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**The influence of genealogical characteristics
on Derby elands' striping**

Bachelor Thesis

Prague 2016

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Declaration

I hereby declare that this bachelor thesis entitled The influence of genealogical characteristics on Derby elands' striping is my own work and all the sources have been quoted and acknowledged by means of complete references.

In Prague, 15th April 2016

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Acknowledgement

I want to express my sincere thanks to my supervisor Ing. Karolína Brandlová, Ph.D. and consultant Ing. Pavla Jůnková Vymyslická, Ph.D. for their guidance and patience during the writing of my bachelor thesis and also for providing me with materials and photographs which I used for my analyses.

My gratitude also belongs to my parents for their moral and financial support during my studies and to my sister Kateřina who has always shared her great knowledge and experience with me.

Abstract

Animal coloration reflects evolutionary adaptations of species to their habitat or protection against parasites and predators, and represents an ideal tool for studying evolutionary changes generating intraspecific and interspecific differences. Derby eland (*Taurotragus derbianus*) is an even-toed ungulate with a small range in Central and Western Africa and is divided into two subspecies. The western subspecies (*Taurotragus derbianus derbianus*) is classified by IUCN Red List as “critically endangered” and its population consists of about 200 wild individuals living only in the Niokolo-Koba National Park and cca 100 individuals in human care in Bandia and Fathala Reserves in Senegal. The eastern subspecies (*Taurotragus derbianus gigas*) with the population of 15–20 000 animals in the wild and cca 50 individuals in captivity is considered as “least concern”. However, the small populations of the Derby elands kept in human care face a high risk of decrease in genetic variability.

The main aim of this thesis was to determine with help of the studbook and photographs of both Derby eland subspecies, whether breeding management and possibly some rapid evolutionary changes in genotypes of individuals can cause also changes in their phenotypic characteristics, specifically in number of stripes on body flanks. We were interested in the influence of pedigree data (mainly coefficient of inbreeding) on striping in western subspecies, if individuals of eastern subspecies in the wild differ in number of stripes from those in human care, and in the end we wanted to find a difference in number of stripes between both subspecies living in the wild. The analyses confirmed our hypotheses that the number of stripes in the population of Western Derby eland in human care increases with level of inbreeding, and also that the populations of eastern subspecies from human care have more stripes than the wild populations. The results also confirmed that the wild individuals of western subspecies have more stripes compared to those of eastern subspecies. We could explain the changes in striping by genetic drift, founder effect or for example by sexual selection. However, without a detailed knowledge of genealogy and analyses with more generations we cannot even exclude the possibility, that all the significant correlations in our studied samples were generated only by chance.

Key words: Derby eland, striping, coloration, genealogy, ungulates

Abstrakt

Zbarvení živočichů odráží evoluční adaptace druhů na daný typ jejich habitatu či na ochranu před parazity a predátory, a představuje ideální nástroj pro zkoumání vývojových změn generujících vnitrodruhové i mezidruhové rozdíly. Antilopa Derbyho (*Taurotragus derbianus*) je sudokopytník s malým areálem rozšíření ve střední a západní Africe rozlišovaný do dvou poddruhů. Západní poddruh (*Taurotragus derbianus derbianus*) je na Červeném seznamu IUCN klasifikován jako „kriticky ohrožený“ a jeho populace ve volné přírodě čítá kolem 200 jedinců žijících pouze v Národním parku Niokolo-Koba a cca 100 jedinců v lidské péči v rezervacích Bandia a Fathala v Senegal. Východní poddruh (*Taurotragus derbianus gigas*) je naproti tomu s populací 15 - 20 000 zvířat ve volné přírodě a cca 50 jedinci v lidské péči považován za „málo dotčený“. Malé populace antilop Derbyho v lidské péči jsou však dlouhodobě vystaveny vysokému riziku poklesu genetické variability.

Hlavním cílem této práce tedy bylo s pomocí plemenné knihy a fotografií obou poddruhů antilopy Derbyho zjistit, zdali způsob managementu a s ním související možné rychlé evoluční změny v genotypu jedinců mohou mít za následek také změny jejich fenotypových vlastností, konkrétně pak počtu pruhů na bocích těla. Zajímalo nás vliv rodokmenových hodnot (především koeficientu inbreeding) na pruhování u západního poddruhu, zda se u východního poddruhu v počtu pruhů liší jedinci ve volné přírodě a ti v lidské péči, a nakonec rozdíl v počtu pruhů mezi oběma poddruhy žijícími ve volné přírodě. Analýzy potvrdily naše předpoklady, že počet pruhů u populace západního poddruhu antilopy Derbyho v lidské péči stoupá se stupněm jejího inbreeding a že populace východního poddruhu v lidské péči mají větší počet pruhů nežli populace ve volné přírodě. Výsledky také potvrdily, že divoce žijící jedinci západního poddruhu mají v porovnání s jedinci východního poddruhu pruhů více. Vysvětlením změn v pruhování může být genetický drift, efekt zakladatele či například pohlavní výběr. Bez podrobných znalostí původu zvířat a analýz na větším množství generací však nelze vyloučit ani možnost, že zjištěné vztahy byly v našem zkoumaném vzorku vygenerovány vlivem pouhé náhody.

Klíčová slova: Antilopa Derbyho, pruhování, zbarvení, rodokmen, kopytníci

Content

1 Introduction	1
2 Literature review.....	3
2.1 Genesis and alteration of coloration and color patterns in mammals.....	3
2.1.1 Genes and color pigments	3
2.1.2 Mechanisms of (micro)evolution	5
2.2 Coat colors and patterns in ungulates	14
2.3 Derby eland (<i>Taurotragus derbianus</i>).....	16
2.3.1 Western Derby eland (<i>Taurotragus derbianus derbianus</i>)	18
2.3.2 Eastern Giant eland (<i>Taurotragus derbianus gigas</i>)	21
3 Aims of the Thesis	23
4 Materials and Methods	24
4.1 Animal data collection.....	24
4.3 Data analysis.....	24
5 Results	26
6 Discussion.....	29
7 Conclusion.....	33
8 References	34

List of figures

Figure 1. Characteristics of stripes in Derby eland: a – pre-stripe, b – stripe with arc, c – split on the back, d – split on the belly, e – fork on the back, f – fork on the belly, g – arc on the back.

Figure 2. Western Derby elands (*Taurotragus derbianus derbianus*)

Figure 3. An Eastern Giant eland (*Taurotragus derbianus gigas*) killed for trophy hunting

Figure 4. An example of Western Derby eland's identification card

List of graphs

Graph 1. Correlation between the coefficient of inbreeding (F) and the number of stripes on the right flank in Western Derby eland.

Graph 2. Comparison of the average number of stripes on the flank of Eastern Giant eland living in human care and living in the wild.

Graph 3. Comparison of eastern and western subspecies of Derby eland from the wild in the average number of stripes on the flank.

List of the contractions used in the thesis

WDE - Western Derby Eland

EGE - Eastern Giant Eland

NKNP - Niokolo-Koba National Park

ASIP - Agouti Signaling Protein

IUCN - The International Union for Conservation of Nature

Mc1r - Melanocortin-1 receptor

α MSH - α - Melanocyte Stimulating Hormone

cAMP - Cyclic Adenosine Monophosphate

ZIMS - The Zoological Information Management System

SPEFS - Society for Protection of Environment and Wildlife in Senegal

1 Introduction

The study of animal pigmentation has had an excellent opportunity to gain a detailed understanding of the mechanisms of phenotypic evolution from genetics to development and physiology through behavior and adaptation (Hoekstra, 2006). Pigment patterns represent an ideal system which helps identify individuals and understand the way how developmental changes generate differences in form both within and between species (Mills and Patterson, 2009). During evolution, organisms have always been influenced by biotic and abiotic changes in their environment, which have led them to avoid or adapt *in situ* conditions to avoid extinction (Zimova *et al.*, 2016).

In captive populations, the evolutionary changes may be an important but poorly understood factor that can affect their sustainability. An intensive management of threatened species and preserving high level of genetic diversity is an essential goal, especially for small populations that are sources for translocation or re-introduction programmes (Frankham, 2008). There is a high risk of inbreeding depression that universally appears to reduce fitness. However, the magnitude and specific effects show a high variability and depend both on the genetic constitution of the species or populations and on how the genotypes interact with the environment (Hedrick and Kalinowski, 2000). Therefore, breeding programmes should be usually based on knowledge of an individual registered in studbooks (Glatson, 1986) and on pedigree analyses (Ralls and Ballou, 2004).

Derby eland (*Taurotragus derbianus*), an antelope occurring in relatively small and isolated range in central and western Africa (Zemanová *et al.*, 2015), has been divided into two subspecies, the Western Derby eland (*Taurotragus derbianus derbianus*) (Gray, 1847) and the Eastern Giant eland (*Taurotragus derbianus gigas*) (Heuglin, 1863). The western subspecies has been classified as “critically endangered” (IUCN, 2015) and its only natural range is in the Niokolo-Koba National Park in Senegal with less than 200 wild elands (Renaud *et al.*, 2006). To avoid its extinction, two semi-captive herds with 6 founders have been established in Senegal for conservation purposes. On the other hand, the eastern subspecies has been classified as “least concern” and we can still find about 15,000-20,000 animals in the wild and also

in several zoo facilities (IUCN, 2015). Both subspecies have typical white body striping which is unique for each individual and varies in number of stripes or in shapes of each stripe (Böhmová, 2013).

As the population sizes of Derby elands held in human care are low and they face high risk of decrease in genetic variability, this thesis aims to find out if there is any relationship between inbreeding level and pigmentation, specifically the number of stripes. Our main aim was to test if some evolutionary changes of genotype running at short time scale in connection with wildlife management can be expressed by changes also in phenotype, particularly the striping. We were also interested if there is any difference in striping between a wild population of the eastern subspecies and its population in human care, and also between wild populations of the eastern and western subspecies of Derby eland.

2 Literature review

2.1 Genesis and alteration of coloration and color patterns in mammals

Animals generally display various coloration and color patterns which help us diagnose and classify them into appropriate taxa. Knowledge of cellular interactions and signaling pathways producing pigment patterns is required to understand the development and evolution of these patterns (Mills and Patterson, 2009). The most important point in animal coloration in evolution is that different species and different parts of the body are subject to different selective pressures (Cott, 1940). Historically, biologists have used two parallel methods to study evolutionary changes in coloration, where the first is based on genotype level and the second is based on phenotype (Lewontin, 1974). Specifically, for example population geneticists have been knowledgeable in spatial and temporal changes in allele and genotype frequencies, while organismal biologists have studied individual difference in phenotypic traits across natural habitats (Hoekstra, 2006).

2.1.1 Genes and color pigments

The highly conserved pigmentation biology in vertebrates is based on the melanin that can be characterized as a culmination of a complex process with inception, migration and regulation of melanocytes (Jackson, 1994). Development and regulation of melanocytes lead generally to two types of variation in pigmentation phenotype:

- 1) Variation of the spatial distribution of pigmentation across the body,
- 2) Variation of the density or distribution of pigmentation along individual hairs (Hoekstra, 2006; Mills and Patterson, 2009).

Melanin-based coloration in vertebrates has very often pleiotropic linkage (i.e. gene has more phenotypically different effects) and is associated with variation in physiological and behavioural traits within species. Darker pigmented individuals are found to be more aggressive, sexually active, and more resistant to stress and diseases than lighter individuals (Rushton and Templer, 2012). Connection between behavioral dominance and coloring was studied in some mammals, for example in white-tailed deer, soay sheep (Ducrest *et al.*, 2008) or African lion (West and Packer, 2002; Ducrest

et al., 2008). Ducrest *et al.* (2008) observed, that melanocortin hormone levels predict the amount of testosterone and other sexual steroids, which can affect the behavior.

2.1.2 Changes in pigmentation

Pigmentation is influenced by two types of pigments, which are produced by melanocytes. First is eumelanin, responsible for black to brown color, and the second is pheomelanin, causing red to yellow coloration. Switching between their synthesis is coordinated by interaction of two primary genes: the melanocortin-1 receptor (Mc1r) and ASIP (agouti signalling protein) (Barsh, 1996).

Mc1r is a G-protein-coupled receptor important in determining the type of pigment, responding to two ligands of signalling molecules: the α -melanocyte stimulating hormone (α -MSH) and Agouti. α -MSH works as agonist and activates cells caused by increase in the intracellular level of cyclic adenosine monophosphate (cAMP), leading to the eumelanin production by melanocytes. Dermal papilla cells from the base of hair follicles release the Agouti gene (Bradley and Mundy, 2008). If the Agouti protein is present, it inhibits Mc1r activity, levels of cAMP are reduced and it causes that production of eumelanin is stopped by melanocytes and the production of pheomelanin starts (Hoekstra, 2006).

The system between Mc1r and Asip provides useful tool for better understanding the natural adaptation by linking molecular changes to functional traits during evolution. It also leads us to understand gene evolution and genetic architecture formed by long-term selection (Suzuki, 2013).

Many biologists have been interested in pigmentation patterning because of the huge diversity in color patterns among animal species (Hoekstra, 2006). However, still little is known about molecular or cellular processes which create patterns such as stripes or spots (Mills and Patterson, 2009).

During embryogenesis in vertebrates, pigment cells are derived from the neural crest along the dorsal neural tube, and some distinguish into melanoblasts - precursors of melanocytes migrating ventrally along the body. Some melanoblasts remain in the epidermis after entering and others are localized to the hair follicles and then differentiated into melanocytes producing pigment. This pigment is packaged into melanosomes and transported to keratinocytes, which build hair or epidermal cells

(Hoekstra, 2006). Although several genes responsible for proper dispersion and development of melanocytes have been identified, a little is known about their temporal and spatial control. It has been presumed that important role in generating regular patterns is played by developmental timing (Baxter *et al.*, 2004).

Genomics, molecular and evolutionary biology have revealed genes and pathways involved in skin patterning of poikilotherm vertebrates like fish (for example zebrafish- *Danio rerio*) and amphibians, but birds and mammalian models of stripes are lacking (Mills and Patterson, 2009). However, Eizirik *et al.* (2010) decided to map mammalian coat pattern genes in a cat as a model organism. They hypothesized that mammalian coat patterns are formed by two distinct processes. The first is a developmental mechanism that is spatially oriented and lays down a species-specific pattern of skin cell differentiation. The second is a pigmentation-oriented mechanism using information from pre-established pattern to control the synthesis of melanin. After establishing three independent pedigrees to map four pattern variants (unpatterned agouti, spotted, mackerel and blotched) which were considered to be specified by only a single locus *Tabby*, their results indicated that coat markings in domestic cat are leded at least by three different loci: the *Tabby* locus establishing the shape of the pattern and loci which create spotted coats are involved in the first process and the *Ticked* locus may control the second process. The connection between pigmentation pathways and the preexisting pattern determined by *Tabby*, so the variants may show different amounts of pigmentation on coat areas oriented to be stripes or spots. There is also an alternative hypothesis, that *Ticked* locus may also affect the first process by leading progressively thinner and more numerous stripes that can cause them to disappear amid the agouti color of individual hairs (Eizirik *et al.*, 2010).

2.1.2 Mechanisms of (micro)evolution

Generally, evolution can be divided into two processes: 1) macroevolution, that requires long periods of time and relates to higher systematic categories and 2) microevolution, that occurs in shorter time scale and lower systematic categories, likely within and among populations characterized as groups of individuals of the same species that live in the same area, can interbreed and produce fertile offspring (Reece and Campbell, 2011).

Universally, altered selection pressures lead to adaptive changes and many of these changes have a genetic basis (Losos *et al.*, 2001). Reznick and Ghalambor (2001) deduced by studies, that general condition favoring adaptive evolution is colonization followed by an opportunity for population growth. Colonization opportunities can include new host or food resources, new biophysical environment, new predator, or human-modified environments.

When populations are exposed to new conditions, microevolution is a frequent phenomenon in nature. Microevolution is always driven by some deterministic mechanisms. The main are natural selection, mutation, gene flow and genetic drift (Simpson, 1944)

- **Natural selection**

Organisms have always been influenced by biotic and abiotic changes in their environment, which lead them to move or adapt in situ to avoid extinction (Zimova *et al.*, 2016). Individuals in populations vary in their heritable traits. Those with traits that are better suited to their environment tend to produce more offspring than the individuals having traits not as well suited. So the natural selection is based on different ability to survive and reproduce (Reece and Campbell, 2011).

When we study coloration from an evolutionary perspective, one question always comes to mind: “What is the main role of particular pattern?” (Protas and Patel, 2008). In the case of mammals, scientists have agreed on three main hypotheses on function of specific color patterns leading to natural selection: i) camouflage, ii) communication, and iii) regulation of physiological processes (Ortolani, 1999; Caro, 2009; Vaduva, 2016).

- i) Camouflage*

Camouflage is considered as the most important single function of coloration in mammals. Animals can be concealed when their coat coloration and patterns resemble the natural background (Endler, 1978). This effect is caused by crypsis, when the body color is similar to the general color of the environment, or by pattern blending, in case when the light or dark body patterns match patterns in the surrounding area. For example, climate change poses a serious threat to persistence of wild species. Zimova *et*

al. (2016) focused on climate change-induced phonological mismatch which occurs from shortened duration of seasonal snow cover that can be caused for example by anthropogenic greenhouse gas emissions. As the white animals having a coat color extremely conspicuous to their background, they might face a higher predation risk. At least 14 species are in danger when undergoing color molts from white to brown to reduce color contrast when the snow is seasonally present or absent (Mills *et al.*, 2013). As an example, Snowshoe hares (*Lepus americanus*) are under the strong background matching selection, as 85-100 % of mortality is predation related (Hodges, 2000).

Another way how animals can be concealed is disruptive coloration caused by contrasting patterns or irregular marks which break up body silhouette (Merilaita, 1998). Common concealment in many animals is ensured by lighter ventral surface and darker dorsum, also termed as countershading, when the sun's effect shades the ventrum and lights the dorsum (Kiltie, 1988).

We can distinguish at least five different coat colors across mammalian species, which are typically concealed with their background. Most of the species with white color can be seen particular in arctic and tundra biomes, species with pale coat in desert and open habitat, grey and red animals live more in rocky environment, while dark-colored animals mostly in dense forest. Nevertheless, this classification is not clearly influenced only by background, but it can also be an important attribute for body thermoregulation (Caro, 2005).

For most taxa, it is hard to relate coloration or patterning to camouflage or conspicuousness. Some species are able to be noticed only close up, but not from the long distance. A good example for this case is zebra, which is easy to be seen rather from a short distance. Contrast dependent on ambient illumination and spectral reflectivity between an animal and its environment can be also a reason, why the animal can be seen only at some given period during the day or in specific environment (Endler, 1990).

Research by Von Helversen *et al.* (2013) has suggested that animals with stripes positioned in parallel to the direction of their movement are more likely to be captured than animals with stripes vertical to movement direction. However, other researches did not find any difference in speed perception (Scott-Samuel *et al.*, 2011) or success of capturing (Stevens *et al.*, 2008) between animals with these two kinds of stripes. Stripes can cause "confusion effect" in animals living in groups as their predator is confused

and unable to pick out and attack a particular member of the group (Krause and Ruxton, 2002). Striped and spotted mammals are also less attractive for tabanid flies than individuals with homogeneous white or dark coat color (Vaduva, 2016). Thus Vaduva (2016) suggests that appearance of stripes could be an evolutionary force reducing attraction of tabanids to many striped animals, and therefore reducing a disease transmission risk.

ii) Communication

Color patches in animal coat may also be used in intraspecific or interspecific communication (Caro, 2005).

The intraspecific signals may help animals keep visual contact between female and young (Leyhausen, 1979), as well as they may signal conditions for reproduction, health, superiority, or genetic quality to conspecific mates (Pagel, 1994).

Caro (2005) have pursued systematic evidence of artiodactyls, carnivores and lagomorphs, which is tied by markings on the face, tail, ears, legs and rump used for intraspecific signalling. Specifically, we can see dark or white faces especially in social ungulates, white patches on ears in carnivores living in forests, dark ear patches in lagomorphs living in groups, and also conspicuous legs in diurnal grassland and desert ungulates.

By interspecific coloration such as aposematic signals preys deter predators by advertising their harmfulness or aggression (Caro, 2005). Aposematic species often use combination of bright red, orange, yellow, or white color with black color (Cott, 1940). One of the most famous example of aposematism might be the spotted skunk with its contrasting combination of black and white fur patches on its body. In mustelids, seven other species also producing noxious anal secretions have this specific black-and-white coloration too (Caro, 2005). Markings may be the most effective as visual badge, when they are related with conditions in which they can be most visible (in open habitat and in case of diurnal activity), if they are associated with gregarious species, or used for interspecific communication with particular predators (Stoner *et al.*, 2003). Some characteristics of dominance are mostly located at the front of the animal body, while indicators of body condition signalling an ability of their owner to evade predators or its willingness to mate are likely to be at the rear. Also, marks of recognition are likely to

be found on rumps, tails or on the rear-facing surface of pinnae (Ortolani, 1999). Stevens (2005) has suggested that marks on the tail may serve to distract predators from vulnerable parts of the body or to mesmerize a potential prey.

Communication by coloration has been developed completely in primates. In contrast to all other mammals, primates manifest brilliant sexual dichromatism, however, the functions of color signals of males or females are still largely unknown. In some species with polygynous or polygynandrous mating system males display colorful skin which may be used in solving relations (Caro, 2005). Waitt *et al.* (2006) have suggested in their research on rhesus macaques that male coloration might mediate more attractiveness as females visually prefer males with red instead of pale faces. Skin coloration is regulated by testosterone, which is considered to have immunosuppressive effects, so only the males in good condition may be able to stand costs of color displays (Folstad and Karter, 1992).

Other mammal species with sexual dichromatism is for example a lion. Females live in pride, but males prefer living in a small coalition and carry manes, which can vary between light or dark color. Black mane is a mark of higher food intake, age, concentration of testosterone and cooler environment. The darker-maned males have better chance to survive wounds in fights, thus they have longer reproductive life span and higher offspring survival. Therefore, they are likely to be preferred by females to males with lighter mane (West and Packer, 2002).

iii) Regulation of physiological processes

Coloration of pelage can play a major role also in reducing sun glare or regulating a body temperature. Different coat colors can absorb or reflect radiation and raise or reduce evaporation. Of course, these functions are dependent on a hair structure, density, orientation and ambient factors, as a wind velocity (Walsberg, 1983).

Gloger (1833) noticed that temperature and humidity accounted for geographic variation in birds. This fact was a base for Gloger's rule (Caro, 2005) explaining why animals, including mammals and insects (Stoner *et al.*, 2003), supposed to be dark in warm and humid areas, although animals with light coloration should live in colder and drier habitats (Roulin and Randin, 2015). This pattern can be explained by several selective processes. For example melanin pigments take part in thermoregulation, or

heavily pigmented feathers repel water better, so the body can be dry more quickly (Burt, 1981; Clusella-Trullas *et al.*, 2008). Also melanin can protect integument against bacteria and ectoparasites that thrive in warmer habitats with higher humidity (Guernier *et al.*, 2004). Melanin pigments also play a role in improving hardness of feather, which prevent abrasion (Bonser and Witter, 1993). Eumelanin in black fur or skin may be able to secure a protection against ultraviolet radiation (Diamond, 2005), especially a dark dorsum (Kiltie, 1988). It has been also suggested, that white face markings in ungulates are instrument in reducing heat in desert and grassland habitats by reflecting the heat. Ortolani (1999) has claimed that crepuscular and riparian species have dark eyes to coneract glare of horizontal sun or in cases when it is reflected off water.

- **Mutations**

The term “mutation” is used for describing an alteration in DNA sequence to characterize a phenotypic variation in a heritable trait. Mutations of coat color are usually classified on the basis of cellular and developmental disrupted processes, as a pigment cell differentiation/survival/migration, pigment type switching, biochemical synthesis of melanin, intracellular trafficking membrane sorting of pigment granules (Barsh and Barsh, 2001).

In early 1900s, Mendel’s rules were applied to examine the genetic basis of coat coloration in rodents. Later, several various model species were used for more studies of coloration, primarily the fly *Drosophila melanogaster*, the mouse (*Mus musculus*) and the zebrafish (*Danio rerio*) (Barsh and Barsh, 2001). For color mutants, the large-scale mutagenesis screens were carried out, the mutations were mapped and scientists could identify the causative (i.e. mutated) genes and clone them (Protas and Patel, 2008).

When natural color variation is studied, it is necessary to keep in mind, that coloration mutants, which are created by mutagenesis, may be viable in the laboratory with controlled environment, but may not be able to survive in the natural environment. The phenotype of null alleles can be most obvious in a screen, but the variants in nature may still use weaker alleles of the same gene. There is a difference between genetic background, timescale and population size in a genetic screen and in evolutionary processes that generate natural variation. Specifically, phenotypes resulted from the mutation of a single gene in the lab may be produced by the sum of several mutation processes in the nature (Protas and Patel, 2008).

As we have already mentioned, Mc1r and Asip are two genes that have the major role in red-yellow and black-brown melanization and are able to cause a rapid change in phenotype, so they do in evolution (Hoekstra and Price, 2004). Mutations that change amino acids of Mc1r single exon gene have potential to change the affinity of the receptor for interacting with ligands and G-protein (Bultman *et al.*, 1992).

Extreme changes in phenotypes in the hair color patterns connected with single mutation of Mc1r and Asip have been detected in a variety of animals. Allelic variation in Mc1r and Asip may be classified as gain-of-function or loss-of-function mutation. For example a destructive mutation of Mc1r that stops production of functional receptor molecules and causes extreme yellow coat colors. Also, expression of the antagonist ASIP can generate totally yellow or white color, what can be seen for example in domestic sheep (Norris and Whan, 2008) or laboratory mice (Miller *et al.*, 1993). Characteristic coloration when melanin is reduced in skin, hairs and eyes is called albinism and it is caused by a single genetic mutation. The albino individuals are widespread across divergent taxa, however, they are likely to be removed from population due to no adaptive significance (Caro, 2005).

Besides of light color, Mc1r and Asip can cause also the opposite phenotype- melanism. About twenty percent of individuals in some populations of mammals have melanistic color. It is mostly seen in predators in tropical forests, such as black panthers (melanistic jaguars), or also in burnt habitat, when the fur on the dorsal body side is correlated with frequency of lightening causing wildfires (Kiltie, 1988).

- **Gene flow**

Gene flow is another phenomenon which affects allele frequencies. It transfers alleles into or out of a population due to the movement of fertile individuals or their gametes (Reece and Campbell, 2011) and can affect how well adaptable the populations are to conditions of local environment. Patterns of gene flow and population genetic structure are influenced by dispersal. Habitat loss and fragmentation (for example potential barriers including secondary roads, highways, creeks, agricultural pastures, etc.) may lead to reduced gene flow among small, fragmented populations and a subsequent decline of genetic diversity in remaining populations (Frankham *et al.*, 2002). As the genetic diversity is connected with population fitness, understanding the

patterns of gene flow and dispersal is necessary for conservation of wildlife in fragmented landscapes (Reed and Frankham, 2003).

- **Genetic drift**

Genetic drift is characterized as a change in allele frequencies through time caused by the random combination of parental alleles that can fluctuate unpredictably from one generation to the next (Reece and Campbell, 2011). It can occur in populations of all sizes, however, the process is particularly important in small populations (Slatkin, 1987). Frequency of a particular allele can also increase in one year and decrease in the next. Elimination of alleles from the population can lead to a loss of genetic variation and impossibility to adapt to an environmental change. However, there is also a possibility, that alleles that are neither harmful nor beneficial can be lost or fixed by chance through the genetic drift (Reece and Campbell, 2011).

When a few individuals become isolated from a bigger population, they establish a new population, which has different gene pool than the source population. This process is called “**founder effect**” (Reece and Campbell, 2011).

When an inbred offspring increase in homozygosity, there is a high risk of **inbreeding depression**. This causes negative fitness outcomes relative to less-inbred or non-inbred population (Keller and Waller, 2002). The magnitude of inbreeding depression can be influenced by effective population size and demographic history, including rate and magnitude of historical inbreeding (Charlesworth and Charlesworth, 1987). Some contemporary processes, such as environmental conditions, can be factors for magnitude of inbreeding depression. Thus we can say that the impact of inbreeding depression on the viability of individuals or population of a species is typically assessed on case-by-case basis. In a pedigreed population, inbreeding depression is usually quantified by declining vitality or reproductive rates against pedigree-based inbreeding coefficients, where a negative slope is considered a measure of inbreeding depression (Keller and Waller, 2002).

Also some environmental changes such as fires, floods etc. may drastically reduce the population size and cause a “**bottleneck effect**”. Then some alleles may be overrepresented, some underrepresented and some may be absent among survivors. In this case, the genetic drift substantially affects the gene pool until the population

becomes large enough, when chance events have smaller impact (Reece and Campbell, 2011).

Selection induced in captivity by humans can cause changes in allele and genotype frequencies at short time scale, with potential negative impacts on animal survival after release (Frankham, 2008). Frankham (2008) suggests that alleles or genotypes which may be beneficial in the nature can be lost if they are deleterious in captivity, or the other way around when the characteristics are more deleterious in the wild can appear in captivity. Comparing genealogical data with genetic markers have been often used in domesticated animals and this method is highly recommended also for captive breeding of wildlife, as well as for population management of endangered species (Jordana *et al.*, 2010).

For example Trut *et al.* (2009) surmised that regulatory changes in activity of genes may generate the remarkable level of variety and resemble patterns among domestic animals. These regulatory changes were mainly caused by selection of animals for tameability as a marker for tolerance and adaptation to the human social environment. These authors used silver fox (*Vulpes vulpes*) as a model example for an experiment mapping changes in behavior, morphology and physiology that appear during domestication. After several generations, the standard silver coat color was changed and some specific characteristics as for example Star depigmented spots appeared. This fox domestication experiment showed that artificial selection has an impact on genes regulating the neurohormonal system. Some of the genes that are responsible for the association between tameability and hormonal and transmitter levels might have become fixed by 8-10 selected generations. Fixation of these genes might have modifying effect on activity of many other downstream genes and might cause destabilizing and shifting development timing and uncovering some genome potentialities which were phenotypically hidden. So this detection can explain, why interactions between genetic variants altered during selection may produce new patterns of gene expression and new phenotypes (Trut *et al.*, 2009). Another example is domestication in horses against wild coat coloration with striping. These stripes, which were very similar to all other species of the family *Equidae* almost disappeared, but in primitive breeds still persist in some structures, as a spinal stripe, a next horizontal zebroid stripes on legs or rudiments of stripes on the vertical system (Lusis, 1941).

2.2 Coat colors and patterns in ungulates

The type of coat coloration in ungulates varies from black to grey and red to pale (Stoner, 2003). Many species take on lighter coats during the winter season (Cott, 1940), and some have white color over the whole year, as for example muflon (*Ovis orientalis*) and North American mountain goat (*Oreamnos americanus*) (Caro, 2009). Many artiodactyls have also black or white marks on a uniform background, mainly on their flanks, legs, neck and face.

Artiodactyls use color patches to highlight pursuit-deterrent signals at predators, which may warn the predators that they have been noticed, or they may inform about prey's condition. The size or brightness of color marks could be related to condition, although this hypothesis has never been researched (Caro, 1995; Stoner *et al.*, 2003). Stoner *et al.* (2003) have found that in ungulates, a lot of aspects of coloration are related to concealment and that communication and thermoregulation have less significant role. As there is a small number of sexually dichromatic ungulate species, the role of coloration in mate choice is also minor. However, Caro and Stankowich (2010) came with a hypothesis, that prominent marking on an otherwise uniform pelage background of artiodactyls has also a significant role as signals in communication. These authors have proved that taller species of even-toed ungulates have markings placed lower than shorter species, but only the markings on elbows and knees remained significant after phylogenetic correction. The reason might be that the lower parts of the bodies of shorter species are rather occluded by vegetation than the lower parts of the bodies of taller species. They have also found an association between flank markings and leaping or stotting, when the markings can increase the effect of vertical leaps made during antipredator behaviour. Thomson's gazelle (*Eudorcas thomsoni*) is an example of a species using stotting, while leaping is characteristic for impala (*Aepyceros melanopus*). This marking serves as a deterrent signal in interspecific communication and makes it difficult for a predator to follow an individual prey in a group or catch a solitary victim (Caro and Stankowich, 2010).

Ungulates with conspicuous markings on their flanks are diurnal and can be usually found in open habitats where the markings are more visible and where they might be used in intraspecific communication, for example to keep animals in a herd together (Stoner *et al.*, 2003).

In forests or grasslands, solitary artiodactyls have spotted young, which exhibit a hiding strategy used when their mothers leave them alone while they forage. Stripes in young also aid in concealment and in the species that are rather hiders than followers (Stoner *et al.*, 2003). For concealment in deserts, ungulates use countershading, but this hypothesis has not been supported in other open habitats (Stoner *et al.*, 2003).

All six species of the Hippotraginae subfamily have bodies in white or light color and faces with black wigs, cheek patches, patches between eyes and nostrils (Caro, 2009). Artiodactyls with both black and white markings on the face are diurnal and live in intermediate-sized groups. Dark faces can be found in intermediate- and large-sized social groups, which implies an intraspecific communicatory function (Kingdon, 1982). White faces are characteristic for diurnal species which live in open environments. Caro (2005) suggested that light faces help reflect heat. In many artiodactyls we can find black or white eye rings, as for example in dik-dik (*Madoqua kirkii*), or spots on the face, which are characteristic for saola (*Pseudoryx nghetinhensis*). Caro (2009) has suggested that these patches probably draw attention to pre-orbital glands used for scenting and marking their territories.

Contrasting coloration of rumps and legs in artiodactyls is common compared to other mammals (Caro, 2009). Contrasting rumps are characteristic for example in okapi (*Okapi johnstoni*) with its horizontal black stripes extending from the rump to half way down the hindlegs. White rumps can be seen in deer (Cervidae), most of *Capra* and *Ovis*, some *Bos*, *Kobus* and *Cephalus* species, and in all gazelles (Caro, 2009). Stoner *et al.* (2003) suggested that artiodactyls with white rumps are in most of the cases diurnal and living in large groups in open environment, principally in deserts. The role of this patterning can be in communication with conspecifics or predators, but also in thermoregulation, as the white patches can be easily turned toward or away from the sun to regulate reflectance.

Dark legs marking is associated with open habitat and can be seen mostly in species living in deserts and in social groups, whereas white legs marking is connected with diurnal species living in grasslands or bushland habitats (Stoner *et al.*, 2003).

White spots on fetlocks are typical for nilgai (*Boselaphus tragocamelus*), saola (*Pseudoryx nghetinhensis*) and also Derby eland (*Taurotragus derbianus*). White stockings can be seen on goral (*Naemorhedus goral*), bontebok (*Damaliscus pygargus pygargus*) or gemsbok (*Oryx gazella*) (Caro, 2009). Species as *Kobus* sp., *Capra* sp.,

Pseudovis sp., and chiru (*Pantholops hodgsonii*) have a characteristic black frontal surface on forelegs and for example gemsbok (*Oryx gazella*) and blackbuck (*Antelope cervicapra*) have black upper legs. Black stockings can be found in a few species of *Cephalus*, black spots on the fetlocks in nilgai, Derby eland, impala (*Aepyceros melampus*), and common eland (*Taurotragus oryx*) has black spots elsewhere on the legs (Caro, 2009)

Finally, conspicuous tail tips are strongly associated with diurnal species living in groups (Stoner *et al.*, 2003).

2.3 Derby eland (*Taurotragus derbianus*)

The Derby eland (also called a Giant eland) (*Taurotragus derbianus*) belongs to family Bovidae, Tragelaphini tribe and genus *Taurotragus* (Groves and Grubb, 2011). This species is classified in two subspecies - the Western Derby eland (*Taurotragus derbianus derbianus*) (Gray, 1847) and the Eastern Giant eland (*Taurotragus derbianus gigas*) (Heuglin, 1863).

Both subspecies can be found in almost the same environment regarding the climatic conditions and the composition of vegetation. As herbivores they prefer mainly trees, shrubs, leaves and some types of fruits in their diet, but very rarely they eat grasses (Hejzmanová *et al.*, 2013).

The Derby eland is considered as the world's largest antelope. Males can reach up to 907 kg of weight. If we compare appearance of both subspecies, the Western Derby eland (WDE) is smaller than the Eastern Giant eland (EGE) (Kingdon, 1982).

The main visible characteristics common to both subspecies are their long spiralled horns, white and black markings on the face, limbs, ears and dewlap, and also vertical white stripes on flanks (Kingdon, 1982; Böhmová, 2013). Böhmová (2013) described four main coat color variants of Derby eland: light beige, beige, light red and light brown, when the dominant body coloration of WDE is beige but the most frequent color in EGE is light brown. In both subspecies, there are three color variants of neck: light brown, brown and black. Böhmová (2013) has suggested that color of body and neck can be dependent on sex and age. She has also found out that the body stripes can have about 7 possible characteristics- split on the back, split on the belly, pre-stripe, fork on the back, fork on the belly, stripes with arc and arc on the back (Figure 1).

The number of stripes varies among subspecies, individuals, and also between each side of an eland's body and remain the same during the whole life of the animal. Wilson and Mittermeier (2011) and Böhmová (2013) have agreed that WDE has more body stripes than the EGE.

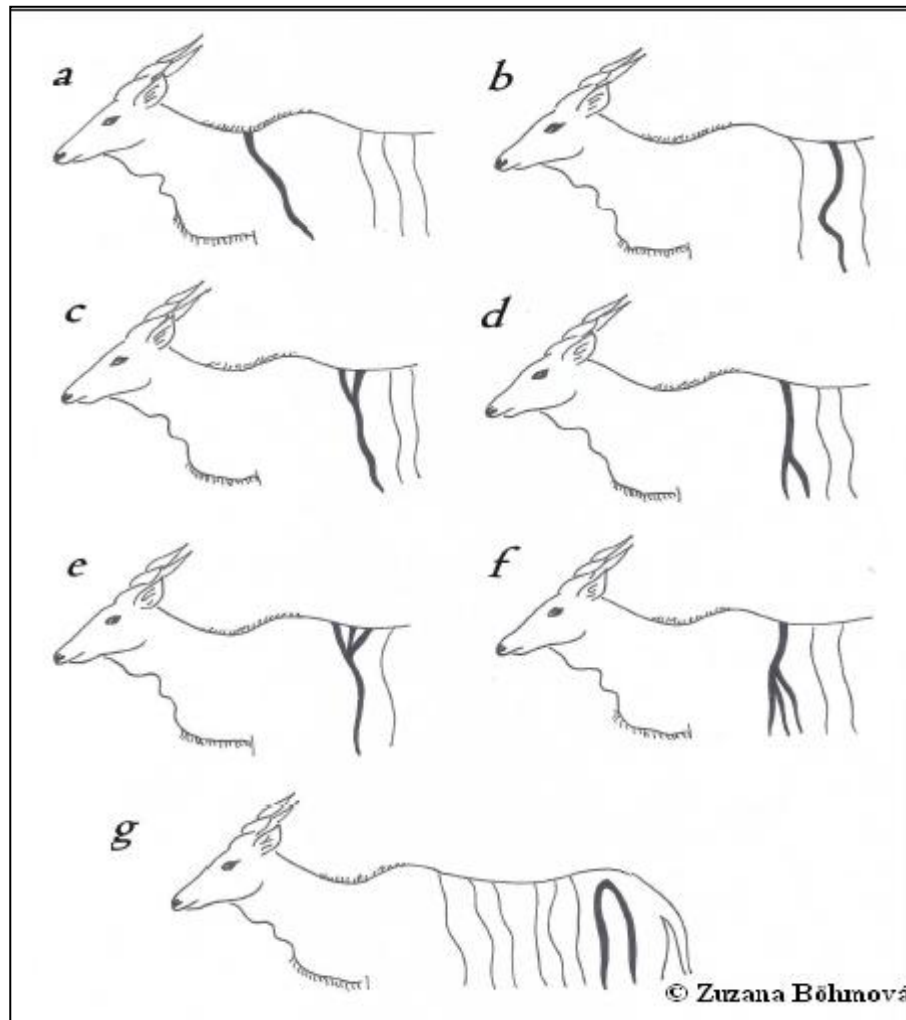


Figure 1. Characteristics of stripes in Derby eland: a – pre-stripe, b – stripe with arc, c – split on the back, d – split on the belly, e – fork on the back, f – fork on the belly, g – arc on the back. (Source: Böhmová, 2014)

2.3.1 Western Derby eland (*Taurotragus derbianus derbianus*)

Western Derby eland (Figure 2) is considered by IUCN (2015) as a “critically endangered” subspecies and its only range of occurrence in the world is in Senegal, specifically in the Niokolo-Koba National Park (NKNP), and also in the Natural Bandia and Fathala Reserves, where two semi-captive breeding groups have been established (Koláčková et al., 2015). The main threats for WDE in NKNP is poaching, livestock grazing, habitat loss and degradation, fragmentation by expansion farmlands and also economic and political decisions. For the semi-captive population, the serious risk is inbreeding depression, founder effect, genetic drift and bottleneck effect (Brandlová et al., 2013)



Figure 2. Western Derby elands (*Taurotragus derbianus derbianus*)

(Photo by: Pavel Brandl)

Natural range

The **NKNP**, which has been listed as World Heritage in Danger by UNESCO since 2007 (UNESCO, 2015), covers 913,000 ha in south-eastern Senegal and is known as the Senegalese largest and oldest national park. It supports a high diversity of plant and animals species, and it is also the only range of a wild Western Derby eland’s population (Kingdon, 2003). Renaud *et al.* (2006) estimated the size of this population

to about 170 individuals during the aerial count in 2006, after a herd of 69 individuals was seen.

Semi-captive population

The **Bandia Reserve** was created in 1994, and in 2000, six wild individuals (1 male and 5 females) of Western Derby eland were transported there by the Society for Protection of Environment and Wildlife in Senegal (SPEFS) (Antonínová *et al.*, 2004). The Bandia Reserve is located about 65 km south-east from Dakar (14°35'N, 17°00'W), in the Sudano-Sahelian ecosystem (Hejčmanová *et al.*, 2010). It is surrounded by a fence to protect the environment, enable wildlife conservation and also to provide conditions for a safari-tourism (Antonínová *et al.*, 2004). The aim of the reserve was to establish a new conservation programme, because the population of WDE was at high risk of extinction. After establishing the herd with the 6 founders (i.e. unrelated wild-born individuals) in 2000, a total of 145 offspring of WDE were born until 2015 in both Bandia and Fathala Reserves (Brandlová *et al.*, 2015).

The game species occurring in Bandia Reserve were either native to Senegal, and introduced from South Africa. The large game species are for instance African buffalo (*Syncerus caffer brachyceros*), kob (*Kobus kob*), deffasa waterbuck (*Kobus ellipsiprymnus defassa*), roan antelope (*Hippotragus equinus koba*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), common eland (*Taurotragus oryx oryx*) and white rhino (*Ceratotherium simum simum*) (Antonínová *et al.*, 2004).

There are 3 breeding herds of Derby eland in the reserve (Brandlová *et al.*, 2015). There are two reproductive herds – Bandia 1 (18 males, 14 females) with the area of 3,500 ha and Bandia 3 (4 males, 6 females) which in total covers an area of 80 ha. There is also a bachelor herd Bandia 4 (9 males) in enclosure of 100 ha (Brandlová *et al.*, 2015).

The fenced **Fathala Reserve** lies in the Sudano-Guinean savannah (13°39' N, 16°30' W) on the west coast of Senegal, as a part of the Delta du Saloum National Park (Nežerková-Hejčmanová *et al.*, 2005). In the reserve there are some native game species as bushbuck (*Tragelaphus scriptus*), warthog (*Phacochoerus africanus*), patas monkey (*Erythrocebus patas*), several Senegalese game species such as deffasa waterbuck

(*Kobus ellipsiprymnus defassa*), roan antelope (*Hippotragus equinus koba*), African buffalo (*Syncerus caffer brachyceros*), but also white rhino (*Ceratotherium simum*) and giraffe (*Giraffa camelopardalis*) from South Africa (Brandlová *et al.*, 2015). The Fathala Reserve was established in an area separated from the Bandia Reserve to avoid a risk of any disease outbreaks and to provide a diet safety (Snyder *et al.*, 1996). It consists of two reproductive herds - Fathala 1 (6 males, 6 females) covering 160 ha of the land and Fathala 2 (15 males, 2 females) with enclosure of 1,800 ha (Brandlová *et al.*, 2015).

During an ex-situ conservation programme of small populations it is always necessary to ensure a proper genetic management to avoid a genetic variation loss and inbreeding depression of animals (Zemanová *et al.*, 2015). In the Bandia and Fathala Reserves a team from Derbianus Conservation- is concerned with some field work every year. The main activity is identifying the new-born calves by behavioral observations (suckling) and controlling a number and health condition of elands in bachelor and breeding herds (Brandlová *et al.*, 2015). Since 2000, the team has managed to monitor the whole semi-captive population and has published a studbook with genetic and geographic data every year since 2008 (Zemanová *et al.*, 2015). Pedigree data are stored in SPARKS (the Single Population Analysis and Record Keeping System) and validated by PMx software for pedigree analyses (Brandlová *et al.*, 2013).

The studbook notices:

- ID- the studbook unique number of an animal from semi- captive population
- Location- location within the conservation programme
- Sex (F- female, M- male, U-unknown)
- Known- percentage of known kinship
- Birth date
- Death date
- Sire/Dam- identification of parents of an animal
- Gen- generation
- F- inbreeding coefficient
- MK Rank- mean kinship
- Age
- Total number of offspring, number of living offspring

- Last reproduction date (Brandlová *et al.*, 2015).

The semi-captive breeding population has become crucial for the whole wild Western derby eland population. It provides a gene pool, stock of animals, but it is also a unique tool for fundraising and public knowledge activities towards the unique ecosystem of Niokolo National Park (Brandlová *et al.*, 2013).

2.3.2 Eastern Giant eland (*Taurotragus derbianus gigas*)

Eastern Giant eland (*Taurotragus derbianus gigas*) has a status of “least concern” on IUCN Red List (2015), although this subspecies is one of the most sought for antelope trophies (Figure 3). In the past, the Giant eland suffered from habitat loss, massive uncontrolled poaching and high mortality because of rinderpest epizootic. During rinderpest outbreak in 1983-1984, populations in the Central Africa region crashed by 60-80 %. However, through time the populations recovered from the huge loss (East, 1999). Nowadays, the main problem is political instability and armed conflicts that forestall the implementation of effective protection and well-established management (McCaffree, 2011). The total population number was estimated in 2008 by IUCN to 15,000-20,000 but the trend is still decreasing (IUCN, 2015).



Figure 3. An Eastern Giant eland (*Taurotragus derbianus gigas*) killed for trophy hunting (Source: <http://hwwmag.com>)

Natural range

The main natural range of EGE is located in the Central African Republic and Cameroon, where the human population density is still low (IUCN, 2008). Occasionally, some individuals may enter the territory in Nigeria. Their occurrence can be registered also in south-western Sudan, where they can cross borders to north-eastern Democratic Republic of Congo and Uganda (East, 1999). Small population reappeared in the hunting blocks on the Central African Republic border between Aoukale and Aouk rivers, and also two populations occur in the Chad Bouba Ndjidda National Park and Manda National Park, which was established in 1965 with the aim to protect Giant elands (McCaffree, 2011).

Captive population

Unlike the Western Derby eland, the Eastern Giant eland is bred in a few ZOOs in the USA, United Arab Emirates and Republic of South Africa. The Eastern Giant eland has also its studbook, which maps the whole captive population from all holding institutions in the world (McCaffree, 2011).

In November 2011, the studbook reported that the historical population reached 262 individuals and the living captive population of total 54 individuals as bred in 8 institutions (McCaffree, 2011).

The studbook notices:

- Studbook number- the studbook unique number of an animal (not chronological number, due to animals being recorded when they are known to the Studbook keeper)
- Sex-(M- male, m- castrated male, F- female, f- contracepted/neutered female, U-unknown)
- Sire/ Dam
- Birth date
- Location- the institution holding the animal
- Date- the date on which the event occurred
- Local ID- the identification assigned by the location
- Event- some type of activity that occurred (birth, capture, transfer, death, etc.)
- Transponder- a device inserted under the skin serving as an identifier (McCaffree, 2011).

3 Aims of the Thesis

The objective of this thesis was to compare the number of stripes on flanks in individuals of the eastern and western subspecies of Derby eland (*Taurotragus derbianus*) in connection with their genealogical characteristics and also with their habitat (e.g. if in captivity or in the wild). The results may show, if the effect of smaller populations in human care can cause changes in pigmentations due to some rapid evolutionary processes.

We also wanted to compare average numbers of stripes in Western Derby eland (WDE) and Eastern Giant eland (EGE) living in the wild.

We set following hypotheses:

- 1) Number of stripes increases with higher coefficient of inbreeding and number of generation.
- 2) Number of stripes is higher in EGE living in human care than in EGE living in the wild.
- 3) Number of stripes in WDE is higher than in EGE.

4 Materials and Methods

4.1 Animal data collection

To determine the influence of genealogical characteristics on Derby elands' striping, we first collected data from the African Studbook of **Western Derby eland** (published between 2008 and 30 June 2015 by Czech University of Life Sciences in Prague and Derbians Conservation) and supplemented it with information about number of stripes of each individual known from identification cards (see Figure 3). We gathered data of 151 individuals, but in 8 of them the number of stripes was unknown due to their early death. Therefore, we worked only with 143 of all WDE coming from the Bandia and Fathala Reserves (e.g. 6 founders and 137 individuals of semi-captive population). We gained also extra photos of 7 wild WDE from NKNP that were seen and photographed by Mamadou Doha Kane during a random spotting and we added these animals with the 6 founders, so we had sample of 13 wild WDE for our analysis.

In case of **Eastern Giant eland**, we had the International Studbook, where, unfortunately, the information about number of stripes of each individual was missing and neither photographs for identification were available. Thus we only found some photographs of one body side of 65 individuals (28 in the wild, 37 in human care) from websites of zoological gardens, safari parks or websites for hunters, but without any specific designation. Therefore, we could only evaluate whether the average number of stripes on the flank can differ between individuals living in human care and in the wild.

4.3 Data analysis

For our statistical analyses of quantitative data we used a programme STATISTICA 13. As the data were not normally distributed, we used non-parametric tests for data evaluation.

To analyze dependence of number of stripes on the coefficient of inbreeding and the number of generation in WDE we conducted Spearman correlation. We compared number of stripes on the left and right flank separately in each individual.

To compare the average number of stripes on the flank between EGE living in the wild and in human care, we used Mann-Whitney U test.

We applied the same test to compare average number of stripes on the flank in WDE and EGE living in the wild.


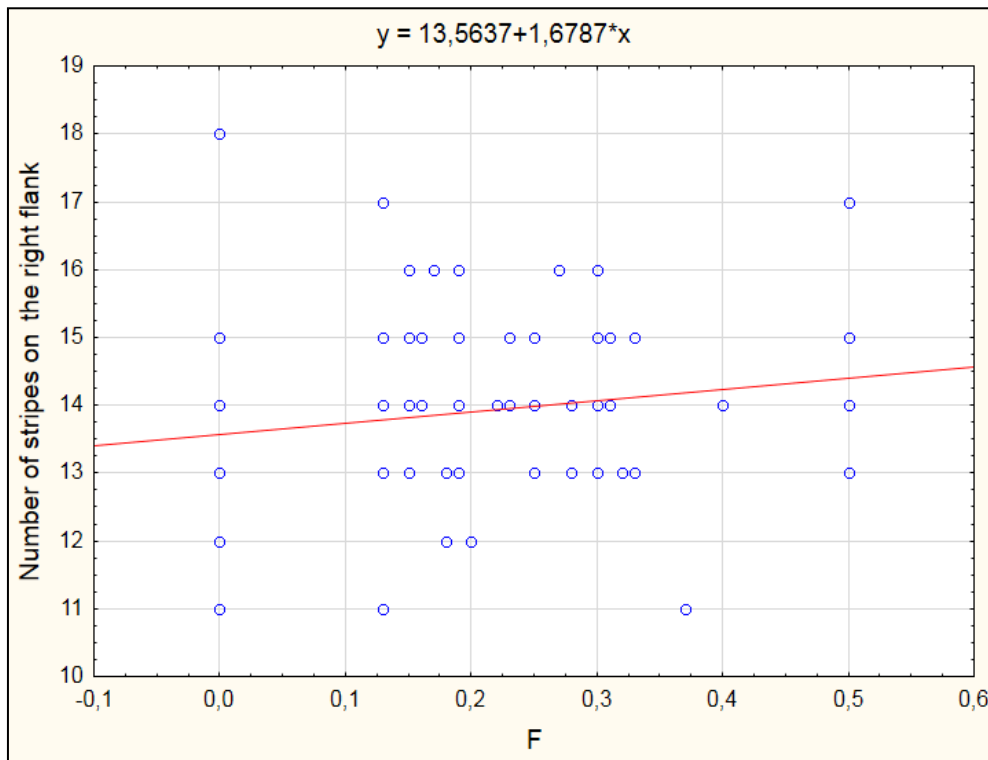
DIDI	
Scientific name: <i>Taurotragus derbianus derbianus</i>	Identification number: 1050
Name: Didi	English name: Western Derby eland
Date of birth: 18. 12. 2007	Birth type: in captivity
Sex: female	Birth location: Bandia 1, Senegal
Sire: Niokolo	Hybride status: not a hybride
Dam: Dalaba	Current location: Bandia 1, Senegal
Number of stripes on: left flank/ right flank	15/13
Other characteristics:	
	

Figure 4. An example of Western Derby eland's identification card (Source: Brandlová *et al.*, 2015)

5 Results

The influence of coefficient of inbreeding (F) and number of generation (Gen)

In our studied sample of 143 individuals (6 founders and 137 individuals of semi-captive population) of Western Derby eland with 14 ± 0.94 SD stripes on the flank on average, we first computed correlation of number of stripes with the coefficient of inbreeding. The correlation was only significant when we counted with the number of stripes on the right flank ($r = 0.2502$; $p < 0.05$) (see Graph 1), in contrast with the left flank which was not relevant ($r = -0.026763$; $p < 0.05$).

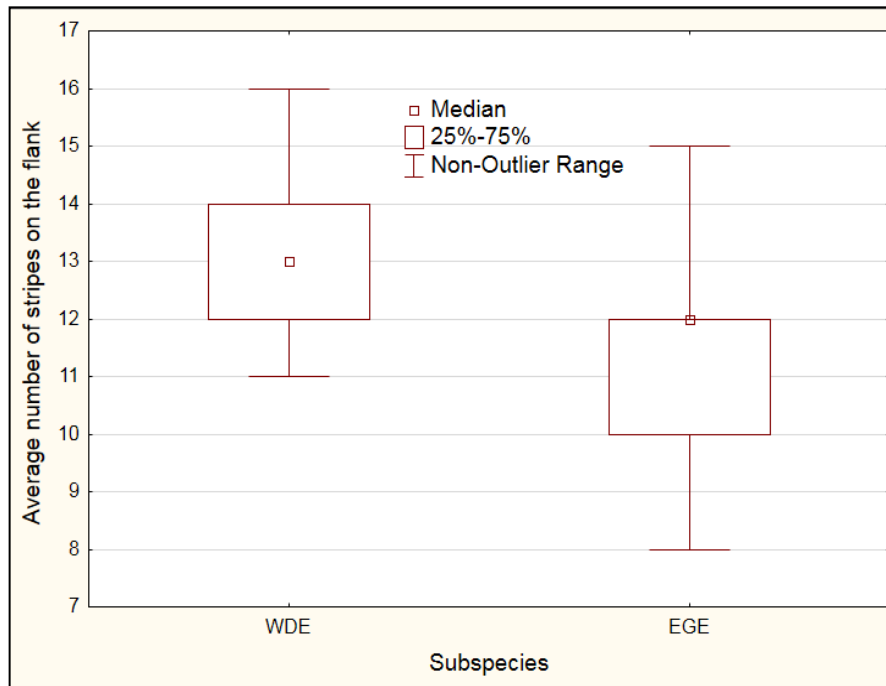


Graph 1. Correlation between the coefficient (F) of inbreeding and the number of stripes on the right flank in Western Derby eland.

In case of the number of generation, the results showed that the number of stripes on the right flank ($r = 0.1513$; $p < 0.05$) and the left flank ($r = 0.0329$; $p < 0.05$) were not correlated.

EGE in the wild versus in human care

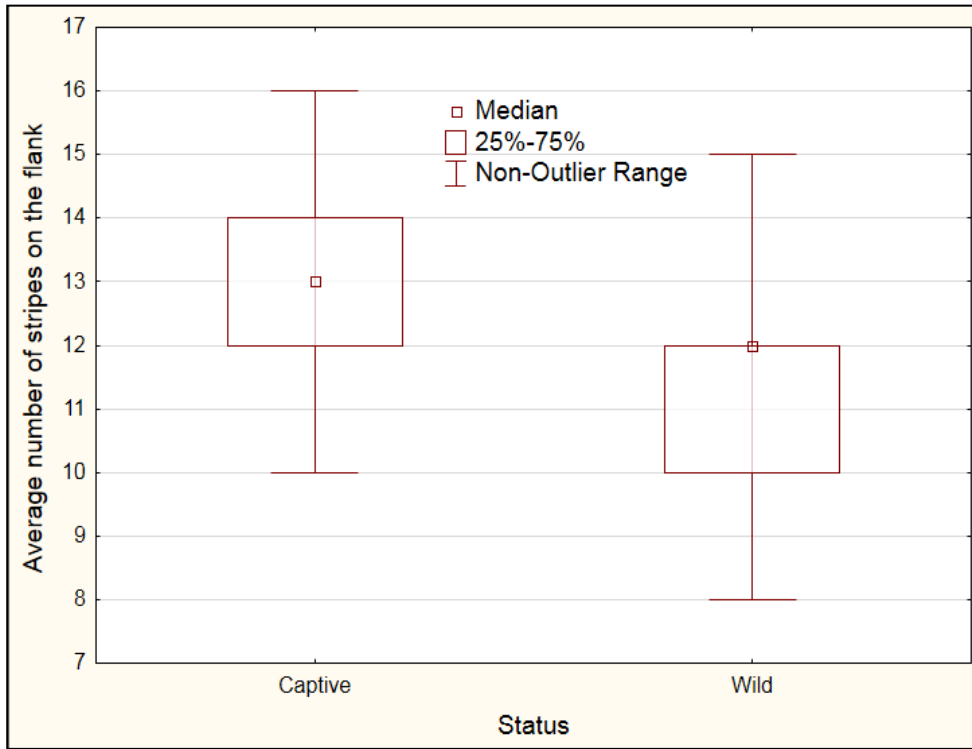
Sample of all Eastern Giant elands had 11 ± 1.39 SD stripes on the flank on average. Comparing the average number of stripes on the flank in Eastern Giant eland living in human care and living in the wild showed that individuals in human care had higher average number of stripes on the flank than those from the wild ($U = 239.5$; $p < 0.05$) (see Graph 2).



Graph 2. Comparison of the average number of stripes on the flank of Eastern Giant eland living in human care and living in the wild.

Comparison of average number of stripes on the flank in wild EGE and WDE

Finally we compared the average number of stripes on the flank of Western and Eastern Giant elands living in the wild. Our studied sample consisted of 13 individuals of WDE and 28 individuals of EGE had average number of stripes on the flank equivalent to 11.90 ± 1.67 . The results showed that Western Derby eland has higher average number of stripes on the flank than the eastern subspecies ($U = 71$; $p < 0.05$) (see Graph 3).



Graph 3. Comparison of eastern and western subspecies of Derby eland from the wild in the average number of stripes on the flank.

6 Discussion

Our results have shown a significant correlation between number of stripes on the right flank and the coefficient of inbreeding in the semi-captive population of Western Derby eland (WDE). However, the analysis with number of generations cannot confirm this outcome. As we know, each side of elands can differ in number of stripes, so for this reason we counted with numbers of each flank separately. For example, results of Böhmová (2013) showed that differences in quantitative characteristics of stripes in both subspecies are significant only on the left flank, while number of splits of stripes is different on the right flank. The semi-captive population was established by only 6 founders (1 male and 5 females) in 2000, thus we can argue that our sample of the population presents a relatively short life history (Koláčková et al., 2011), so some significant correlation could be more visible later with more generations. As we know, in small populations there is always a high risk of genetic drift and inbreeding depression that, in the short term, would most likely cause reproductive problems (Koláčková et al., 2011). However, no studies explaining changes in striping or other color patterns by inbreeding depression are known. Therefore, it is a question whether more white stripes mark lower viability and fitness of elands. This hypothesis would need more observation of correlation between number of stripes and reproductive ability, number of offspring, etc. Nevertheless, thanks to a good breeding management, the overall mean level of inbreeding in WDE was estimated to be 0.1788 (Brandlová et al., 2015), which is still relatively low despite the small number of founders.

Another explanation could be the founder effect. The population was established by only one male, called Niokolo, all the other males born later were theoretically able to reproduce from two years of their age (Koláčková et al., 2011). However, between 2000 and 2009, the dominant bull Niokolo was the only sire of all offspring, because other young males were removed from breeding herds to avoid mating. After Niokolo's death in July 2012, the founder genome equivalents increased, however, founder genomes surviving decreased due to the genetic drift (not all the genes have been passed to the next generation (Brandlová et al., 2015). Therefore the population has retained 78.99 % of genetic diversity (Brandlová et al., 2015). Böhmová (2013) has found out that number of stripes is a characteristic inheritable from parents, so there is also some chance that some males bring genes for more stripes into the population and they spread

it. In the specific case of the Niokolo male, the number of stripes was 16 (left flank) and 14 (right flank), which is above the average, and as he was the sir of all the offspring, he could spread genes for higher number of stripes in the population. However, as one breeding herd is usually shared by several males, we do not know for sure which male is the sir of the offspring. This is the reason why we, unfortunately, are not able to investigate this possibility.

However, we cannot forget to allow for an influence of natural selection. Captive environments are different from the natural environments and can impose different selection pressure which can lead to adaptation to captivity affecting behavior (McDoughall *et al.*, 2006), morphology and reproductive output (O'Regan and Kitchener, 2005). Particularly, populations of species with short generation times are able to adapt more rapidly to captivity than those with longer generation times (Frankham, 2008). Striping in mammals has a lot of functions which could be the main force for natural selection, but the most important one has still not been specified. Larison *et al.* (2015) claims that thermoregulation and protection against insects is the main force in pigmentation in zebra (*Equus* sp.) Vaduva (2016) has also suggested that the number of stripes can play a significant role in sexual selection. As an example, he evidenced a Grevy's zebra (*Equus grevyi*) and bongo (*Tragelaphus imberbis*), where males with more stripes are preferred by females. But he could not prove it statistically. Because the character of zebra and Derby eland stripes are very different, comparing this patterning would not bring any clear solution. However, striping in bongo is very similar to Derby eland, so we cannot disclaim the possibility of sexual selection, where females choose males with more stripes. On the other hand, the function of stripes in most artiodactyls is mainly ascribed to camouflage and communication. Nevertheless, Schulte-Hostedde and Mastro Monaco (2015) explain that captive populations are out of interest of natural selection, because these populations are usually removed from their environment which they were adapted to and which is probably much more complex than an artificial environment.

In the analysis of striping in Eastern Giant eland (EGE), the results showed that the average number of stripes in elands living in human care exceed the average number of stripes in elands from the wild. Genetic adaptation to the artificial environment influenced by human selection criteria is synonymous to domestication (Pelletier *et al.*,

2009). Differences between pigmentation (switching between eumelanin and pheomelanin) in domestic animals (e.g. pigs, horses, cows, etc.) were assigned to action of Agouti protein and melanocortin receptor 1 (MC1R) (Barsh, 1996). In an intensive selection for some temperament this could lead to different coloration in animals, as for example in domesticated silver foxes which have been selected for tameness (Trut *et al.*, 2009). Also striping in domesticated horses almost disappeared by long-term human selection (Lusis, 1941). However, the increase of number of stripes in Derby elands in captivity is very unlikely to be a result of human selection. Although populations of both subspecies are kept in reserves or ZOOs and the animals can get in touch with people more frequently than in the wild, the breeders do not do any selection for tameness or special color variants. The aim is only to avoid inbreeding depression and preserve a high genetic diversity.

Furthermore, it should be mentioned that our result from the analysis of eastern subspecies could be influenced by poor quality of the photos, and also that we were able to count only with the average number of stripes on the flank, because the photographs were taken only from one side. Some stripes were hidden because of lying position of elands killed for trophy, or some elands were photographed from a long distance and the stripes were too light and thin to be seen. We also did not know any origin and genealogical details about the elands, so we can have some doubts if the individuals kept in zoo facilities were also born in captivity or if they were recently removed from the wild and thus should be included among wild individuals. We cannot solve these inconsistencies without proper genealogical data. However, according to this simple analysis we can confirm our second hypothesis that number of stripes is higher in EGE living in human care than in EGE living in the wild.

Our last analysis showed that wild WDE has in average more stripes than wild EGE. This is in accordance with findings of Böhmová (2013), who compared both subspecies in many aspects of appearance. In case of number of stripes on flanks in both subspecies, she observed 14 stripes in WDE and 13 stripes in EGE on average in her studied sample. Kingdon (2003) declared that the both subspecies have 8-12 stripes, and according to Wilson and Mittermeier (2011) and Gray (1847), the Western Derby eland has 14-15 stripes. My results regarding an average of 13 stripes in WDE are identical with those of Akakpo *et al.* (2004), who counted 11-16 stripes in this subspecies, while the eastern subspecies in my sample has range between 8-15 stripes only 11 in average.

Although Böhmová (2013) counted with all WDE including the semi-captive population, we counted with wild individuals of both subspecies. This example can show how the ranges can vary according to different origin and breeding management of the subspecies.

The long-time observation of semi-captive population of WDE by scientists and members of Derbianus Conservation and also the photos of eastern subspecies show an evident increase in stripes. Our statistical analyses have confirmed almost all our hypotheses, except for the significant correlation of number of stripes with number of generation. These outputs can signify that the number of stripes on flanks of Derby elands may increase in captivity and therefore, hypothetically, with higher level of inbreeding. Unfortunately, we cannot explain what the main force is. We must consider the possibility that this change has been caused only by chance.

7 Conclusion

This bachelor thesis is the first study determining changes in striping within and between populations of both subspecies of Derby eland with different management in connection with the level of their inbreeding.

In Western Derby eland, the results showed that the level of inbreeding has a significant influence on increase of the number of stripes, however, only when we counted with stripes on right flanks. The results of comparing populations of Eastern Giant eland living in the wild and in human care supported our hypothesis that the average number of stripes on the flank is higher in the population in human care. Both these analyses could confirm that some rapid microevolutionary changes can appear in pigmentation due to a higher inbreeding level in captivity. To explain why the number of stripes is increasing and what it might mean for the fitness of future populations, we would need a proper pedigree and a long-term observation of more generations. We have also proved that number of stripes on flanks is higher in the wild population of Western Derby eland than in the wild population of the eastern subspecies.

This study has revealed that there is a lack of detailed information about genealogical characteristics and appearance of individuals in captive population of Eastern Derby eland, which makes study of genealogy and its impact on changes in striping very difficult. Also because of the differences between breeding management and environment in captive populations of Derby elands, the results cannot be unified.

In general, intensive monitoring of both captive populations of Derby eland ensuring a proper breeding management and protection of the gene diversity is needed. Bringing new blood into a population by introducing elands from the wild is one of the inevitable steps necessary for improvement of the gene pool and increase of healthy population in a conservation programme.

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