	0.40	10
2011/1	Bonheur	51	3	M	3M	-1.00	10	0.50	10.5	0.33	11
2011/1	Nguekokh	15	1	M	1M	-3.00	11	0.25	13	0.20	12
2011/1	Ndiogoye	98	3	F	3F	-22.00	19	0.18	15	0.14	13
2011/1	Touba	14	1	F	1F	-8.00	12.5	0.50	10.5	0.12	14
2011/1	Teranga	26	2	M	2M	-16.00	16	0.21	14	0.08	15
2011/1	Marabout	15	1	M	1M	-18.00	17	0.09	17	0.06	16
2011/1	Mirabelle	15	1	F	1F	-8.00	12.5	0.11	16	0.05	17
2011/1	Nanuk	27	2	M	2M	-23.00	20.5	0.08	18	0.04	18
2011/1	Bisaab	15	1	M	1M	-12.00	15	0.08	19	0.03	19
2011/1	Fort	15	1	M	1M	-21.00	18	0.05	20	0.02	20
2011/1	Dara	27	2	F	2F	-26.00	22	0.04	22	0.01	21
2011/1	Gaanga	26	2	F	2F	-23.00	20.5	0.04	21	0.01	22
2011/2	Toubab	87	3	M	3M	61.89	1	17.75	1	17.50	1
2011/2	Dewene	50	3	F	3F	44.11	2	7.56	2	8.50	2
2011/2	Toko	27	2	M	2M	25.68	3	2.04	3	1.40	3
2011/2	Sindia	76	3	F	3F	22.17	4	1.82	4	1.33	4
2011/2	Minna	75	3	F	3F	12.29	5	1.45	5	1.12	5
2011/2	Didi	39	2	F	2F	1.48	6	1.27	6	0.96	6
2011/2	Dagou	51	3	F	3F	-8.00	7	0.61	7	0.67	7
2011/2	Bandiagara	39	2	F	2F	-21.20	10	0.39	8	0.29	8
2011/2	Sabar	27	2	M	2M	-16.40	9	0.38	9	0.26	9
2011/2	Salut	15	1	M	1M	-29.13	11	0.22	11	0.23	10
2011/2	Mango	27	2	M	2M	-15.79	8	0.29	10	0.13	11
2011/2	Demba	15	1	F	1F	-31.90	12	0.10	12	0.04	12
2011/2	Mirabelle	15	1	F	1F	-41.78	13	0.02	13	0.01	13

#### 4.4. SUCKLING BEHAVIOUR OF ELAND ANTELOPES (*TAUROTRAGUS SPP.*) UNDER SEMI-CAPTIVE AND FARM CONDITIONS

Hejzmanová P., Vymyslická P., Koláčková K., Antonínová M., Havlíková B, Stejskalová M., Policht R., Hejzman M. 2011. Suckling behaviour of eland antelopes (*Taurotragus spp.*) under semi-captive and farm conditions. *Journal of Ethology*, 29, 161-168.



Photo by Tom Junek



## Suckling behavior of eland antelopes (*Taurotragus* spp.) under semi-captive and farm conditions

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**Abstract** Mother–offspring interactions soon after parturition play a key role in the survival of mammals. We investigated the suckling behavior of semi-captive Western Derby eland (*Taurotragus derbianus derbianus*) in a 60-ha enclosure covered by dense savanna vegetation in Senegal and farmed Common eland (*T. oryx*) on an open 2-ha pasture in the Czech Republic. We hypothesized that the basic pattern of suckling bout duration and mother–offspring interactions would be similar between species, but would vary in response to the environmental conditions and breeding system. During three calving periods, we observed the suckling of 27 and 23 calves of Derby and Common elands, respectively, between the ages of 1–5 months, and the interactions between mother and calf before and during suckling. Suckling bout duration increased with the age of the calves for both elands. However, in Derby elands we recorded longer suckling

bouts in male than female calves and shorter suckling bouts in primiparous mothers than multiparous ones; no differences were found in farmed Common elands. The animals' active approach to mother–offspring contact, for example naso–anal contact, and initiation and termination of suckling, resulted in longer suckling bouts in Derby elands. The results suggest that Derby elands that range over a large enclosure with dense vegetation cover adjust their maternal behavior in compliance with potential predator risk, facing a trade-off between nursing and vigilant behavior in the wild. The suckling behavior of farmed elands, on the other hand, reflects the conditions of captivity without predators and with the small available area enabling permanent visual contact of animals.

**Keywords** *Taurotragus* spp. · Antelope · Mother–offspring interaction · Maternal care · Breeding management · Trade-off

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### Introduction

Mother–offspring interactions soon after parturition play a key role in the survival of mammals. Maternal behavior in ungulates, manifested particularly during suckling, is generally intensive after birth and declines with the age of the calves (Rubin and Michelson 1994; Sarno and Franklin 1999; Cassinello 2001). In ungulate species, multiparous and older mothers generally display a higher level of maternal care than primiparous or younger ones, and this is because of their greater level of experience (Ozoga and Verme 1986; Green 1990; Cameron et al. 2000) or is the effect of residual reproductive value (Clutton-Brock 1991). On the other hand, because ungulates are highly susceptible to predation during the initial weeks and months of life,

their mother–offspring interactions are variable within and across species and reflect the strategy adopted in the trade-off between nursing and vigilance (Rachlow and Bowyer 1998; Toïgo 1999; Hamel and Côté 2008). The protection of offspring and the resulting anti-predator behavior is one of the most conspicuous features of maternal care. Besides the general “follower” and “hider” strategies (Lent 1974; Leuthold 1977; Ralls et al. 1986), mothers naturally adopt an anti-predator pattern that is specific for the conditions and environment they experience (Braza et al. 2000; White and Berger 2001; Ciuti et al. 2006). In ungulate hider species, mothers may move directly towards neonates at very close distance or they may use other maternal behavioral tactics to stay at a distance of several meters and wait for the calf to approach (Hnida 1985; Thompson 1996; Wronski et al. 2006). Maternal females do trade off between the distance from a hiding place and the detectability of the offspring and thereby balance the risk of neonate predation (Byers and Byers 1983; Bongi et al. 2008; Panzacchi et al. 2009). The success of the adopted anti-predator strategy is thus inevitably related to the type of habitat (Jarnemo 2004; Bongi et al. 2008).

Mechanisms acting in maternal care appear conservative among and within species but, despite this, wild and captive populations may exhibit different attitudes in the care of their offspring. In the wild, vigilance against predators brings constraints to females with offspring in terms of the time devoted to foraging (Bowyer et al. 1999) and satisfying the higher nutritional requirements arising from energetically costly lactation (Oftedal 1985). Consequently, the time intended for maternal care is highly limited and females facing these constraints may allocate energy to their own maintenance and/or survival and postpone reproductive success (Festa-Bianchet and Jorgenson 1998; Gaillard et al. 2000; Therrien et al. 2007). Captivity, which offers an environment without predators, may have a crucial impact on maternal expenditure and nursing behavior. Indeed, the permanent availability of food resources may increase reproductive success (Andersen et al. 2000). The small area and the lack of predators enable more frequent visual contact between the mother and her offspring and, consequently, a different approach to a hidden calf, the reuse of hiding places (Murdock et al. 1983; Thompson 1996), or a higher suckling rate (Manski 1991; Rubin and Michelson 1994). However, both in captivity and in the wild the mothers contact the offspring before and during suckling for mutual identification to prevent the loss of invested energy, for instance by allosuckling (Roulin 2002; Zapata et al. 2009).

In this study, we investigated the suckling behavior of two species of eland antelopes bred under different conditions (semi-captive extensive ranch and intensive farm

system). The Derby eland (*Taurotragus derbianus*) and Common eland (*Taurotragus oryx*) are sister-species within the monophyletic lineage of African spiral-horned antelopes, Tragelaphinae (Rubeš et al. 2008); are large body-sized, gregarious, polygynous species that inhabit African woody savanna (Kingdon 1982; Estes 1992; Pappas 2002; Nežerková et al. 2004). They display identical auditory, visual, and defense traits in vigilance and anti-predator behavior (Caro et al. 2004) and have similar foraging habits (Wallington et al. 2007 for Common eland; Hejzmanová et al. 2010b for Derby eland). They may, however, display differences in their maternal behavior, related to species, their different “life history”, and environment, which may be critical either for breeding and/or conservation success.

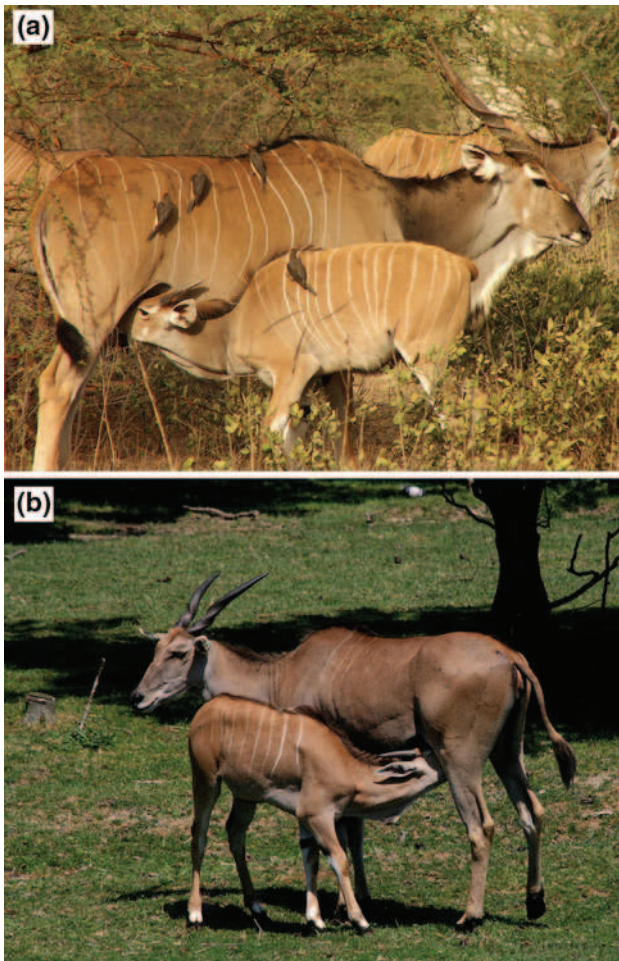
The objectives of this study were to fill the gap in the understanding of mother–offspring interactions. We describe the suckling behavior of the semi-captive Western Derby eland (*T. d. derbianus*) in a 60-ha conservation breeding enclosure along with that of tame and farmed Common elands. We used suckling bout duration as it represents an integral part of maternal effort to raising offspring and may also indicate offspring growth and survival (Cassinello 1996; Sarno and Franklin 1999; Therrien et al. 2008). Because of the critically endangered status of the Western subspecies of Derby elands (IUCN 2010), we were not allowed to manipulate animals for weighing. However, despite the restricted access to the enclosure and the dense vegetation cover, we were able to observe the rarely recorded behavior of suckling.

We examined whether the two species of elands differ in their basic suckling pattern, via the suckling bout duration. We predicted that the antelope calves would have longer suckling bouts after birth and that these would become shorter with age, and that multiparous mothers would have longer suckling bouts than primiparous ones. We predicted that the mother–offspring contact interaction before and during suckling would differ between species, as a response to the different breeding systems and the environment, namely vegetation cover.

## Material and methods

### Study area, breeding management, and investigated animals

The study was performed on the Western subspecies of Derby eland (*Taurotragus derbianus* GRAY 1847) and Common eland (*Taurotragus oryx* PALLAS 1766) (Fig. 1), which are related antelope species (Rubeš et al. 2008) but were handled under different breeding-management systems.



**Fig. 1** Mother–offspring pair while suckling: **a** Western Derby eland in the conservation breeding enclosure in the Bandia Reserve, Senegal (photo by M. Stejskalová); **b** Common eland at the University Farm Lány, Czech Republic (photo by B. Havlíková)

A herd of 36 Western Derby elands (8 males, 20 females, and 8 calves) was bred in a 60-ha enclosure in the Bandia Reserve, a nature wildlife reserve in Senegal (Antonínová et al. 2008). The breeding enclosure was covered by natural Sahelian savanna vegetation with a high density of woody species (Hejčmanová et al. 2010a). During the wet season, the natural vegetation was sufficient to satisfy the animals' feeding requirements. During the dry season, the antelopes were offered a food supplement daily at an open-air feeding-place; hence the animals had contact with a keeper during this period. The animals' movements and reproduction were allowed to be as close to the conditions in the wild as possible. The investigated Derby eland females were wild born and the first generation born in the Bandia Reserve. The data were collected over three calving seasons, between December 2005 and March 2006, between February and March 2007, and in December 2007 and April 2008. A total of 27 calves was observed suckling

between the ages of 1–5 months from a total of ten females, all of which reproduced repeatedly.

A herd of 36 Common elands was bred at the University Farm Lány (Czech Republic), in an enclosed stable and an open pasture of approx. 2 ha. The stable and pasture were divided into two separate parts, one for 19 adult and sub-adult males and the other for seven suckling females and their seven calves and three females without calves. The animals were regularly fed with alfalfa hay and fodder concentrate and had ad libitum access to pasture. The animals were in daily contact with a keeper and were tame. Reproduction and parturition were synchronized by farm management. The investigated animals were descendants of elands that had been bred in the Dvůr Králové Zoo for at least eight generations. Suckling was observed during three calving periods, between June and September 2005, between March and September 2007, and between February and May 2008. A total of 23 calves aged 1–5 months were observed suckling from a total of 11 females, eight of which reproduced repeatedly.

#### Behavioral observation and definition

We observed Derby elands between 0800 hours and 1900 hours when a hidden calf was found or a herd with calves was detected. The focal animal observations were not continuous because of the dense vegetation cover and the animals' frequent movements over the enclosure. Animals were individually recognized on the basis of the unique morphological characteristics of each animal (Antonínová et al. 2008) at a distance of 20–40 m, according to actual visibility in the savanna vegetation. We observed animals from birth up to the age of 5 months. At the farm, Common elands were observed regularly from 0800 hours to 1900 hours once a week from the birth of the first calf in the herd up to the age of 5 months. Animals were tagged for individual recognition and observed in the stable or at pasture at a distance of 5–40 m.

We observed animals directly and used binoculars when necessary. We measured suckling duration using a stopwatch. We collected data using an ad libitum sampling method (Altmann 1974). Each observation was carried out to cover most of the suckling that occurred in the herd during the observation session. We considered a suckling bout to occur when a calf took a teat in its mouth for at least 5 s. During observation, we recorded the suckling behavior, including mother–offspring naso–anal contact, the initiator and terminator of the suckling event, and the duration of the suckling bout. We recorded individual information about the age of the mother and calf, the sex of the calf, and mother parity. We collected data from a total of 123 and 328 suckling bouts in Derby and Common elands, respectively.



## Statistical analyses

Statistical analyses were performed using the Statistica 8.0 package (StatSoft, Tulsa, USA). The data were not normally distributed, and we therefore used non-parametric Mann–Whitney  $U$  tests and Kruskal–Wallis ANOVA to test the effects of calf sex (male/female), calf age (in months), parity (primiparous, multiparous), naso–anal contact (yes/no), and the initiator and terminator of the suckling event (mother/calf) on suckling bout duration separately in both species. Multiple comparisons were performed where there were more than two levels of the variable. Data for different calves from the same mother were considered as independent units (Cassinello 2001).

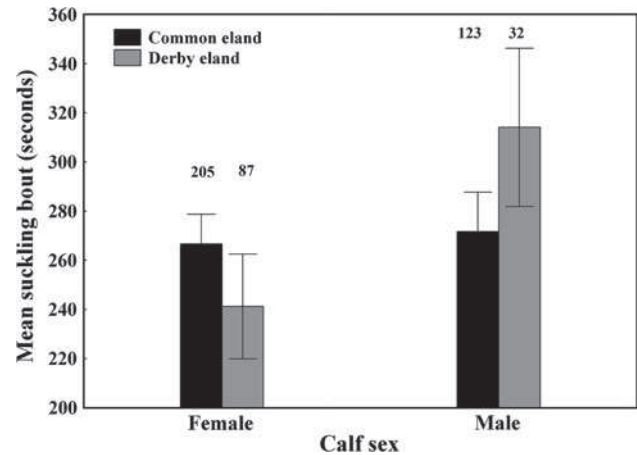
## Results

There was no difference in the average suckling bout duration of Derby elands (mean = 260.8 s, SE = 17.9 s,  $n = 119$ ) and that of Common eland calves (mean 268.5 s, SE = 9.6 s,  $n = 328$ ) (Mann–Whitney test,  $U = 19062$ ,  $P = 0.706$ ).

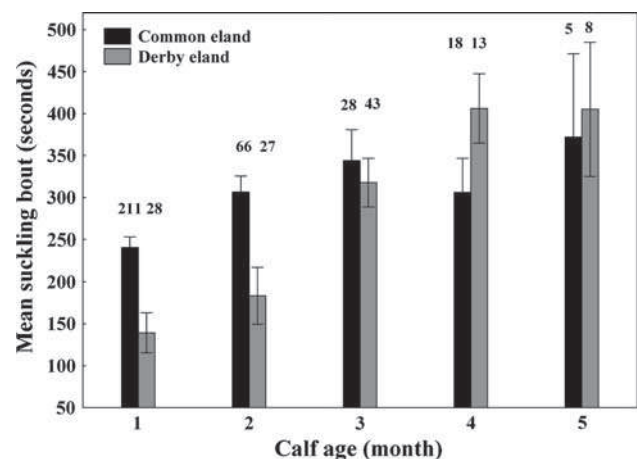
The male calves of the Derby elands on average suckled significantly longer (mean = 314.1 s, SE = 32.2,  $n = 32$ ) than female calves (mean = 241.2 s, SE = 21.3 s,  $n = 87$ ) (Mann–Whitney test,  $U = 1042.5$ ,  $P = 0.036$ ), whereas no difference was found between the average suckling bout of male (mean = 271.6 s, SE = 16 s,  $n = 123$ ) and female (mean = 266.6 s, SE = 12.1 s,  $n = 205$ ) calves of Common elands (Mann–Whitney test,  $U = 12515$ ,  $P = 0.91$ ; Fig. 2). The suckling duration increased continuously up to the age of 3 months (Fig. 3), and then remained constant (Kruskal–Wallis test,  $H_{(4,119)} = 28.52$ ,  $P < 0.001$ ) in the Derby eland calves. The Common eland calves showed the same increasing trend of average suckling bout in relation to age (Kruskal–Wallis test,  $H_{(4,328)} = 16.81$ ,  $P = 0.002$ ). However, in comparison with Derby eland calves they suckled significantly longer at the age of 1 and 2 months (1 month: Mann–Whitney test,  $U = 1979$ ,  $P = 0.004$ ; 2 months: Mann–Whitney test,  $U = 547$ ,  $P = 0.004$ ) and there was no difference at 3 months of age (Mann–Whitney test,  $U = 552$ ,  $P = 0.55$ ).

The effect of parity on the length of suckling bouts differed between the two elands. Whereas the average duration of a suckling bout was significantly higher in multiparous mothers in Derby eland (Mann–Whitney test,  $U = 526$ ,  $P = 0.02$ ), there was no difference in Common eland (Mann–Whitney test,  $U = 9286$ ,  $P = 0.52$ ; Fig. 4).

The duration of suckling was affected by the first mother–calf contact and their mutual interaction. Before suckling, the mother made naso–anal contact with the calf

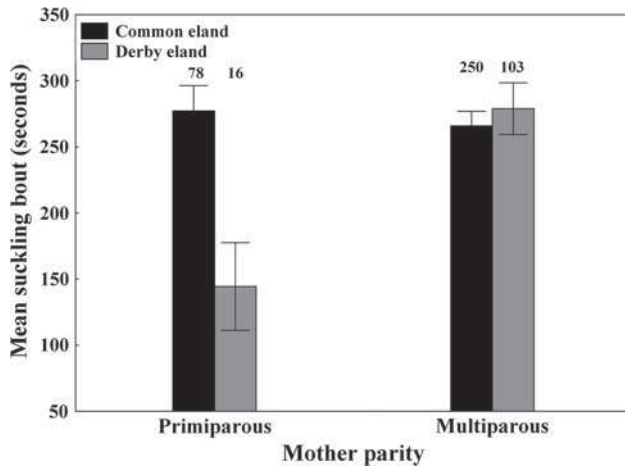


**Fig. 2** Mean suckling bout duration of male and female calves of farmed Common and free ranging Derby eland. Error bars indicate SE; numbers above bars represent sample sizes



**Fig. 3** The effect of calf age on mean suckling bout duration of farmed Common and free ranging Derby eland calves. Error bars indicate SE; numbers above bars represent sample sizes

in 40% of cases in Derby eland and in 52% of cases in Common eland. In such cases, the average suckling bout duration was significantly higher than in cases in which naso–anal contact did not occur in both species (Derby eland: Mann–Whitney test,  $U = 620$ ,  $P = 0.036$ ; Common eland: Mann–Whitney test,  $U = 11081.5$ ,  $P = 0.02$ ; Fig. 5a). Although in most cases (93% in Derby eland and 62% in Common eland) suckling was initiated by the calf, the average suckling bout was longer when suckling was initiated by the mother, significantly so in Derby eland (Mann–Whitney test,  $U = 97.5$ ,  $P = 0.017$ ) and non-significantly in Common eland (Mann–Whitney test,  $U = 11239$ ,  $P = 0.08$ ; Fig. 5b). Suckling was terminated by the mothers in 95 and 65% of cases in Derby and Common eland, respectively, and was shorter than in cases in which suckling was terminated by the calf (Derby eland: Mann–Whitney test,  $U = 40.5$ ,  $P = 0.096$ ;



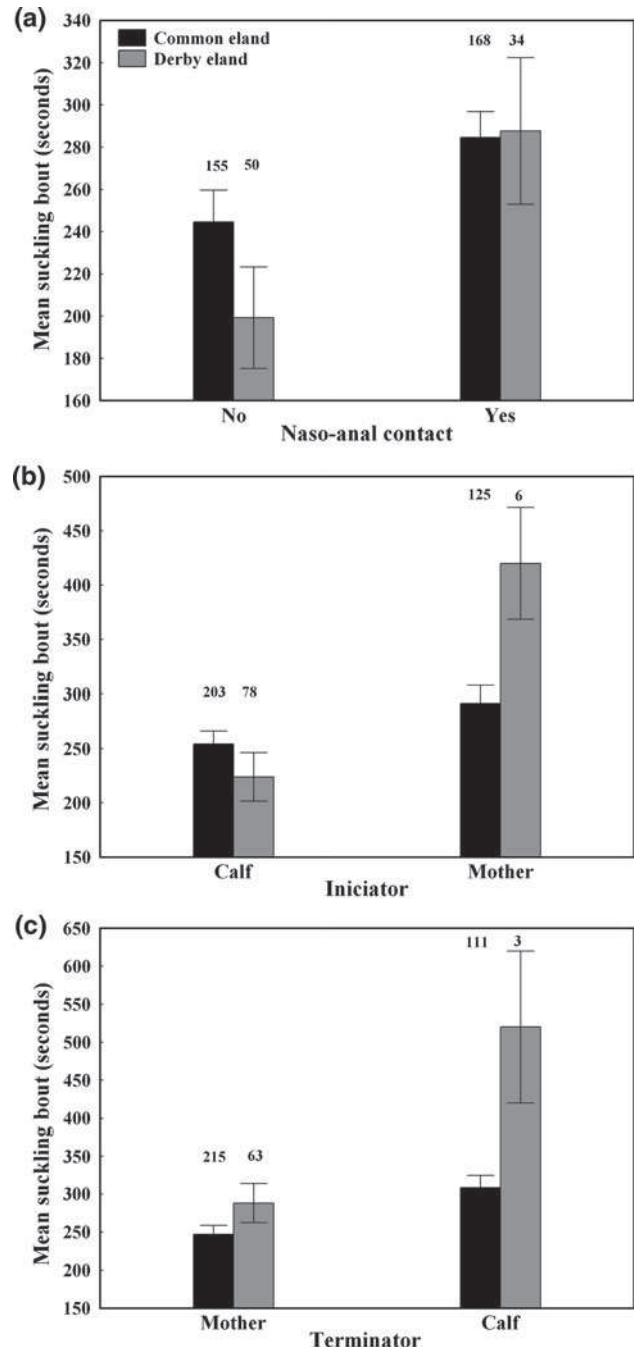
**Fig. 4** Mean suckling bout duration of farmed Common and free ranging Derby eland from primiparous and multiparous mothers. Error bars indicate SE; numbers above bars represent sample sizes

Common eland: Mann–Whitney test,  $U = 9358$ ,  $P = 0.001$ ; Fig. 5c).

**Discussion**

The general suckling pattern for the two elands appears similar in terms of the average suckling duration and the increasing trend as the calves grow, reflecting the fact that animals have increasing nutritional requirements in concordance with their growth (Robbins et al. 1981). The time spent suckling, however, generally declines at the end of the first month of life when physiological weaning occurs (Sarno and Franklin 1999; Cassinello 2001; Therrien et al. 2008). The increasing duration of suckling bouts of elands probably reflected a decrease in the suckling rate (Manski 1991). For Derby elands ranging in a large enclosure with dense vegetation, the suckling bouts during the first 2 months of life were shorter, probably because of the short contact between mother and offspring as a tactic to reduce predator risk (Bongi et al. 2008). The farm breeding system that lacked predators and had a restricted area, on the other hand, offers animals an opportunity to monitor the surrounding area and to nurse without restrictions.

Another aspect in which semi free-ranging and farmed elands demonstrated differences concerns the sex of the calves. In Derby elands male calves suckled for longer than female calves, which may suggest sex-biased maternal care (Clutton-Brock 1991). However, we consider the difference to be due primarily to the higher physiological energy requirement to support the higher growth rate of male calves (Verme 1989; Green and Rothstein 1991). This might not be manifested under farm conditions where mothers may have more milk available for their offspring



**Fig. 5** Mean suckling bout duration of farmed Common and free ranging Derby eland: **a** the effect of naso–anal contact before suckling; **b** the effect of the initiator of suckling; **c** the effect of the terminator of suckling. Error bars indicate SE; numbers above bars represent sample sizes

(Manski 1991) or milk of higher quality (Wilson and Hirst 1977; Rognmo et al. 1983), or where calves may have a higher suckling rate and thus balance their requirements better.

We predicted longer suckling bouts in multiparous mothers. Our results on the effect of parity support this

hypothesis for semi-captive Derby elands, while parity had no effect on suckling duration in farmed Common elands. Experience improves the targeting of females' investment in raising offspring (Cameron et al. 2000) and helps mothers to cope better with vigilant versus nursing behavior trade-offs (Kohlmann et al. 1996). Like other ungulate species (Lent 1974), elands separate from the herd for parturition and the first few days of nursing in order to increase the protection of the neonate against predators. Primiparous mothers may delay nursing (Nowak et al. 2000) and linger more vigilantly in dense vegetation. Farm conditions, on the other hand, offer permanent visual contact with other female herd members and primiparous mothers may therefore acquire more experience. Females in captivity may also have more milk or simply cannot escape from calves that are demanding more milk (Manski 1991). Although our results contrast with the findings of Andersen et al. (2000), who observed no effect of parity on maternal care in a free-ranging roe deer population and a higher level of maternal care by multiparous mothers in a captive population, we consider this to be because of the different measure of maternal behavior and the incompatible environmental conditions.

Naso–anal contact between the mother and calf before suckling plays an essential role in mother–calf recognition (Lent 1974; Wronski et al. 2006). When such contact occurred, the suckling bout was longer in both elands. This indicates that identification of own calf is conservative across species and is purposeful not only in the wild, but also in captivity. Naso–anal contact contributes to mother–offspring bonding (Cowan 1974; Nowak et al. 2000), which is essential for the survival of the calf independently from the environmental conditions. In addition, non-filial suckling, which could jeopardize individual reproductive success and increase maternal costs, occurs in many ungulate species under both wild and farm conditions (Packer et al. 1992; Ekvall 1998; Pélabon et al. 1998; Víchová and Bartoš 2005; Drábková et al. 2008).

The effect of an active approach of the mother or calf to suckling seemed phenotypically plastic. Indeed, both the initiation and termination of suckling are likely to be “life-history-dependent” and “environment-dependent” and thus vary between semi-captive and farmed elands. Although calves initiated suckling in most cases, the mothers generally dictated how long the calves could nurse and generally terminated the bouts, as reported previously by Rubin and Michelson (1994) and Wronski et al. (2006). The longer suckling duration of Derby eland calves when the mother initiated the suckling and the decision about termination of suckling was left to the calf could be explained by the positive motivation of the mother to allow suckling, for instance because of the physiological need to deplete the milk from the udder, or by the active approach of the mother

to a low predator-risk situation. On the other hand, tamed elands under farm conditions did not show any differences in the initiation and termination of suckling, probably because of their non-functional or modified anti-predator behavior (Blumstein and Daniel 2005). These results indicate that, despite the crucial importance of anti-predator behavior to animal survival, living in an environment without predators such as that offered by farm conditions for several generations may cause a reduction in vigilant behavior. Indeed, maintaining vigilant behavior in conditions without predators is costly (Magurran 1999). Such a reduction enables females to adjust their suckling behavior to be more effective for higher reproductive success or may give calves the opportunity to receive higher levels of maternal care than could be obtained in the wild.

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## 5. CONCLUSIONS AND RECOMMENDATIONS

We can conclude that general behaviour patterns of investigated antelopes do not markedly differ from similar large herbivore species, both in the wild and in the space limited by fence, and it is possible to use the experience from these species for the management and conservation implications.

The value of our results on activity pattern should be considered from two, actually contradictory, points of view. First, conservation managers should be aware of possible changes in animal behaviour due to management decisions, and imposing new conditions on animals. If new conditions last for a certain period, the animals may take advantage of behavioural plasticity but, on the other hand, this long-term adaptation may lead to unpredictable behavioural changes, decreasing the animals' natural fitness, which is important for eventual reintroduction or reinforcement in the wild (McDougall *et al.* 2006). Food supplementation should play a role mainly during unfavourable conditions of scarce natural forage availability, in order to surmount such critical periods (Elliot *et al.* 2001), and should be avoided in the opposite situation. Secondly, food supplementation may be used as a key managerial element in conservation activities. For instance, favourable feeding conditions may enhance investment in reproduction, and translate into higher breeding success (Schoech *et al.* 2008), although the genetic variability should be highlighted, particularly in small populations (Bretagnolle *et al.* 2004; López-Bao *et al.* 2010). Or, food supplementation may become a tool to alleviate post-release stress after animals are transported (Teixeira *et al.* 2007), since the animals devote more time to resting.

The social behaviour is mostly influenced by age, although at some age level the effect of age on social rank decreases and body mass becomes the more important factor. Proper knowledge of dominance hierarchies in populations of conservation concern can play crucial role in management decisions. Transfer of animals or medical treatment can be provided without using financially and organizationally demanding anaesthesia that requires capable and well coordinated team of several people and expensive narcotics and pharmaceuticals. Cheaper option is usage of social hierarchy knowledge, through which particular individuals can be separated from the herd, orally treated with medicaments or even transferred. This possibility was already applied in Western Derby eland, when selected individuals were

separated from other group members and were relocated to an enclosure using just preferred supplemental food, thus it can be applicable in similar conditions to other ungulate species.

Results of suckling behaviour of eland antelopes indicate that living for several generations under managed condition where presence of predators is prevented could lead in a reduction of anti-predator behaviour. In contrary loosing vigilant behaviour, in conditions where it is not needed, can bring higher productivity or higher reproductive success which is one of goals of conservation programmes. However increased reproductive success caused by loss of anti-predator behaviour makes difficult or can even disallow the reintroduction in the wild. Balanced management considering all needs for maintaining as natural behaviour as possible together with possibility of application of management measures is necessary.

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