

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences

**Department of Animal Science and Food Processing in
Tropics and Subtropics**



Czech University of Life Sciences Prague
**Faculty of Tropical
AgriSciences**

Calf sex ratio of captive eland populations

Diploma thesis

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Supervisor:
Ing. Karolína Brandlová, PhD.

Author:
Bc. Viktor Neštický

Declaration

I hereby declare that this thesis entitled Calf sex ratio of captive eland populations is my own work and all the sources have been quoted and acknowledged by means of complete references. I agree with storing this thesis in the library of CULS Prague and enabling it for study use.

In Prague, dated 24th of April 2017

Viktor Neštický

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Abstract

This Diploma thesis is focused on calf sex ratio of common elands (*Taurotragus oryx*) and Western Derby elands (*Taurotragus derbianus derbianus*). Calf sex ratio is discussed, but yet still not fully researched topic. Aim of this thesis was to test Trivers-Willard hypothesis and other possible factors affecting sex of offspring of both species. For data collection we chose 3 European institutions holding common elands with different husbandry management and 2 nature reserves in Senegal keeping the only herd of Western Derby eland in human care. Historical records from each institution holding common elands and African studbook for Western Derby eland were used for data analyses. In both species we did not recorded deviations from supposed 1:1 calf sex ratio. None of the mother's quality and her condition predicting factors had a significant impact on offspring sex with slight differences between species. Similar results were obtained from testing herd composition factors of individual groups. Significant difference was observed only in analysing impact of climatic conditions on calf sex, specifically precipitation in previous breeding season. Our results can be used for better understanding of calf sex adjustment mechanism for maximal reproductive utilization of mother's reproductive potential.

Key words: Sex ratio, *Taurotragus oryx*, *Taurotragus derbianus derbianus*, Trivers-Willard hypothesis

Abstrakt

Táto diplomová práca sa zaoberá pomerom pohlaví mláďat u antilop losích (*Taurotragus oryx*) a západného poddruhu antilopy Derbyho (*Taurotragus derbianus derbianus*). Pomery pohlaví u cicavcov je diskutovaná, ale doposiaľ nie úplne preskúmaná téma. Cieľom našej práce bolo otestovať Trivers-Willard hypotézu a ďalšie možné faktory ovplyvňujúce pohlavie mláďat u oboch vybraných druhov. Pre zber dát sme vybrali 3 európske inštitúcie chovajúce antilopy losie v zajatí s odlišným typom riadenia chovu a 2 prírodné rezervácie v Senegale, ktoré ako jediné držia západný poddruh antilopy Derbyho v ľudskej opatere. K analýze sme využili historické záznamy každej inštitúcie s antilopami losími a africkú plemennú knihu pre antilopu Derbyho. U oboch druhov sme nezaznamenali rozdiel v pomere pohlaví mláďat pri narodení od predpokladaného pomeru 1:1. Žiaden z faktorov predpovedajúcich kvalitu matky a jej kondíciu nemal vplyv na pohlavie mláďat s malými rozdielmi medzi jednotlivými druhmi. Obdobné výsledky sme dostali aj pri testovaní ukazovateľov zloženia jednotlivých stád. Výrazný rozdiel sme pozorovali pri testovaní klimatických podmienok jednotlivých krajín, konkrétne zrážok v predchádzajúcej reprodukčnej sezóne. Naše výsledky môžu pomôcť k lepšiemu pochopeniu fungovania mechanizmu upravovania pohlavia mláďat k maximálnemu využitiu reprodukčného potenciálu matky.

Kľúčové slová: Pomer pohlaví, *Taurotragus oryx*, *Taurotragus derbianus derbianus*, Trivers-Willard hypotéza

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1 Introduction

African antelopes of the genus *Taurotragus*, which includes 2 species (*Taurotragus oryx* and *Taurotragus derbianus*), are considered to be the largest antelopes of the world. (Estes, 1991).

Common eland (CE) (*Taurotragus oryx*) is more numerous species from this genus and is considered least concern (IUCN, 2008). Three subspecies of this species have been recognized, which main difference is based on their distribution. *T. o. oryx* inhabits southern Africa, with its range extending north to south of Botswana and northern Namibia. *T. o. livingstonii* occurs in east-central African woodland areas. *T. o. pattersonianus* can be found in northern Tanzania. CE in the southern part of the range are dull fawn in colour, white stripes on the side of the body are not particularly distinct and have a dark brown mark on the upper back region of the forelegs. CE further north have distinct body stripes, but a less distinct mark on the back of the forelegs. (Thouless, 2013).

Derby eland (*Taurotragus derbianus*) can be found in 2 subspecies, each one in different part of Africa (East, 1999). Eastern Derby eland (*Taurotragus derbianus gigas*) occurs in Central African region and according to IUCN (2008) is being considered as least concern.

On the other hand, the Western Derby eland (*Taurotragus derbianus derbianus*) is currently restricted to only one country in the world – Senegal with only one confirmed wild population in Niokolo Koba National Park (Brandlová et al., 2015). In 2000 two semi-captive populations were established in the Bandia reserve and the Fathala reserve as a part of Western Derby eland Conservation Programme organized by Society for the Protection of Environment and Fauna in Senegal, in cooperation with Derbyanus Conservation and Czech University of Life Sciences Prague (Koláčková et al., 2011).

Trivers and Willard (1973) suggested that natural selection should favour the sex ratio adjustment of offspring produced according to parental ability to invest. In sexually dimorphic polygynous ungulates males have to fight for access to mates, so only the strongest and fittest males get to reproduce while weaker ones are rarely able to find mate (Estes, 1991). Therefore it is more beneficial from fitness gains criteria point

of view for female to produce quality male, as they are able to outreproduce the female of same quality. This hypothesis has been tested on numerous species (Clutton-Brock et al., 1986; Hewison and Gaillard, 1999; Blanchard et al., 2004) but yet it has never been researched on elands. As we consider this topic important for captive breeding programme of Western Derby elands we decided to focus closely on this phenomenon with addition of common elands, which are the most related to Western Derby elands, from captivity to enlarge our dataset.

2 Literature review

2.1 Genus Taurotragus

Common eland and Derby eland are the only 2 antelope species forming genus Taurotragus. Individuals of both sexes have horns, males' are usually thicker but shorter, with heavy spiral ridge at the base (Thouless, 2013). Males of both species can reach weigh more than 900 kg (Estes, 1991; Kingdon, 1982).

2.2 Derby eland (*Taurotragus derbianus*)

The largest of all antelopes and often said to show a 'bovine' appearance. Sometimes even exceeding the size of the Cape Buffalo (*Syncerus caffer*). Body is covered in ruddy fawn coloured short hair (Planton and Michaux, 2013) with slight differences between subspecies. The western one (*Taurotragus derbianus derbianus*) is more reddish with approximately 15 stripes on sides, while the eastern subspecies (*Taurotragus derbianus gigas*) coat colour is more sandy and only has 12 stripes on average (Stuart and Stuart, 2007). From neck to the middle of the back runs down shorthaired black spinal crest which is most prominent on the shoulders (Castelló, 2016). A short dark mane can be seen on neck and whither of the bulls (Planton and Michaux, 2013). Large dark dewlap with fringe of hair on its edge runs from the chin to chest (Estes, 1991). Spiralled horns of Derby eland are longer and heavier than those of common eland, reaching maximum size of 123 cm in length (Wilson and Mittermeier, 2011).

2.2.1 Habitat and ecology

Derby elands are more constrained in habitat preferences than common elands (Wilson and Mittermeier, 2011) and typical environment where they can be found are broad-leaved savannas and glades (Castelló, 2016). Habitats that these animals avoid are dry deserts but also dense forests (Estes, 1991). Derby elands are migratory ungulates moving large distances daily (5 – 20 km) and also yearly, but usually spend

same season in same places (Planton and Michaux, 2013). Water abundance is not limiting factor in habitat, but animals will drink daily if the access to the water is granted (Wilson and Mittermeier, 2011).

2.2.2 Distribution

Probable occurrence of Derby elands in the past was narrow belt of savanna extending from Senegal to Nile (East, 1999). Recently the presence of Eastern Derby eland (*Taurotragus derbianus gigas*) is recorded in Cameroon, Central African Republic, Chad, The Democratic Republic of the Congo, South Sudan and Sudan (IUCN, 2008). Estimated population size is between 15 000 to 20 000 individuals considered to be stable in Central African Republic and Cameroon where human population densities are low (Wilson and Mittermeier, 2011), but overall current population trend according to IUCN (2008) is decreasing.

Senegal is considered the only country, where the wild population of Western Derby eland (*Taurotragus derbianus derbianus*) is confirmed (Nežerková et al. 2004).

2.2.3 Social organization

Derby elands form herds consisting of females with calves of both sexes, young adult males and sometimes breeding male joins the herd (Planton and Michaux, 2013). Castelló (2016) states that herds of more than 75 animals have been reported, but groups of 15 – 25 elands are more common. As Derby elands are occurring in less arid areas as common elands, their group sizes are more stable do not change as much seasonally (Wilson and Mittermeier, 2011).

2.2.4 Reproduction

Reproduction of Derby eland have not yet been reported in detail, but due to close relativeness it is likely to be similar to breeding characteristics of common eland (Wilson and Mittermeier, 2011). Gestation period is 265 – 270 days resulting to birth of single calf (Castelló, 2016), weighing 25 – 35 kg (Planton and Michaux, 2013). There is a lack of information about age of sexual maturity, but in conservation breeding

programme females reach suitable age for mating between 15 and 36 months and males in 4 – 5 years of age, but they usually do not succeed in mating before age of 7 years (Brandlová et al., 2013).

2.2.5 Management in captivity

Eastern Derby eland can be found only in 6 institutions on 3 continents – Johannesburg Zoological garden in South Africa which houses only one female, Al Bustan Zoological Center in United Arab Emirates with 7 individuals and 4 institutions in the USA (IAE – African Safari Wildlife Park, Zoo Miami, San Diego Zoo Safari Park and White Oak Conservation Centre) holding altogether the highest number of animals, 31, with increasing population trend (ZIMS, 2016).

Even though Western Derby elands are considered to be critically endangered (IUCN, 2008) there is no captive population held in zoos. Only semi-captive population can be found in 2 wildlife reserves in Senegal (Brandlová et al., 2015), which was founded by six wild born animals (1 male and 5 females) in 2000 with start of the reproduction in 2002 (Brandlová et al., 2013).

Each reserve is additionally divided to smaller breeding paddocks. Bandia reserve consists of 4 different sized enclosures. The largest one of area 3,500 ha also contains the biggest herd, but shares area with other species, including common elands. This situation brings a threat of potential interbreeding (Brandlová et al., 2015).

Fathala reserve is divided in 2 enclosures sized 160 and 1,800 ha. Population size is lower than in Bandia with majority of males (Brandlová et al., 2015).

2.3 Common eland (*Taurotragus oryx*)

Common elands are slightly smaller than Derby elands and have much shorter and tighter spiralled horns (Pappas, 2002). Dewlap is limited only to throat region (Ansell, 1972) occurring in both sexes, larger and darker in males (Kingdon, 2015). The pelage is tawny with short hairs, becoming blue-grey with age, especially in males. Variable white stripes on the sides of the body are present in calves, becoming less distinct with age as well (Thouless, 2013). Males can weigh up to 50% more than

females (Wilson and Mittermeier, 2011), but their horns are thicker and shorter (mean 54.5 cm) than horns of females (mean 60.5 cm) (Estes, 1991).

Males during lifetime develop a tuft of black hair on the nose and forehead (Estes, 1991), which can decline in size, suggesting hormonal control (Kingdon, 2015). The tuft has a strong smell due to secretion from a glandular area in the skin and frequent rubbing in urine (Thouless, 2013).

Mouth and teeth are disproportionately small relative to overall mass, which can be considered as a sign of selective feeders (Wilson and Mittermeier, 2011). Common elands are intermediate type of feeders what allows them adapting to a wide variety of habitats (Estes, 1991).

2.3.1 Habitat and ecology

Common elands occur in savanna, woodland, semi-desert and montane grassland with wide variety of flowering flowers (Rowe-Rowe, 1983). Animals can be found in elevations up to 4600 m (Wilson and Mittermeier, 2011). Even they are considered as one of the most adaptable African antelopes, they avoid true deserts, dense forests or completely open grasslands (Thouless, 2013). Broad habitat tolerance is reflected in variety of their diet consisting primarily of browse, but also including seeds, herbs, fruit, tubers and at the beginning of wet season main component of diet are grasses (Estes, 1991). The size of animal serves as heat storage and good water conservation. Because of this adaptation, common elands do not need to dwell around the water source as much as other large ungulates (Wilson and Mittermeier, 2011). In the case of water lack, elands are able to rise their body temperature up to 7°C higher as a way to avoid increased evaporation (Estes, 1991).

2.3.2 Distribution

Historical range included the savanna woodlands of eastern and southern Africa, from Cape Peninsula to Congo Forest basin (East, 1999). Nowadays common elands can be found in Botswana, Ethiopia, Kenya, Lesotho, Malawi, Mozambique, Namibia, Rwanda, South Africa, South Sudan, Swaziland, Tanzania, The Democratic Republic of the Congo, Uganda, Zambia and Zimbabwe (IUCN, 2008). As popular game specie it

has been introduced to various game ranches in South Africa and Namibia outside of their native range (Thouless, 2013).

2.3.3 Social organization

Common elands are non-territorial gregarious animals (Bothma and van Rooyen, 2005). Animals have large home ranges, up to 422 km² (Hillman, 1979), and are nomadic and mobile in search for food (Estes, 1991). Social structure is very fluid, appearing as there are no stable long-term relationships between individuals (Thouless, 2013), which can stay in herd from several hours up to few months (Pappas, 2002). Herd size varies from 100 to 500 individuals, depending on season of the year (Wilson and Mittermeier, 2011).

Herd composition depends on sex of animals. Having no parental care, bulls enter wooded areas avoided by cows with calves, which prefer open landscapes (Estes, 1999). Males are also less sociable than females, forming groups of 3-5 individuals (Wilson and Mittermeier, 2011), solitary occurring only older 'grey' males (Thouless, 2013). Young elands often form groups a lot larger than adults, sometimes entirely composed of calves and juveniles (Estes, 1991).

2.3.4 Reproduction

In the wild, mating and births occur throughout the year, but peaks are noted late in dry and early in the rainy season (Wilson and Mittermeier, 2011). Females reach sexual maturity around 2.5 years of age while males in the age of 4 years (Hosking and Withers, 1996). Gestation lasts 271 ± 2.9 days at which end one calf is born, rarely two (Posselt, 1963). The observed oestrous cycle length is 21 to 26 days, with oestrus lasting approximately 3 days (Posselt, 1963). Weaning takes place at about 4 – 6 months of age (Estes, 1991). Jeffery (1979) reported the annual inter-calving interval between 281 and 532 days (n = 120; mean = 373).

New-born common eland weighs between 25 and 30 kg (Wilson and Mittermeier, 2011). Calves stand shortly after birth and move freely in their immediate area (Pappas, 2002). New-borns join nursery groups within few days after birth or stay

hidden up to 2 weeks (Wilson and Mittermeier, 2011). Weaning takes place at about 4 – 6 months of age (Estes, 1991).

2.3.5 Husbandry

Common elands are frequently kept in zoological gardens, farms and reserves (Šáda et al., 1998). They possess mild temperament and are easily tamed (Pappas, 2002). Lightfoot and Posselt (1977) stated that common elands can be fully domesticated.

Eland can be raised for meat and dairy production of farm-like environment (Pappas, 2002). According to research done by Bartoň et al. (2014) eland meat can be low-fat alternative to cattle beef. The milk is also easily preserved and lasts much longer than that of domestic cattle (Pappas, 2002).

Relatively large numbers of the common eland now occur on private reserves, particularly in Namibia, Zimbabwe and South Africa, reflecting its value as a trophy animal (East, 1999).

2.4 Ungulate calf sex ratio

There is abundant evidence that among vertebrates breeding adults manipulate the sex ratio of their offspring so as to maximize their own fitness (Charnov, 1982). According to Clutton-Brock and Iason (1986) main circumstances favouring offspring sex ratio are:

1. Variation in the relative fitness of sons and daughters
2. Sibling competition for mates or resources
3. Competition between parents and offspring
4. Cooperation between parents and offspring
5. Cooperation between siblings
6. Sex differences in juvenile mortality during the period of parental investment
7. Fluctuations in the adult sex ratios
8. Inbreeding

2.4.1 Trivers-Willard hypothesis

Trivers and Willard (1973) proposed a model of adaptive offspring sex ratio variation when parental fitness returns differ according to offspring sex. Their model makes three assumptions: (1) that offspring phenotypic quality at weaning is correlated with maternal phenotypic quality, (2) that offspring quality at weaning is correlated with quality when adult, and (3) that adult quality affects reproductive success of one sex more than reproductive success of the other. As a model animal was used caribou (*Rangifer tarandus caribou*) which condition varies from good to poor through the year. It is high likely that female in good condition is better able to bear and nurse her calf than is a female in poor condition. At the end of the period of parental investment, the healthiest, strongest and heaviest calves will be the ones of females in good condition. According to (2) assumption, there is a tendency of calves to maintain this condition into adulthood. This factor is important in polygynous animal species, where females mate only with males bearing the best secondary sexual characteristics and are more likely to outcompete weaker males (Fisher, 1930). On the other hand, increase in reproductive success of females in good condition compared to females in poor condition is only moderate (Trivers and Willard, 1973).

Contrary, to the recent date several studies denied Trivers-Willard hypothesis (TWH). Blanchard et al. (2004) prove the opposite in bighorn sheep (*Ovis canadensis*). Hamel et al. (2015) found out that females of mountain goat (*Oreamnos americanus*) in good condition are more likely to produce calves of the rare sex among adults in the year of conception. According to study of Hewison and Gaillard (1999), who revised several researches focused on application of TWH on different ungulate species, only 4 species from 16 were considered to meet this assumption.

Maternal lifetime reproductive success in species passing on rank of the mother to the daughter, for instance social primates, may not be the highest by producing male sex offspring (Hiraiwa-Hasegawa, 1993). The advantaged daughters model shares similar assumptions with TWH (Hewison and Gaillard, 1999).

Reindeer (*Rangifer tarandus*) was used as a model animal for TWH and thus it also became one of the most studied animals for differential sex ratios amongst juveniles. Skogland (1986) in his study on three wild reindeer population showed influence of physical condition of the females on offspring sex. Three herds occupied poor, medium and good quality ranges with five-fold difference in food availability

during winter between poor and good ranges. Small females on poor ranges showed sex ratio biased towards males (1,15:1), medium sized females from medium quality ranges maintained calf sex ratio near equality (0,91:1) while the heaviest females on the best quality ranges showed strongly female-biased sex ratio (0,67:1). Maternal age did not vary significantly between the three groups. Results are in support of Clark's (1978) local resource competition (LRC) hypothesis, which is explained later in thesis.

By contrast, research on supplementary fed semi-domesticated reindeer population in Finnish Lapland done by Kojola and Eloranta (1989) show support of TWH by significant difference between males and females born to heavier and lighter mothers. Age and parity of mother did not influence sex ratio significantly.

2.4.2 Fluctuations in adult sex ratios and population density

When the adult sex ratio deviates from equilibrium, temporary production of rarer sex would be more beneficial for parents on terms of fitness gains (Burley, 1982). After population decrease that has adjusted sex ratio towards females, the production of an excess of males may be favoured until sex differences in survival reappear with rising population density (Clutton-Brock and Iason, 1986). Studies of unmanaged red deer (*Cervus elaphus*) population on Isle of Rum in Scotland showed the relationship between hierarchy and calf sex ratio, documenting dominant females to be more likely to produce more males than subordinates (Clutton-Brock et al., 1984; Clutton-Brock et al., 1986) disappear in high population density (Kruuk et al., 1999). This may be caused by higher nutritional stress as there is higher competition between animals for food resources, thus the nutritional status of mother can get worse (Kruuk et al., 1999). In study of Guynn and Hamilton (1986) the adult sex ratio played important role in shortening breeding season of white-tailed deer (*Odocoileus virginianus*). With sex ratio in equilibrium, does have less difficulty finding a male during 24-hour period of receptivity, meaning fewer females recycle and conceive in first oestrous cycle. Therefore, calves are born in optimal time for their survival and growth, which should favour the more expensive sex to be raised meaning, in ungulates, males.

2.4.3 Age and reproductive experience

Age of mother influence maternal body condition (Saltz, 2001) and her capacity for motherhood, predicting her reproductive success (Clutton-Brock and Iason, 1986). Females start breeding before reaching final body size and towards the end of reproductive active age their body condition decreases. According to TWH, the sex ratio might be expected to be low among primiparous animals, increasing during the middle years and decreasing in old individuals (Clutton-Brock and Iason, 1986). Côté and Festa-Bianchet (2001) confirmed this model in primiparous mountain goats (*Oreamnos americanus*), except the older females produced more males, which might be explained by ability to provide better maternal care in older mothers.

2.4.4 Competition between parents and offspring

Species which offspring of one sex adopt home ranges of their parents and compete for resources may also influence sex ratio variation (Clutton-Brock and Iason, 1986). Clark (1978) formulated alternative LRC hypothesis predicting in mothers constrained by environmental conditions benefit more from reducing competition with offspring by skewed ratio towards the dispersing sex. In polygynous ungulate species, daughters usually stay in their natal herd while sons disperse and join bachelor groups (Estes, 1991). Therefore, daughters born early in mother lifetime will compete with her for more years than those born later (Cockburn et al., 1985). Females can influence the extent of LRC that she will encounter with her daughters by reducing of females born in the natal group, but she can not reduce competition her sons will encounter, when they disperse after reaching maturity (Silk, 1983). Sex ratio might be expected to favour production of females in later stages of life of females (Clutton-Brock et al., 1982). There are two different way how mothers may limit females born in group: (1) they may adjust calf sex ratio towards male offspring according to LRC formulated by Clark (1978), or (2) by reducing the probability of rearing female offspring by other mother. This can be accomplished by preventing immature females' access to feed resources or by behaving aggressively towards them in other manners (Silk, 1983). These kinds of behaviours are more likely to be manifested on unrelated or distantly related individuals as they benefit more by helping their own kin (Hamilton, 1964).

2.4.5 Ungulate calf survival rate

Survival rates of calves play important role in population growth of ungulates. (Gaillard et al., 2000). Viability of new-borns can be determined by several maternal factors, such as age (Mech et al., 1991), dominance status (Clutton-Brock et al., 1984), reproductive experience (Festa-Bianchet and Jorgenson, 1998), maternal care (Gaillard et al., 2000) and size of group (Ozoga and Verme, 1984).

As Fisher (1930) suggested, sex with lower viability during the parental investment will be favoured in production while it is expected to be balanced at the end of this period. This effect will be applied only if there is tendency of higher mortality of one sex (Leigh, 1970).

Male offspring are less viable than female in several sexually dimorphic mammal species (Ralls et al., 1980; Clutton-Brock et al., 1982; Harris, 2006). In polygynous sexually dimorphic species where male offspring have higher birth weight and higher demands on nutrition than females during the parental investment, their survival might be expected to be related to food availability (Skogland, 1986).

2.4.6 Climatic conditions affecting calf sex ratio

Climatic variation can be considered as another factor influencing female condition in large herbivores (Albon et al., 1987; Estevez et al., 2011; Garroway and Broders, 2007; Hobbs, 1989). Post et al. (1999) formulated extrinsic modification hypothesis (EMH) proposing abiotic factors, such as climate, to be more influential than resource limitation. Thus climatic change may have the potential to alter calf sex ratio in sexually dimorphic species in which maternal condition during pregnancy influences viability of sons and daughters. El Niño Southern Oscillation (ENSO), which induces low rainfall and dry conditions during summer, was confirmed to have effect on sex ratio of captive Iberian red deer provided by additional feeding, meaning that nutritional stress was prevented (Estevez et al., 2011). In White-tailed deer (*Odocoileus virginianus*) severe winters cause females to be less likely to reproduce and increase a probability of daughters to be born in the following year (Garroway and Broders, 2007).

2.4.7 Social stress

High levels of social stress have effect on skewed sex ratio towards males and increased female mortality after birth in non-human primates (Van Schaik and Noordwijk, 1982). In multiparous animals, like yellow-bellied marmot (*Marmota flaviventris*), sex ratio did not differ significantly between stressed and unstressed females, difference was only in probability of weaning a litter which was higher among unstressed females (Armitage, 1986), while in other specie from *sciuridae* family, Richardson's ground squirrel (*Urocitellus richardsonii*), significant positive relationship between cortisol levels during gestation and the sex ratio of litter was observed, with higher proportion of males born (Ryan et al., 2011). The relationship between cortisol levels and sex ratio support Cameron's (2004) glucose metabolism hypothesis suggesting that high stress results in increase of circulating glucose, which during early cell division may alter sex ratios. According to Rosenfeld et al. (2003) more males were born to mothers fed a high-fat diet in comparison with mothers with low-fat diet, with the same caloric value. High-fat based diet can result in increased levels of circulating glucose (Folmer et al., 2003); therefore glucose may be influential to offspring sex determination.

2.4.8 Necessity of studying calf sex ratio

Closer research on sex ratio topic is not only important from academic point of view but also have a relevance to captive breeding programmes (Glatston, 1997). Zoos and other similar institutions provide complex and detailed not only current data but also historical data kept in studbooks for numerous species in captivity (Hardy and Krackow, 1995). Captive breeding allows to easily obtain data which are rather difficult to collect in the wild - certain sire, exact age of animals, parity, interbreeding intervals (Faust and Thompson, 2000; Linklater, 2007). Big potential of zoos in sex ratio research rests on long-term record keeping enlarging sample size by post hoc analyses from studbooks (Glatston, 1997).

Mammal populations in captivity are generally kept in good nutritional condition and lacking of main stress factors (predators, water and food deficiency) thus, according to TWH, polygynous species are expected to produce skewed sex ratio

towards males which would have a large impact on breeding programs as males surplus may compromise use of limited space in captivity (Faust and Thompson, 2000).

3 Aims of the thesis

The aim of this master thesis is focus on the calf sex ratio allocation in captive populations of common Eland (*Taurotragus oryx*) and semi-captive population of Western Derby eland (*Taurotragus derbianus derbianus*).

Firstly we would like to assess calf sex ratio in both populations and compare the deviations from 1:1 ratio. Based on TWH and LRC we predicted that polygynous elands in captive and semi-captive conditions should bias calf sex ratio towards males.

Next aim is to test other selected factors, which according to previous literature review may have an impact on calf sex adjustment in captive eland populations.

Last aim is to find out if any of these factors have a significant influence on sex ratio and possibly which has the strongest effect.

4 Materials and Methods

4.1 Materials

Study is done on 2 species from genus *Taurotragus*. First specie, common eland located in 3 different European institutions with different husbandry management – 2 safari parks and 1 farm.

Second specie is Western Derby eland (*Taurotragus derbianus derbianus*) occurring only in Senegal, Africa. Semi-captive populations are located in 2 reserves as a part of conservancy breeding programme.

4.1.1 Common elands

Knowsley Safari Park, Great Britain

Knowsley Safari Park is located between Liverpool and Manchester in the Knowsley area of Merseyside, England. Edward Stanley, 18th Earl of Derby in 1971, established the park.

Common elands in Knowsley Safari Park are bred on safari drive whole year round. Total number of animals kept was 26, from which 14 were adult females, 2 adult males, 3 female yearlings and 7 calves. Paddock is covered by grass, which provides stable grazing for animals. Elands share enclosure with other ungulate species – Lechwe (*Kobus leche*), Roan antelope (*Hippotragus equinus*), Blue wildebeest (*Connochaetes taurinus*) and Southern white rhinoceros (*Ceratotherium simum simum*). Recently new house for all antelope species were built to improve animal welfare during cold winters. Knowsley Safari Park noted higher calf survival over previous years without house (Personal communication with Leah Drury, keeper, 2016). Nutrition during summer months is almost completely dependent on grazing with occasional addition of hay, browse and pellets for herbivores. During winter months animals have access to wintering stables and to paddock where during milder winters grazing is possible. During harsh winters lucerne hay is provided with equivite multivitamin with salt licks ad libitum. (Personal communication with Leah Drury, keeper, 2016).



Figure 1. Sub-adult male of common eland on safari drive shared with other ungulate species (Knowsley Safari Park, Great Britain, 2016).

Zoo Dvůr Králové, Czech republic

Zoo Dvůr Králové is situated in northwest part of Czech republic near Krkonoše Mountains and was established in 1946.

Zoological garden Dvůr Králové has been breeding common elands since 1970s, after first herd was caught and transported from Africa (Vágner, 1974). Common elands are kept in safari-like condition approximately 6 months and for the rest of the year they are kept in wintering stables. Several species share space on safari drive – common elands (*Taurotragus oryx*), Blue wildebeest (*Connochaetes taurinus*), Lechwe (*Kobus leche*), Plain zebra (*Equus quagga*) and Ankole-Watusi cattle (*Bos taurus*). During summer period grass is the main component of their nutrition, with additive of hay and browse. During winter common elands have to be additionally fed by complete compound feed for herbivores, carrot, vitamin and minerals premixes and hay provided ad libitum (Personal communication with Dominika Stempa, keeper, 2016).



Figure 2. Common elands on safari drive in Zoo Dvůr Králové, Czech republic. © Přemysl Rabas. Source: www.zoodk.cz

School farm in Lány, Czech republic

School farm in Lány was built in 2006 and 20 individuals of common elands were transported from previous institution. Breeding programme was established by 5 founders (1:4) born in Zoo Dvůr Králové as fifth and sixth generation of wild common elands brought from Africa.

Common elands on school farm in Lány are bred differently to previous two institutions. This farm-like environment is very similar to cattle farm. It provides animals barns with 2 paddocks of 1 hectare. Herd is divided in two smaller groups, which can still interact through the fence. From December to March animals are kept on deep bedding inside the barns. For the rest of the year elands are provided permanent access to paddocks and stables. As these paddocks are not as big as in Zoo Dvůr Králové and Knowsley Safari park, nutrition consists of higher amount of additive feeding as a maize silage, lucerne silage, lucerne hay and barley straw during the whole year (Bartoň et al., 2014).



Figure 3. Stables for common elands in School farm in Lány, Czech republic. Source: www.katedry.czu.cz

4.1.2 Western Derby elands

Bandia and Fathala reserve, Senegal

Bandia and Fathala reserve are home of Western Derby eland (*Taurotragus derbianus derbianus*) semi-captive population. Six animals from NKNP were caught and transported to Bandia reserve in 2000. In 2006 new population was established in Fathala reserve (Brandlová et al., 2013). In February total animal count of Western Derby elands in both reserves exceeded 100 animals for the first time since the start of the breeding programme. Nutrition is based on browsing and grazing with occasional addition of peanut hay mainly during the dry season.



Figure 4. Nursery herd of new-born calves of Western Derby eland accompanied by yearling (Bandia reserve in Senegal, 2017).

4.1.3 Data collection

For common elands data were collected using internal records of each institution to gather information about each calf born including calf sex, mother and father identity, age of parents, parity, sex of previous calf, number of males in herd during period when calf was born and calf sex ratio in herd every year. This included 13 calves born in Knowsley Safari Park, 143 calves born in Zoo Dvůr Králové since 1999 and 135 calves born in School farm in Lány since 2003.

Western Derby elands data were gathered through African Studbook which holds records of each individual born since the beginning of the conservation programme, 180 individuals in total from which 174 calves already born in semi-captive conditions including this year calves. We looked for the same factors as in common elands.

For several calves of Western Derby eland was possible to obtain body score condition of mother from historical photos in time of conception. These were used for additional analyses including this parameter.

Body Condition Score was rated from digital pictures of Western Derby eland in Fathala and Bandia reserve, Senegal. Pictures were used to evaluate body condition of animals using Body Score Condition Cards for beef cattle (*Bos taurus*), which is by body structure very similar.

Animals were divided by general appearance of animals to 5 categories representing level of the muscle and fat cover of body; 1 ~ extreme low, 2 ~ low, 3 ~ moderate, 4 ~ high and 5 ~ extreme high.

Precipitations for both countries were acquired through meteorological station with data freely available on Internet.

4.1.4 Data analyses

All data analyses were done using STATISTICA 12 and SPSS Statistics Subscription. Separate analyses were used for each species. Afterwards, analyses were made on merged group data of both species. In each analyses, we tested the probability of offspring sex being a male. We used nonlinear regression for age, parity, BSC and number of males and females in herd. By Pearson's chi-squared test we analysed interbreeding interval, sex of previous calf and precipitation.

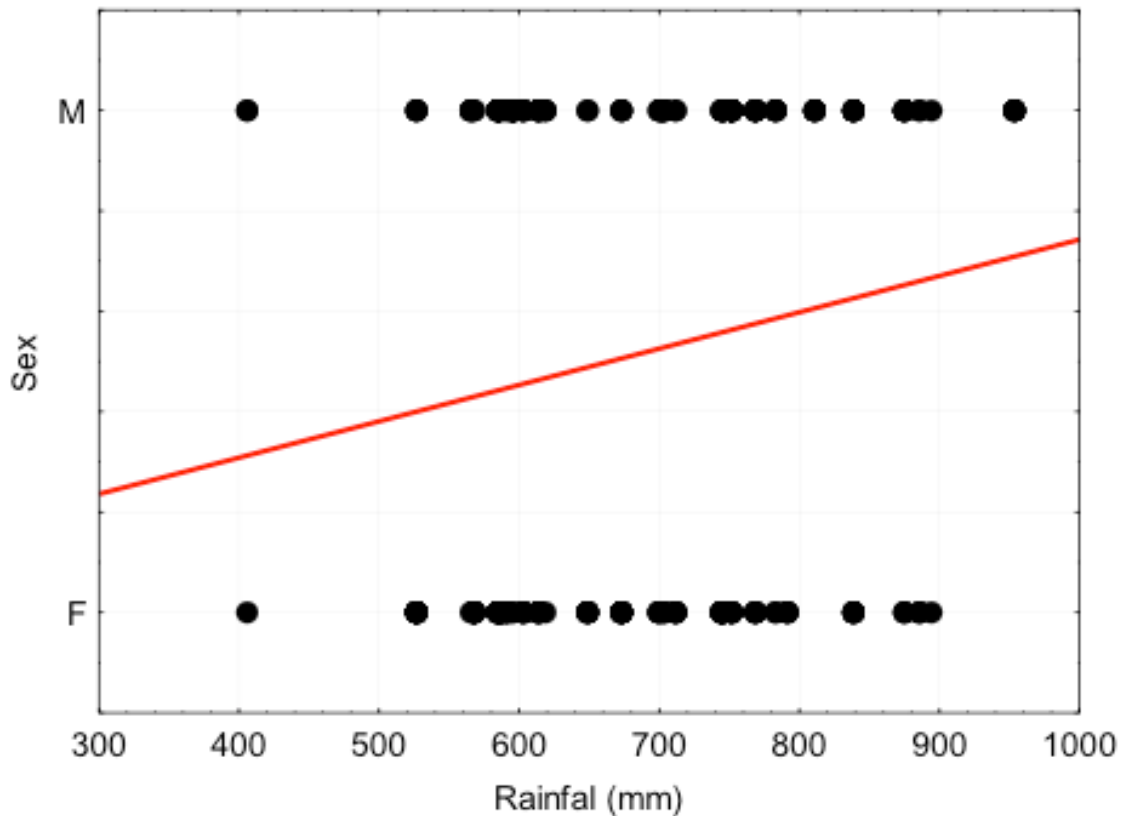
Binomial test was used for testing deviation of the sex ratio at birth from 1:1 at the population level in both species separately.

5 Results

Our studied sample had 291 individuals of common eland and 175 individuals of Western Derby eland.

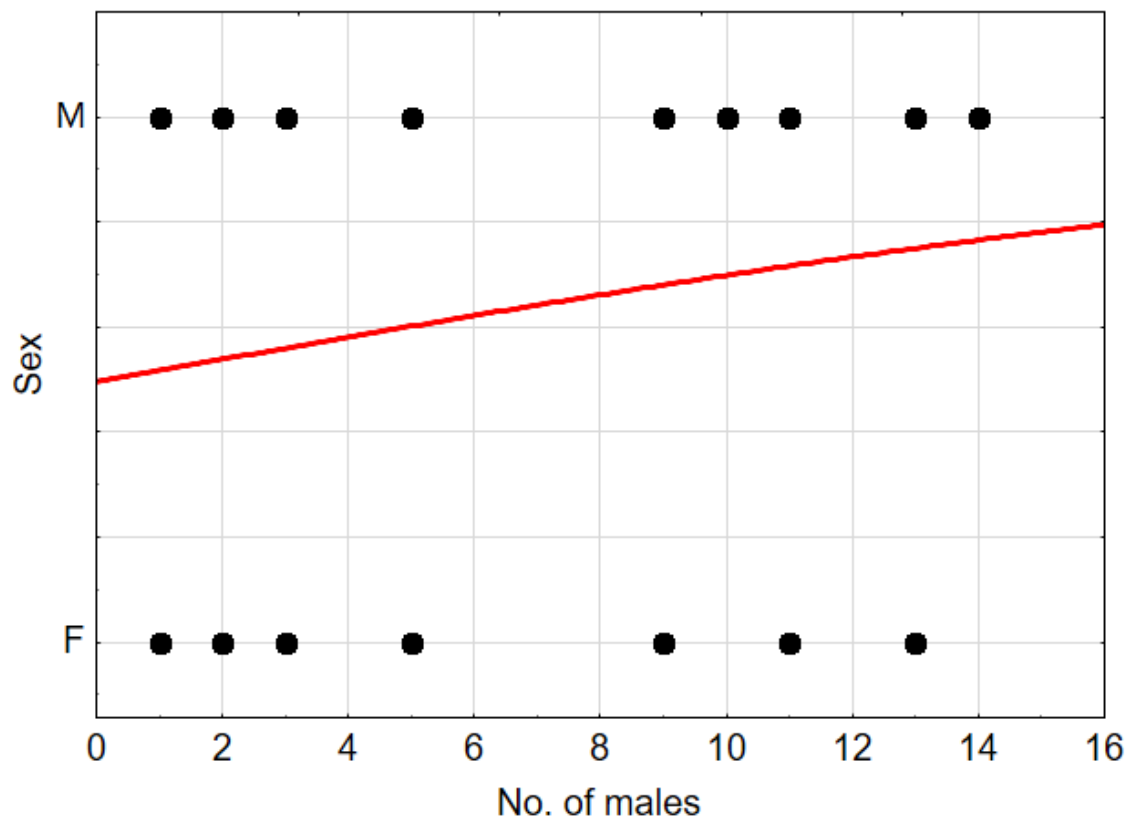
Calf sex ratio of both species at birth on population level was test by binomial test to find deviations from supposed 1:1 ratio. In common elands the birth sex ratio was skewed slightly towards males, but not significantly (149 males and 142 females; $p=0,725$). Western Derby eland sex ratio differed from equilibrium more (55% of males) but no significantly (93 males, 75 females, 7 unknown; $p = 0,190$).

Firstly, we did analyses of bigger sample size of common elands for probability of offspring to be a male. Using quick logit regression on age of mother we found almost stable trend with no significance ($p = 0,9573$), very similar to parity, which is closely related to female's age ($p = 0,9786$). Age of sire was also not significant ($p = 0,7175$). Following factors consisted of herd compositions, which were proven not to have a significant influence on calf sex, but had opposite trend (Number of females, $p = 0,8763$; Number of males, $p = 0,0927$). Last analyses of nonlinear estimations were done to compare breeding success and calf sex ratio in the same breeding season. Observed decreasing probability of calf being a male with higher breeding success was not found to be significant ($p = 0,6281$). For following factors, sex of previous calf, interbreeding interval and rainfall, we used Pearson & Chi-square test. Sex of previous calf did not affect sex probability; only lower proportion of females calves were born when sex of previous calf was also a female ($p = 0,15852$). Interbreeding interval did not differ between males and females with most of data distributed in interval between 300 and 400 days ($p = 0,7223$). Only significant factor to be proven to have an impact on calf sex in common elands was rainfall ($p = 0,0070$) (Graph1).

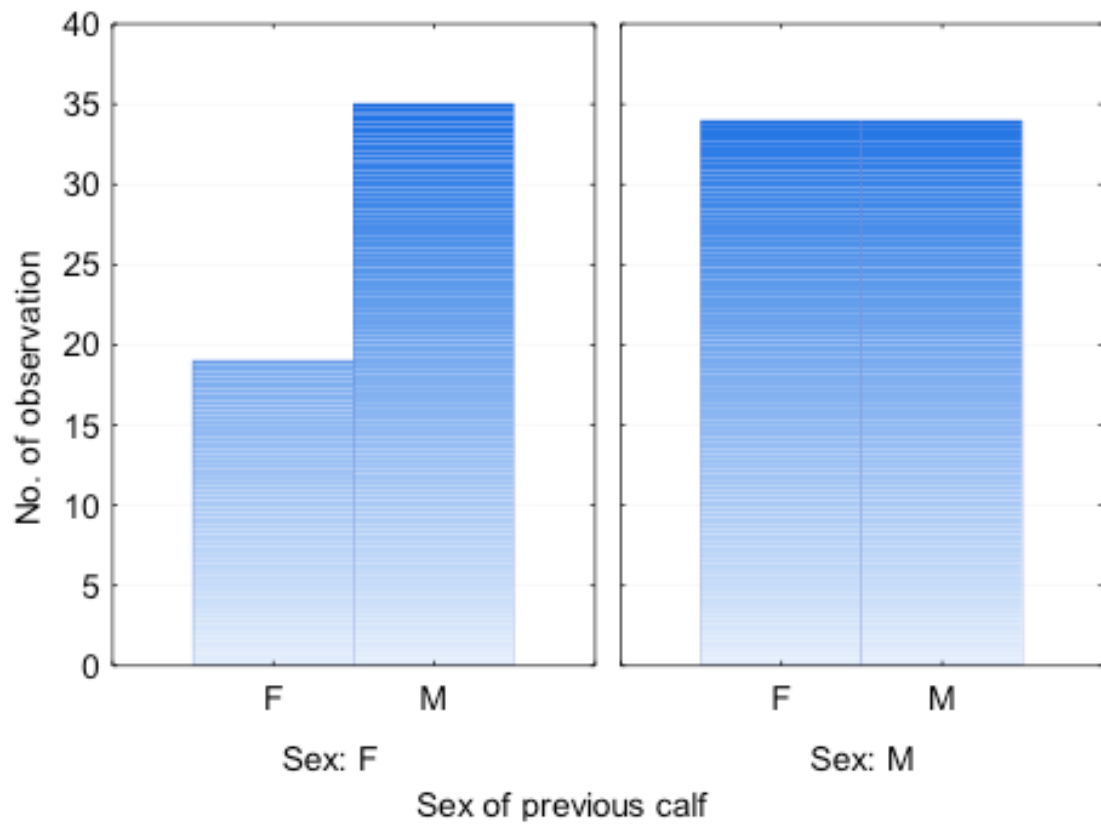


Graph 1. Rainfall influence on calf sex probability in common elands, Pearson's chi-squared test, $p = 0,007$.

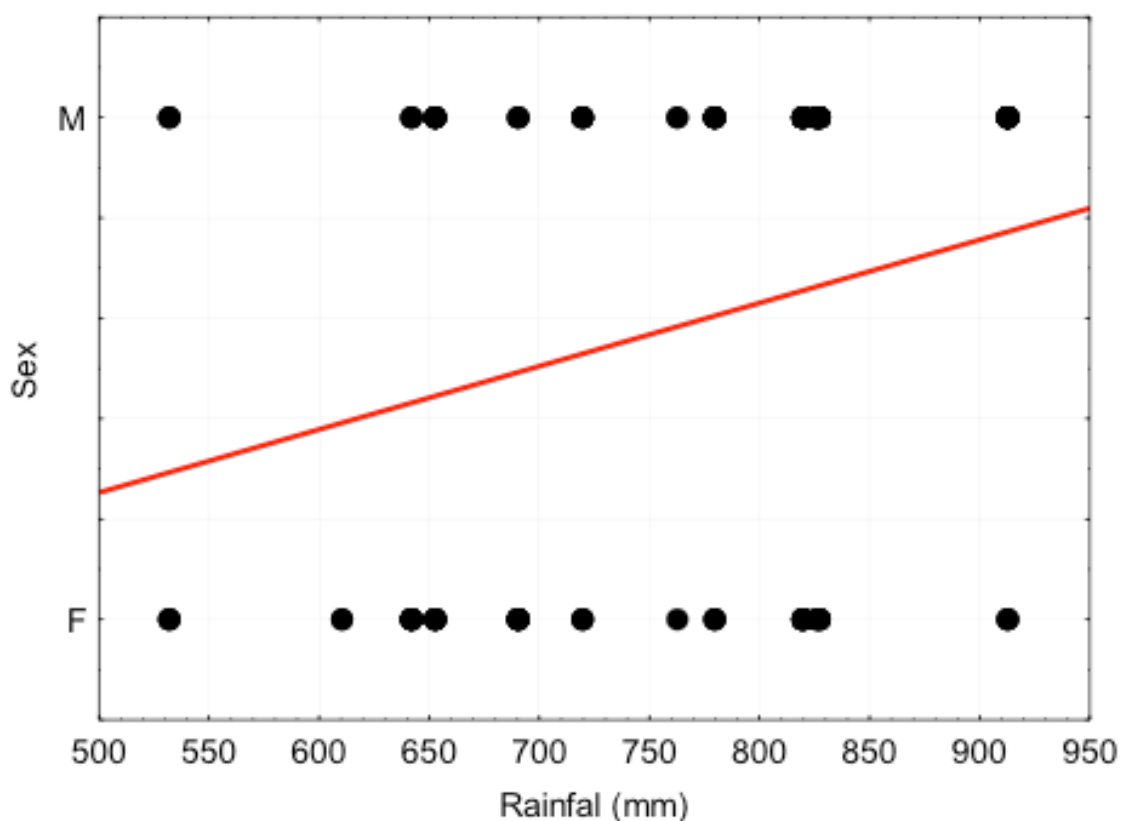
We proceeded with the same analyses for Western Derby eland data set, which was smaller almost by a half. None of the factors tested by quick logit regression were found to have a significant impact on calf sex. Number of males had higher correlation ($r = 0,1356$) and increasing trend of calf being a male ($p = 0,0833$) (Graph 2). Number of females had similar effect and correlation ($p = 0,2704$) together with number of breeding males in herd with slight increase of male probability ($p = 0,1584$). Similar trend with sex of previous calf as in common elands was observed with no significant influence on calf sex probability ($p = 0,101067$) (Graph 3). Only significant factor affecting calf sex in Western Derby eland was rainfall ($p = 0,0049$) (Graph 4).



Graph 2. Probability of calf sex according to number of males in Western Derby eland, Quick logit regression, $p = 0,0833$.



Graph 3. Impact of previous calf sex on current offspring sex, Pearson's chi-squared test, $p = 0,101067$.

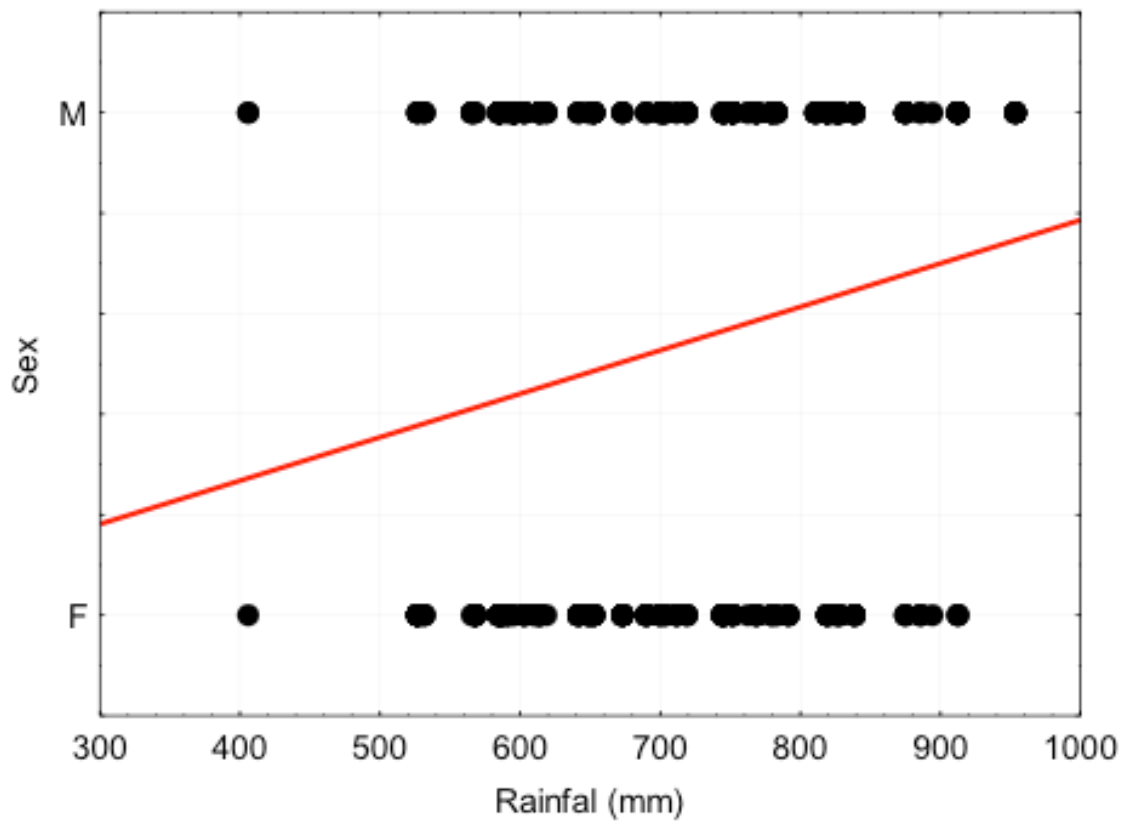


Graph 4. Rainfall impact on calf sex ratio in Western Derby eland, Pearson's chi-squared test, $p = 0,0049$.

Conjoint data of Western Derby elands and common elands were tested for increasing probability of offspring being a male according to different factors. First was age of mother and age of sire, which were not proven to have a significant influence on calf sex ($p = 0,6187$; $p = 0,4385$) with only slight decrease of male calves born in older parents. Another factor, parity, did not have a significant influence and the probability stayed almost the same for each category ($p = 0,91147$). Number of reproductive females in herd showed increase in probability of giving birth to a male but not significant ($p = 0,2704$) with result almost the same with males in herd ($p = 0,1584$). Opposite but not significant trend caused breeding success of females in particular season, meaning the higher breeding success, the lower proportion of males ($p = 0,16035$).

Pearson's chi-squared test showed no significance of interbreeding interval influencing calf sex with most of the data distributed in interval between 300 and 400 days regardless of sex ($p = 0,6125$), however rainfall in the previous year when calf was

born impact sex of offspring strongly with higher precipitation rate favouring males ($p = 0,003$) (Graph 5). We obtained BSC in time of conception only from 18 animals, which is very low number of samples and show no significance in relation to calf sex ($p = 0,177148$).



Graph 5. Rainfall impact on calf sex ratio in conjoint data of Western Derby elands and common elands, Pearson's chi-squared test, $p = 0,00009$.

6 Discussion

Offspring sex ratio is highly studied topic in many not only ungulate species, however there is a high variability amongst factors affecting sex adjustment in different taxa (Hewison and Gaillard, 1999; Clutton-Brock and Iason, 1986). It is problematic to establish most influential factor as many species differ in their social and reproductive systems, therefore the same hypothesis in one specie may favour increased production of males while in another it can be the other way round (Cameron, 2004). For instance, we can focus on TWH (Trivers and Willard, 1973), which was described closely earlier in the thesis. In polygynous sexually dimorphic ungulate species females of good quality may benefit more from sons than daughters in comparison with groups social primates, in which daughters usually inherit high rank of her mother, while sons has to start at the bottom of the hierarchy, mother of better quality should favour female sex offspring to acquire the higher fitness (Silk, 1983; Schino, 2004).

Another important effect is availability of resources on basis of LRC (Clark, 1978) connected with prioritizing sex which disperse more, which may means different sex according to species.

The sex ratio of both species of elands in captivity and semi-captivity did not differ from predicted 1:1 (Fisher, 1930). This result is in order with other similar studies focusing on birth sex ratio of ungulates in captivity (Faust and Thompson, 2000; Moreno et al., 2011).

Previous studies have shown that maternal age can have an impact on calf sex (Landete-Castillejos et al., 2004; Saltz, 2001; Weladji et al., 2003). Female's capacity for motherhood might be strongly age dependent among large mammals (Côté and Fiesta-Bianchet, 2001) and age can be considered as one of the main precursor of maternal body condition (Saltz, 2001). We observed decreasing trend of calf being a male with increasing maternal age in Western Derby elands, which was not significant, but can be considered in line with TWH when we expect decreasing body condition in older females, therefore for females it is becoming harder to bear male foetus. Contradictory trend, almost stable was found in common elands, suggesting there is no effect of age on sex of offspring in this species.

Herd composition and adult sex ratio is considered as one factor influencing calf sex ratio (Clutton-Brock and Iason, 1986). In our study we could not confirm this factor as influential, however it was possible to observe increasing probability of calf being male with both higher numbers of males and also females in Western Derby elands. Higher female count can be connected with LRC (Clark, 1978) when there is a higher competition amongst females with higher density. Then it is beneficial to produce dispersing sex, which will not remain in their natal group, what in ungulates mean males (Kingdon, 2015). The similar trend was observed even with number of adult males what is in conflict with LRC, but with more breeding males around all females may conceive earlier in the mating season as it is less difficult for them to find a suitable male (Ditchkoff et al., 2009). Earlier conception can ensure calving in optimal time of the year in favourable climatic conditions with enough resources for raising males. Reversed effect with males was found in common elands. This can be affected by total amount of males in herd. While in Western Derby elands, it could be up to 14 adult bulls, in common elands was maximum of 3. This is caused by very different management system of institutions, where common elands are kept in zoos and farm not providing the possibility of housing more adult males with all surplus males born needed to be relocated, while the more spacious nature reserves in Senegal provide good conditions for bigger bachelor groups roam in the same area with females with calves.

Sex of calf seems to have an impact on mother's condition in sexually dimorphic ungulates in which males are more demanding to raise (Charnov, 1982). Therefore we could expect females to be better prepared to conceive a male after her previous calf was female. But according to our results there was not such trend visible. This may simply be caused by additional feeding, which all categories received, helping to recover quickly after parturition and get to the optimal body condition sooner.

Interbreeding interval can also be considered as one of possible factors to influence calf sex through its impact on mother's condition. The shorter the interbreeding period, the shorter time a cow has to recover to the time of conception. We could not differentiate between possibility of calf being male or female according to length of interbreeding interval, as it was almost the same for both sexes.

From climatic conditions we searched for rainfall in Senegal and Czech republic during the previous season. In Sahel areas precipitations are main predictor for

availability of food resources in the following year (Moron, 2007), which can be directly connected with adjustment of calf sex to raise possible fitness gains. As we already know the males are more difficult for cows to raise, we would expect to see higher proportion of males calves born following year of higher precipitation, just as it occurred. We found really close relation between sex and precipitation with increasing probability of calf being a male with increasing rainfall in both species. This adaptation seems to be very strong when we take account that Western Derby elands are in captivity for more than 15 years and common elands even longer but they still keep adjusting sex ratio according to climatic condition despite the fact they will receive additional feeding regardless the food resources availability in nature.

However, our data could be affected by many variables. The most important is relatively low sample size. For more reliable results we would need at least 1000 individuals, as it was done with common hippopotamus and pygmy hippopotamus (Pluháček and Steck, 2014) as we could see increasing or decreasing trends in probability, that might be more profound in bigger sample size.

Of course we could not enlarge sample of Western Derby elands as we included all individuals from breeding programme, but for common elands we would be able include other zoos and farms keeping this species. Limiting factor is to find institutions keeping detailed records about every calf born which is not done regularly with this species so well as it is in Zoo Dvůr Králové and School farm in Lány.

Another influential factor can be different management of animals and additional feeding which might impact the condition of cows, which are adjusting calf sex ratio in different way like it would be in the wild. Therefore these results can only be applied to Western Derby elands and common elands in semi-captivity and captivity. It would be beneficial to obtain data even from wild population, but there arise a challenge with data collection and necessity to be able to find and identify every individual.

Several factors we were not able to acquire from animals, as it would necessary to observe animals in the time of conception and record their body score condition every season. Another important factor confirmed in several species (Clutton-Brock et al., 1986; Meikle et al., 1993) and even in humans (Grant, 1994) is maternal dominance, in animals respectively her rank in herd hierarchy. This type of research would require longer period of time than we had for writing of this diploma thesis, as it is necessary to

know rank of every female in herd, what is impossible to obtain from historical data and require long lasting observation as the ranks change during animal's lifetime.

Small probability of potential error could be wrong identification of mother or inability to even recognize them, what mainly could happen in Western Derby eland in Senegal where animals are less monitored as it is possible on smaller paddocks of zoos and farm, but I consider this very unlikely as the new calf born identification of Western Derby eland are held every year.

7 Conclusion

We analysed factors affecting calf sex ratio in Western Derby elands and common elands. Our first hypothesis that the quality of mother can have influence on adjustment of calf sex was not confirmed. The results showed no significance in any factors that may have predict female's quality, such as her age, parity, length of interbreeding interval or sex of her previous calf. There were slight differences visible between both species.

Then we focused on external factors, such as number of males and females in the herd. There we noted the biggest difference in correlation with opposite trends in number of males between Western Derby elands and common elands.

Our last hypothesis focused on impact of climatic conditions of Senegal and Czech republic on calf sex. We confirmed the higher probability of calf being a male with higher rainfall as we expected. This result just shows how strong this drive is when animals still keep tendency to adjust sex ratio even after more than decade of regular supplementary feeding in stable conditions with lack of stress.

These results cannot confirm either TWH or LRC, but we could see some obvious trends to indicate tendency predicted by these hypothesis, which may be used for further research of calf sex adjustment in genus *Taurotragus* with some more factors we were unable to add to our analyses and possibly more individuals.

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